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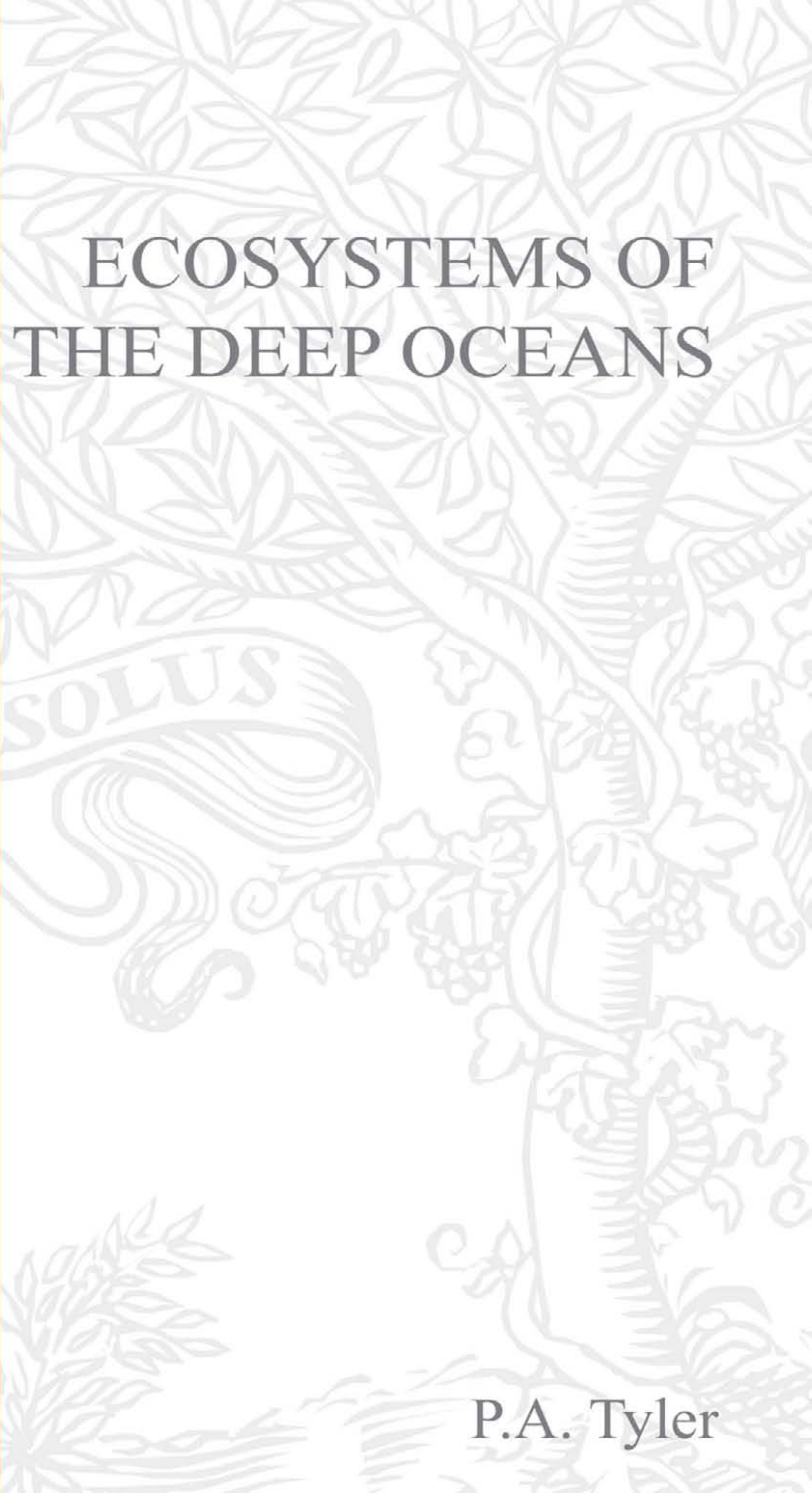
ECOSYSTEMS OF THE DEEP OCEANS



P.A. Tyler

ECOSYSTEMS OF THE WORLD 28

ECOSYSTEMS OF THE DEEP OCEANS

ECOSYSTEMS OF THE WORLD

Editor in Chief:
David W. Goodall
Centre for Ecosystem Studies, Edith Cowan University, Joondalup, W.A. (Australia)

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PREFACE

The deep ocean floor covers over 50% of the surface of the earth. It is often said that we know more about the surface of the moon than we do about the deep ocean floor and the water column above it. While this is not strictly true, we do know remarkably little, as a proportion of the total, of the deep ocean environment. Paradigms are continually changing, and we know now that the deep sea is an ecosystem of high species diversity, that it may have seasons as seen in temperate land ecosystems, and that in certain areas turbulence can be a great as anything seen in coastal shallow waters. Last, but by no means least, the originally perceived idea that the deep sea was an oligotrophic environment in which all environmental processes were gentle and physiological processes slow is no longer valid. We know now that the deep sea is essentially a heterotrophic system fuelled by organic carbon from surface waters, with the notable exception of hydrothermal vents and cold seeps where substantial ecosystems are fuelled by chemosynthetic processes. The continuing theme of this volume is how this energy input affects the deep-sea ecosystem.

All science has its eras of exploration, observation and experimentation. Exploration in deep-sea biology is often considered to have come to a finale with the *Galathea* cruise of 1950 to 1952. Subsequent discoveries of hydrothermal vents and cold seeps show that the deep-sea age of exploration is still with us and will continue. The 1960s saw the first change in our perception of the deep-sea with the introduction of more sophisticated sampling gear. This has been used from then and still continues to be used for much observation work. The introduction of submersibles, and, more recently, remote operated vehicles and landers, has allowed us to conduct manipulative experimentation on the deep sea bed and in the water column.

This volume is a review of where our knowledge stands at this point. All the chapters are written by authorities on their respective subjects, all of whom are still practicing deep-sea biologists. The volume is divided into sections covering the environment of the deep sea, specific deep-water seas and oceans, and lastly a review of the processes that occur there. All the chapters have been peer-reviewed by other experts in deep-sea biology, to all of whom I extend my thanks for their care and advice.

I wish to say a special thank you to all the authors. As I have said above, all are active research scientists, often working for extended periods at sea. I know their scientific lives are full, and I am delighted they were willing to write chapters and put up with my impatient prodding. I would also like to thank the series editor David Goodall for his advice, enthusiasm, patience and his unremitting courtesy when I failed to answer his requests! Lastly, I would like to express my sincere thanks to Lida de Maaijer Hoek of Isys Prepress Services for her patience, good humour and exceptional care in the desk editing of this volume.

Paul A. Tyler
Editor

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CONTENTS

To my wife Amanda for her love and support over the years, and
her patience with the amount of time I spent at sea!

Chapter 1

INTRODUCTION

Paul A. TYLER

The largest single ecosystem on earth is the deep sea. The sea surface occupies ~70% of the surface of the earth, and 50% of the surface of the earth is covered by more than 3000 m of ocean, with a mean depth of ~3800 m. It is the very remoteness of the deep sea and the difficulties encountered in its exploration that have resulted in it being one of the least understood environments on earth. At the present time there is detailed information about specific areas of the deep sea, but these are mere pinpricks in the vastness of this environment. The understanding of the deep-sea ecosystem is entwined with some of the most exciting aspects of scientific exploration and with the development of technologies for sampling and penetrating this environment. This volume is a status report, at the beginning of the 21st century, on current knowledge of the deep sea, on how perceptions of it have changed and where the exciting scientific discoveries will be made in the future.

CHANGING PARADIGMS

Explorers and commercial interests have used the sea as a means of transport for millennia. However, they always looked to the horizon, and it was only in the latter part of the 19th century that scientists went to sea with the specific aim of looking downwards into the impenetrable depths.

One of the first was Forbes (1844), who sampled down to a depth of 600 m in the Aegean. Today one would consider this choice of sampling station as unfortunate, since this region of the Mediterranean deep sea is faunistically very poor, and the lack of animals in Forbes's samples led to the 'azoic theory' that little or no life existed below 600 m. The establishment of such a paradigm was in direct opposition to observations of the ophiuroid *Astrophyton* being brought up on a sounding line from a depth of 1800 m in Baffin Bay (Tyler, 1980), and the pioneering work of Michael and G.O. Sars in Norwegian fjords (Sars, 1864, 1868).

Establishing the presence of a fauna in the deep sea presented irresistible challenges to a small group of scientists led by Charles Wyville Thomson. Wyville-Thomson used HMS *Porcupine* to sample the ocean to the northwest of Scotland and to the west of Ireland in the late 1860s, and found a fauna at depths exceeding 4000 m (Thomson, 1873). This series of cruises established the first ecological observation in the deep sea by showing that there was a marked temperature difference associated with faunal change as one moved across what is now called the Scotland–Faroes–Iceland Ridge from the warm deep North Atlantic to the cold deep Norwegian Sea (see Chapter 6). The results of the *Porcupine* sampling programme led directly to the HMS *Challenger* expedition of 1872 to 1876. This expedition traversed the oceans of the globe and demonstrated a widespread and varied fauna in the deep sea, as well as taking numerous physical and chemical measurements. The results of this cruise, now considered the forerunner of modern oceanography, were published in a series of detailed volumes edited by, and at the expense of, John Murray. A readable account of the *Challenger* expedition has been published by Linklater (1972).

The *Challenger* expedition led directly to the 'heroic' age of deep-sea exploration, with expeditions sampling many areas of the world's oceans (Menzies et al., 1973; Mills, 1983). The heroic age culminated in the Danish *Galathea* expedition of 1950 to 1952, which demonstrated that life could be found in the deepest of all the oceans, in the ocean trenches. One of the main outcomes of this age of exploration was the publication of descriptions of the fauna collected on these voyages.

Taking stock of deep-sea ecology at this point in time would have led to the establishment of the following paradigms:

- The deep sea was species-poor.
- It was a tranquil quiescent environment.
- There was a slow rain of material from surface to the deep (although see Moseley, 1880).
- No primary production occurred within the deep sea.

The 1960s heralded a new approach to deep-sea ecology, driven by technology. Quantification became the name of the game, and to get accurate data it was necessary to replace the coarse-meshed qualitative sampling gear of the heroic age with more refined quantitative gear. This was initially achieved by Howard Sanders and Robert Hessler from the Woods Hole Oceanographic Institution, who used an anchor dredge (later an anchor box dredge: Gage and Tyler, 1991) to sample a series of stations down to a depth of 5000 m between Gay Head, Massachusetts and Bermuda. The fine mesh of the anchor dredge collected a wide variety of species, many new to science, which had been missed by the coarse dredges of the heroic age. Thus the concept of high biodiversity in the deep sea was established, although the absolute diversity is still very much subject to debate (see Chapter 10); but it is now believed that the deep oceans are as diverse as tropical rain forests.

Although known to be diverse, it was assumed that the deep-sea system was heterotrophic, relying on the slow sinking of material from surface waters to provide an energy source for the inhabitants. The 1970s and 1980s provided evidence that this environment was more dynamic than originally thought. The first example was the discovery of hydrothermal vents along the Galapagos Ridge in 1977 (see Chapter 4). For the first time there was evidence that primary production could take place within the deep sea, and an ecosystem independent of sunlight had been discovered. This discovery led to one of the most active programmes in deep-sea biology, and the discovery of hydrothermal vents continues to this day. There can be few people interested in the natural environment who have not seen photos or videos of these spectacular environments. Subsequently, a second type of primary-production environment was observed in the form of cold seeps (see Chapter 4). Both hydrothermal vents and cold seeps are driven by the availability of reduced chemicals such as hydrogen sulphide and methane, the main difference being the temperature of emission.

In terms of energy availability a parallel, but no less important, revolution was occurring in understanding the input of material from surface primary production. The concept of the slow rain of surface primary production to the seabed was challenged by technological advances, particularly in the use of sediment traps to collect the sinking material. Such sediment traps, together with other techniques (see Chapters 2 and 11) showed that, particularly at temperate latitudes, surface production sank rapidly to the seabed – on average, at a rate of ~100 m d^{-1}. As a result, the signal of seasonal surface production was transmitted to the seabed, and it is now known that a number of organisms on the deep-sea bed respond seasonally to this input. This theme is explored in many chapters in this volume.

This seasonal perturbation is mild in comparison to the last major shift in paradigms. Over certain areas of the seabed, especially under areas of high surface-eddy kinetic energy, benthic storms are created by the input of energy to the seabed. These storms are analogous to the blizzards of Antarctica. They create strong currents transporting sediment, which is then deposited in drifts on the seabed, smothering the local fauna (see Chapter 2).

Lastly, technology has allowed humans to penetrate this ‘remote’ environment. SCUBA diving is limited to the top 30 m of the water column; but the development of submersibles has allowed scientists to dive to the deep-sea bed and conduct manipulative experiments as though they were working at the laboratory bench. Current knowledge of hydrothermal vents and cold seeps would be insignificant if it were not for the submersible. Submersibles are still used today; but the Remote Operated Vehicle (ROV) allows similar access from the comfort of the surface tender without the potential dangers of manned submersibles.

Today one may summarize the paradigms for the deep-sea environment as:

- High species diversity.
- Periods of benthic storms perturbing an apparently gentle environment.
- Seasonal input of surface-derived energy for heterotrophic organisms.
- Primary production at vents and cold seeps.

The change in understanding of the deep sea has been a function of an increase in the ability of scientists to gain knowledge from this environment. Despite recent recognition of the above paradigms, all of them are natural phenomena. As yet the deep sea is exploited only to a very limited extent, but this may change in the future. Disposal of waste has become prominent on the political agenda, particularly as land-based disposal areas become saturated. The deep sea has already been used for the disposal of low-level radioactive waste, pharmaceuticals and dredge spoil (see Chapter 13). Possibly more insidious is the use of the deep sea in relation to climate change. There is evidence of 'natural' decadal-scale changes in the fauna of the northeast Atlantic, possibly related to climate change. The deep sea has also been suggested as a repository for the excess carbon dioxide causing the so-called 'greenhouse effect'. The vastness of the deep ocean aids its very stability, but in localized areas this is already being challenged. The public outcry over the 'Brent Spar' (see Chapter 13) demonstrates that public awareness of this environment is increasing rapidly. Finally, with the decline of continental-shelf fisheries, fishing fleets are moving into deeper and deeper water, and there is evidence that at least one deep-sea fish, the orange roughy (*Hoplostethus atlanticus*), is already overexploited.

THE DEEP SEA TODAY

What is the deep-sea? Ask virtually any deep-sea biologist and you get a slightly different answer. For most, it is the region below 200 m, representing the transition from the continental shelves to the continental slope. This is the boundary that has been selected for this volume (see Chapter 2). Definitions based on light penetration, depth of the mixed surface layer, or temperature may be just as valid (see Gage and Tyler, 1991).

The approach to this volume has been to examine the deep sea from a number of facets, and differs from the approach of most previous volumes in this series. The linking theme between all the chapters is the availability of energy for organisms in the water column and at the deep-sea floor. Chapters 2, 3 and 4 examine environmental aspects of the deep sea – specifically the deep-sea floor, the water column and reducing environments. Chapters 5, 6, 7, 8, and 9 examine the ecology of the major oceans and those seas peripheral to the main ocean that have waters of oceanic depth. Chapters 10, 11 and 12 examine some of the specific processes that occur within the deep-sea ecosystem; and Chapter 13 explores the anthropogenic impact that has taken place or that may occur in the future.

ACKNOWLEDGEMENTS

I would like to take this opportunity to thank all the authors who have contributed to this volume. I may be editor but it has been a collective enterprise by a series of world-class scientists whose passion is for the marine environment and the deep sea in particular. I would also like to thank David Goodall for his forbearance throughout its production.

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Chapter 2

THE DEEP-SEA FLOOR: AN OVERVIEW

David THISTLE

INTRODUCTION

This chapter provides a general introduction to the ecosystem of the deep-sea floor, beginning with a description of the physical environment of the deep sea. A section on how information is obtained about the deep-sea-floor ecosystem follows, because knowledge of this ecosystem is greatly influenced by the effectiveness of the available technology. Introductions to the fauna of the deep sea where the substratum is sediment (soft bottoms) and where it is not (hard bottoms) follow. The chapter concludes with a section on the pace of life in the deep sea.

The geographic extent of the deep-sea-floor ecosystem

The deep sea is usually defined as beginning at the shelf break (Fig. 2.1), because this physiographic feature coincides with the transition from the basically shallow-water fauna of the shelf to the deep-sea fauna (Sanders et al., 1965; Hessler, 1974; Merrett, 1989). The shelf break is at about 200 m depth in many parts of the ocean, so the deep sea is said to begin at 200 m.

The deep-sea floor is therefore a vast habitat, covering more than 65% of the Earth's surface (Sverdrup et al., 1942). Much of it is covered by sediment, but in some regions (e.g., mid-ocean ridges, seamounts) bare rock is exposed. In the overview of environmental conditions that follows, the information applies to both hard and soft bottoms unless differences are noted. The ecosystems of hydrothermal vents and cold seeps are special cases and are described in Chapter 4.

Environmental setting

The deep-sea floor is an extreme environment; pressure is high, temperature is low, and food input is small. It has been characterized as a physically stable environment (Sanders, 1968). Below I review the major environmental variables and indicate circumstances under which these environmental variables constitute a biological challenge. I also show that the image of the deep-sea floor as monotonous and stable

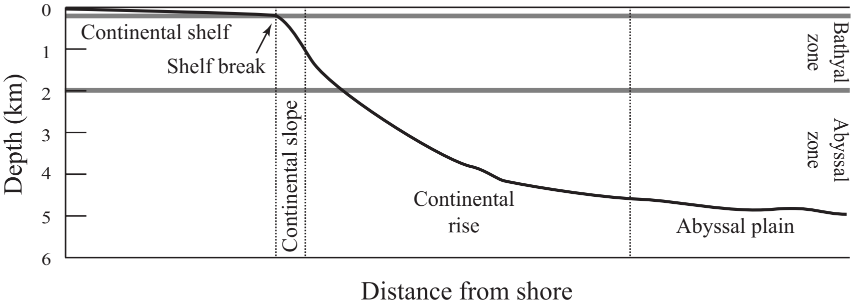

Fig. 2.1. Diagrammatic cross section of the ocean showing the major physiographic features and major depth zones. The sublittoral zone (0–200 m) is not labeled, and the hadal zone (6000–10 000+ m) is not shown. Modified from Gage and Tyler (1991). Copyright: Cambridge University Press 1991. Reprinted with the permission of Cambridge University Press.

must be tempered for some variables and some locations.

Pressure

Pressure increases by one atmosphere (10^5 Pascals) for every 10-m increase in water depth, so pressure varies from 20 atm at the shelf-slope break to >1000 atm in the deepest parts of the trenches. Pressure can affect organisms physiologically. For example, high deep-sea pressures oppose the secretion of gas. Many bottom-associated deep-sea fishes that use a gas-filled swim bladder to regulate their buoyancy (Merrett, 1989) overcome this problem, in part, by increasing the length of the *retia mirabilia* (Marshall, 1979), a component of the system that secretes gas into the swim bladder.

Pressure also affects an organism biochemically because the performance of proteins (e.g., enzymes) and lipid structures (e.g., membranes) changes with pressure. For example, any biochemical reaction that involves an increase in volume at any step in the transition from reactants to products will proceed more slowly as pressure increases (Hochachka and Somero, 1984). A species that lives in the deep sea must have adaptations that reduce or eliminate the pressure effects on reaction rates. Such adaptations include modifications of the enzymatic machinery (e.g., changes to the amino-acid sequence of an enzyme) to reduce or eliminate volume changes during catalysis (Siebenaller and Somero, 1978). These adaptations come with a cost; pressure-insensitive enzymes are not as efficient at shallow-water pressures as are those of shallow-water species (Hochachka and Somero, 1984). This requirement for molecular-level adaptations has been postulated to constitute an evolutionary barrier that must have been overcome by those species that successfully entered the deep sea.

Bottom-water temperature

Bottom-water temperatures generally decrease with increasing depth, reaching ~2ºC on the abyssal plain, but the pattern varies with latitude and region (Mantyla and Reid, 1983; Fig. 2.2). Above about 500 m in mid-latitude, temperature varies seasonally, but with diminishing amplitude with increasing depth (Figs. 2.2, 2.3). It should be noted that, at high latitudes, the vertical gradient in bottom-water temperature is small (Sverdrup et al., 1942). A small vertical temperature gradient also occurs in regions where the bottom water is warm (e.g., the Mediterranean Sea and the Red Sea).

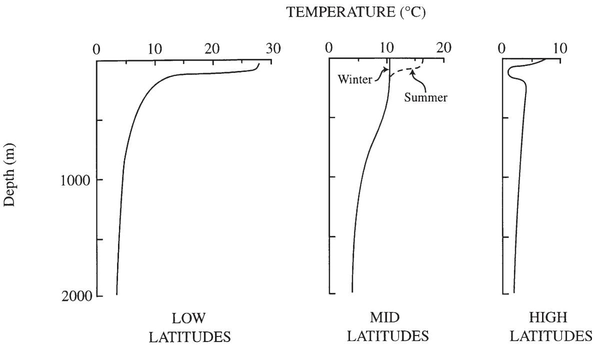

Fig. 2.2. Typical profiles of mean temperature versus depth for the open ocean. Modified from Pickard and Emery (1990). Reproduced by permission of Butterworth Heinemann.

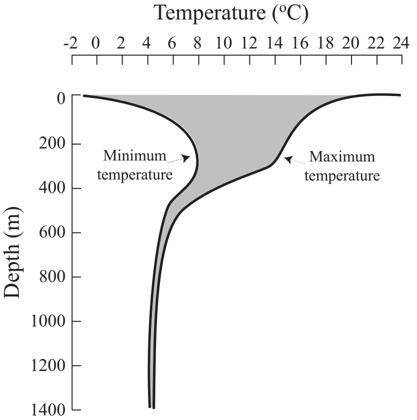

Fig. 2.3. Annual temperature variation in the western North Atlantic illustrating the diminishing amplitude of seasonal variation with depth. Modified from Sanders (1968). Reproduced by permission of the University of Chicago Press. Copyright 1968 by the University of Chicago.

In summary, most of the water overlying the deep-sea floor is cold compared to that over most shallow-water habitats. At depths below ~800 m, temperature is remarkably constant (Fig. 2.3). In the abyss, temporal variation is measured in the second decimal place and occurs, for example, because internal tides and waves cause the oscillation of isothermal surfaces. Hydrothermal vents are exceptions; they occur in the cold deep sea, but temperatures near them are elevated and variable (see Chapter 4).

The low temperatures have consequences for deep-sea-floor organisms because the cold reduces chemical reaction rates and shifts reaction equilibria toward reactants and away from products (Hochachka and Somero, 1984). To metabolize at reasonable rates, deep-sea species must have biochemical machinery that compensates. For example, low temperatures decrease enzyme flexibility and, therefore, catalytic rates. This effect can be offset over evolutionary time by changes in the amino-acid sequence of an enzyme to reduce the number of weak interactions (e.g., hydrogen bonds) that stabilize its three-dimensional structure (Hochachka and Somero, 1984). The necessity for such adaptation to low temperatures, like that to high pressure, may constitute a barrier which a warm-water shallow-water lineage must overcome evolutionarily to colonize the cold deep sea.

Salinity

In shallow, coastal waters, salinity can affect benthic species. For example, in estuaries, the organisms must be adapted physiologically to live in water that changes salinity with the tides. In most of the deep sea, on the other hand, the salinity of the bottom water is fully marine (*c.* 35‰). Exceptions include the Mediterranean and Red Sea (>39‰) and hypersaline basins such as the Orca Basin in the Gulf of Mexico (*c.* 300‰: Shokes et al., 1976). At most locations in the deep sea, salinity varies little with time, and that variation appears to be irrelevant to the ecology of deep-sea organisms.

Oxygen

Oxygen enters the ocean by exchange with the atmosphere and as a by-product of photosynthesis by marine plants in the euphotic zone. The dissolved gas is carried to the deep-sea floor by the descent of surface waters. The water overlying most of the deep-sea floor is saturated with oxygen or nearly so (5–6 ml ℓ^{-1}), and the variation in space and time of oxygen concentration on the scale of an individual organism is small in absolute terms and does not constitute an environmental challenge for organisms living in the near-bottom water or on the seabed.

Two major conditions reduce oxygen concentration to levels that are problematic for organisms. First, organic material (e.g., fecal pellets) that falls from the euphotic zone is decomposed by aerobic bacteria and is consumed by zooplankton as it sinks. The decomposition and animal respiration reduce the oxygen concentration, producing an oxygen-minimum layer in mid-water, usually between 300 m and 1000 m depth (Fig. 2.4). Where this layer intersects the deep-sea floor, the bottom fauna can be reduced or eliminated (Sanders, 1969). For example, the water bathing Volcano 7 (in the eastern tropical Pacific) above 750 m has an oxygen concentration of 0.08–0.09 ml ℓ^{-1}, and the mean abundance of sediment-dwelling animals caught on a 0.300-mm mesh sieve is 1854 individuals m^{-2}. Just below 750 m, the oxygen concentration is slightly higher (0.11–0.16 ml ℓ^{-1}), and the mean abundance quadruples to 8457 m^{-2}. The pattern for the hard-bottom fauna on Volcano 7 is similar (Wishner et al., 1990).

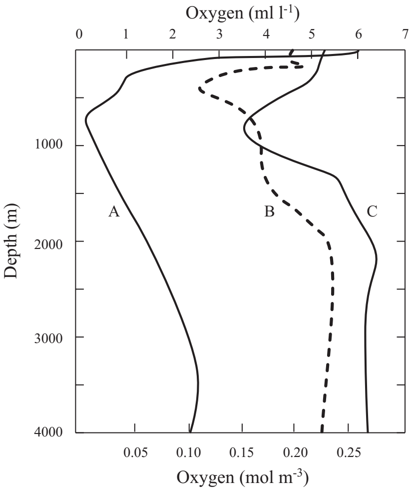

Fig. 2.4. The vertical distribution of dissolved oxygen illustrating the oxygen minimum zones in different regions: (A) south of California, (B) the eastern part of the South Atlantic, and (C) the Gulf Stream. Modified from Anonymous (1989). Reproduced by permission of Butterworth Heinemann.

The second circumstance concerns basins where the bottom water does not freely exchange with that of the surrounding region, for example, because of a topographic barrier. The reduced exchange decreases the oxygen-supply rate to the bottom waters of the basin. Organic material settles into the basin and is decomposed by microbes. Depending on the balance between the rate at which oxygen is supplied and the rate at which it is consumed, the oxygen concentration in the bottom waters can be much less than that of the surrounding region, or even zero. Such conditions can reduce or eliminate the aerobic benthic fauna. It should be noted that oxygen conditions need not be constant; for instance, the Santa Barbara Basin has alternated between oxic and reduced-oxygen conditions many times in the last 60 000 years (Behl and Kennett, 1996; Cannariato et al., 1999).

The ecological effects of low oxygen concentration in the overlying water are complex. For the macrofauna[1], diversity begins to decline at oxy-

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[1] Macrofauna, meiofauna: see Table 2.1, p. 11.

gen concentrations of ~0.45 ml ℓ^{-1} (Levin and Gage, 1998).

In terms of abundance, standing stocks at some low-oxygen sites are very low (Sanders, 1969; Levin et al., 1991), whereas at others they are remarkably high (Levin et al., 2000). Sites of high abundance seem to occur where oxygen concentration exceeds ~0.16 ml ℓ^{-1} (Levin et al., 2000) and the flux of organic carbon is high (Sanders, 1969). Where abundances are high, the number of species that constitute the fauna tends to be low relative to that at comparable, high-oxygen sites, suggesting that only a few species have solved the physiological problems presented by the low oxygen concentration and that the ecological reward for those that have is substantial. Interestingly, the identity of the successful species varies from site to site, suggesting that adaptation to low oxygen concentrations has occurred many times. In general, tolerance of reduced oxygen increases from crustaceans to molluscs to polychaetes, but some exceptions are known (Levin et al., 2000).

Meiofauna[1] are also sensitive to reduced oxygen. In oxygen-minimum zones, the diversity of benthic foraminiferan faunas tends to be reduced, and most individuals belong to a small number of species (Sen Gupta and Machain-Castillo, 1993). Experimental evidence from shallow water reveals that tolerance to oxygen stress generally decreases from benthic copepods to nematodes and soft-shelled foraminifers to hard-shell foraminifers (Moodley et al., 1997). These taxon-specific differences in tolerance imply that as oxygen-stress increases the meiofauna will change in composition.

Oxygen concentration also varies with depth in the sediment. Oxygen enters the pore water of deep-sea sediments by diffusion and by the activities of organisms that pump or mix water into the sediment. Oxygen is consumed by animal and microbial respiration and by chemical reactions in the sediment. Where the deposition rate of labile organic matter is relatively high and the oxygen concentration in the bottom water is low, as in the basins of the California Continental Borderland, free oxygen disappears within the first centimeter (Reimers, 1987). Where organic-matter deposition rates are low and the bottom water is well oxygenated, as beneath the oligotrophic waters of the central North Pacific, abundant free oxygen is present several centimeters into the seabed (Reimers, 1987). The depth of oxygen penetration into the sediment limits the vertical distribution of organisms that require it, such as most metazoans.

Light

Light intensity decreases exponentially with depth in the water column because incident photons are absorbed or scattered. Particles suspended in the water (sediment particles, phytoplankton cells) increase both absorption and scattering, but even in the clearest ocean water no photosynthetically useful light reaches the sea floor below about 250 m (Fig. 2.5). Therefore, the deep-sea floor (except the shallowest 50 m) differs from more familiar ecosystems in that plant primary production does not occur. Except for hydrothermal-vent and cold-seep communities, the food of deep-sea-floor organisms must be imported (see Chapter 11). The paucity of food reaching the deep-sea floor has profound consequences for the ecology of organisms living there.

The decrease of light intensity with increasing depth has other consequences for deep-sea species. For example, in shallow water most isopods have eyes. As depth increases, the proportion of isopod species without eyes increases until, at abyssal depths, eyes are absent (Hessler and Thistle, 1975; see Thurston and Bett, 1993, for amphipods). The implication of this pattern is that vision is of decreasing importance for some animal groups as depth increases. Its role in the ecology of these species (in prey location, in mate location, in movement) must be taken over by other senses such as chemoreception and mechanoreception. Also, the blindness suggests that they do not use bioluminescence, which is important to many animals of the deep water column (Chapter 3). Demersal fishes (e.g., Macrouridae) show a parallel pattern. They can have eyes, even at great depth, but eyes are smaller in deeper-living species (Marshall, 1979).

Near-bottom flow

In much of the deep sea, the near-bottom water moves slowly compared to that in shallow-water environments. Speeds in the bathyal zone tend to be less than 10 cm s^{-1} at 1 m above the bottom, those in the abyssal zone less than 4 cm s^{-1}. Speeds in both environments vary little from day to day at a location (Eckman and Thistle, 1991). Because the horizontal flow speed must decrease to zero at a solid boundary (Vogel, 1981), the horizonal speeds just above the seabed will be much less than those 1 m above. These flows are benign in that they are too slow to erode sediment or benthic organisms. The flow does move

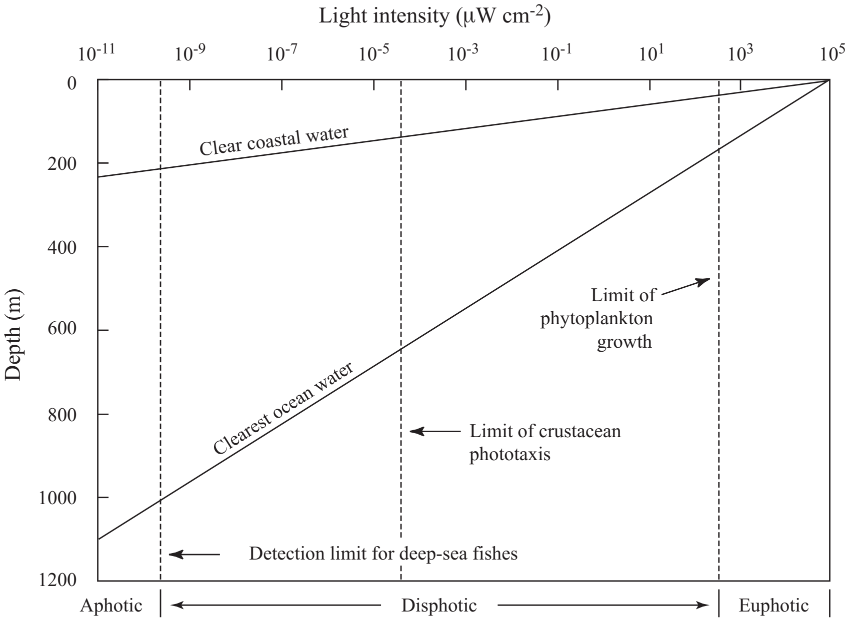

Fig. 2.5. The attenuation of light under different conditions of water clarity. Modified from Parsons et al. (1977). Reproduced by permission of Butterworth Heinemann.

some material, in particular phytodetritus (flocculent material of low specific density consisting of phytoplankton cells in an organic matrix, Billett et al., 1983), which accumulates in depressions (Lampitt, 1985). The water is never still, because tidal forces move water at all ocean depths. As a result, the water bathing all sessile sea-bed organisms slowly changes, bringing food and removing wastes.

Near-bottom velocities are not slow everywhere in the deep sea. At a site at the base of the Scotian Rise (North Atlantic), near-bottom flows 5 m above the bottom can approach 30 cm s^{-1} (Gross and Williams, 1991). During periods of fast flow, the sediment can be eroded. These “benthic storms” occur several times each year and have consequences for the fauna. The fast flows can have positive effects. For example, the increase in the horizontal food flux benefits some species (Nowell et al., 1984). In contrast, surface-living crustaceans can be significantly less abundant than at quiescent deep-sea sites (Thistle and Wilson, 1996). Many soft-bottom regions experience erosive flows (see Fig. 1 of Hollister and Nowell, 1991). Such flows also prevent sediment settling from above from covering the horizontal surfaces of some deep-sea hard bottoms.

The soft-bottom seafloor

Deep-sea sediments consist, in part, of particles derived from the weathering of rock on land (= terrigenous particles), which are transported to the sea by wind and in rivers. In consequence, the supply of terrigenous particles is highest near the continents. The rate of supply and the size of the particles decrease with distance from land.

Deep-sea sediments also contain particles produced by planktonic organisms in the overlying water. Diatoms, radiolarians, and silicoflagellates make silica shells; foraminifers, coccolithophores, and pteropods make calcium carbonate shells. As depth increases, the rate of silica and calcium carbonate dissolution increases, but at a given depth, calcium carbonate dissolves more rapidly. The contribution of shells to the sediment depends on the rate at which they are produced in the overlying water and the rate at which they dissolve in the water column and at the seafloor. If shells constitute more than 30% by volume of the deposit, the sediment is called a biological ooze (Gage and Tyler, 1991).

The balance between the rates of supply of terrestrial and biological particles and the rate of dissolution of biological particles controls the local sediment composition. For example, only a small amount of terrigenous material reaches the areas farthest from land, but the productivity of the overlying waters in these areas (oceanic central gyres) is so small that the few shells that are produced and fall to the seafloor are dissolved away. As a result, the sediment (abyssal red clay) consists of terrigenous particles. Accumulation rates are low, *c.* 0.5 mm per thousand years.

Where productivity is high, the production rate of both siliceous and calcium carbonate shells is high. If the water is deep, the calcium carbonate shells that reach the seafloor dissolve. The sediment will be composed of terrigenous and siliceous particles, a diatomaceous or a radiolarian ooze. For example, a radiolarian ooze occurs under the band of high productivity along the equator in the Pacific. Some productive regions occur where the underlying water is relatively shallow. In these regions, the rate of calcium carbonate dissolution is much reduced, and foraminiferan and coccolithophorid oozes occur (e.g., along most of the Mid-Atlantic Ridge) because production by these plankters is greater than that by those producing silica shells. Biological oozes accumulate at a relatively rapid rate of centimeters per thousand years. Near continents, the supply of terrestrial particles overwhelms that of biological particles, and biological oozes do not form. Accumulation rates vary, but they are higher than for biological oozes.

A substantial portion of the surface area of soft bottoms can be occupied by pebble- to cobble-sized manganese nodules. Manganese nodules are accretions of metals (mostly iron and manganese) that grow slowly (~1 mm per 10 000 y). They occur in a few regions of the deep Atlantic, but widely in the deep Pacific, particularly beneath the central gyres. At their most abundant, nodules can almost completely cover the surface of the seabed.

Large-scale processes control sediment composition, so it tends to be uniform over hundreds of square kilometers. At the spatial scale at which most individual organisms experience their environment (millimeters to meters), the seafloor is made heterogeneous by two processes. The organisms themselves structure the seafloor by building tubes, tests, and mudballs in which to live (Fig. 2.6). These structures are used by other organisms as habitat (Thistle and Eckman, 1990). The second process is small-scale disturbance that creates patchiness in the deep-sea floor – in, for example, species composition, sediment texture, and food content (Grassle and Sanders, 1973; Grassle and Morse-Porteous, 1987). Where they occur, manganese nodules impose a third type of small-scale heterogeneity on the surrounding soft bottom.

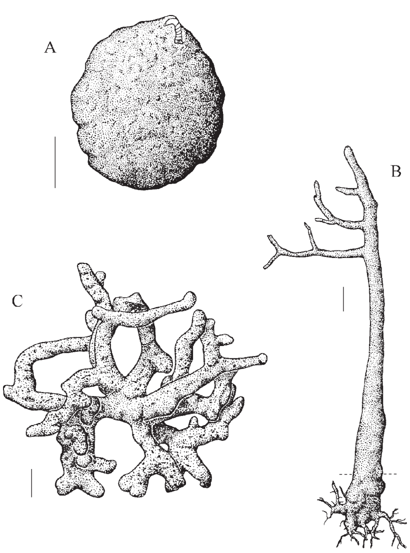

Fig. 2.6. Some representative organism-constructed structures from deep-sea soft-bottom habitats. A. Empty test of the foraminiferan *Oryctoderma* sp., which is inhabited by a polychaete. B. and C. Foraminifers (the dashed line indicates the surface of the sediment). Scale lines equal 1.0 mm. Modified from Thistle (1979). Reproduced with permission of Plenum Press.

Environmental variation in geologic time

The preceding description of physical conditions in the deep sea applies to the modern ocean, but an understanding of modern deep-sea communities cannot be achieved without the incorporation of a historical perspective, because environmental changes at many time scales have helped to shape the present fauna. For example, since the early Eocene (~54 Ma BP)[2], deep-water temperatures have decreased from about 12°C to their present values (Flower and Kennett, 1994) in four major cooling phases, in the early Middle Eocene, Late Eocene, Late Miocene, and Plio-Pleistocene (Lear et al., 2000). These abrupt temperature changes have been correlated with changes in the deep-sea fauna. For example, the sharp drop at the Eocene–Oligocene boundary (~38 Ma BP) is correlated with large changes in the benthic foraminifer (Kennett, 1982) and ostracod (Benson et al., 1984) assemblages. Within the Pliocene (2.85–2.40 Ma BP), bottom-water temperatures varied by 2°C on a 40 000-yr time scale in the North Atlantic, as glaciers advanced and

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[2] 1 Ma = 10^6 years.

retreated because of variation in the Earth's axis of rotation. These temperature changes are correlated with changes in ostracod diversity (Cronin and Raymo, 1997). In the last 60 000 years, global warming and cooling cycles on a 1000-yr time scale are correlated with changes in foraminifer assemblages in the deep sea off California (Behl and Kennett, 1996).

Summarizing, in much of the deep sea the variability in temperature, salinity, and oxygen over ecological time at a location is not important, and current velocities are nonerosive. In this sense, the deep-sea-floor environment is physically stable (Sanders, 1968). Even in regions with these physical characteristics, the sediment is heterogeneous at the millimeter-to-meter scale because of the modifications made by the organisms, small-scale disturbances, and manganese nodules. In contrast to these physically quiescent areas, some deep-sea locations experience erosive currents (Hollister and Nowell, 1991; Levin et al., 1994).

OBTAINING INFORMATION ABOUT THE DEEP-SEA-FLOOR ECOSYSTEM

By definition, 200 m or more of seawater separates deep-sea ecologists from the environment that they study. They, therefore, depend totally on technology to obtain information. Any shortcomings of their sampling devices must be understood, because defects can distort perceptions of the deep-sea-floor ecosystem. For example, the deep-sea floor was thought to be a species-poor environment until Hessler and Sanders (1967) showed that this erroneous view resulted from the inadequacies of older samplers.

No single device can sample the entire size range of deep-sea organisms (from bacteria ~1 μm to fish >50 cm) quantitatively and efficiently. Fortunately, the sizes of deep-sea organisms are not spread evenly over this range but tend to fall into a small number of size classes (Mare, 1942; Schwinghamer, 1985; Table 2.1, Fig. 2.7). Sampling techniques have been developed for each. The size classes have the additional advantage that major taxa tend to occur primarily in a single size class, at least as adults. For example, polychaetes, bivalves, and isopods are macrofauna; nematodes and copepods are meiofauna. The technologies in current use differ in their suitability for the study of the various size classes.

Table 2.1
Published size categories of deep-sea benthic organisms

Category	Lower size limit	Sampler	Representative taxa
Megafauna	centimeters	trawls, photographs	fishes, sea urchins
Macrofauna	250–500 μm	corers	polychaetes, bivalves
Meiofauna	32–62 μm	corers	nematodes, harpacticoids
Microbiota	microns	corers	protists

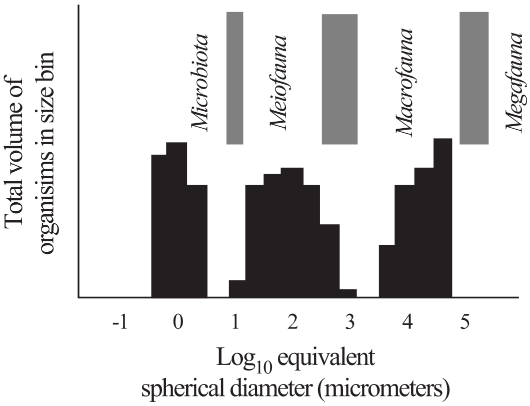

Fig. 2.7. Size–abundance relationships in the benthos showing the gaps in the distribution that underlie the use of size classes. Equivalent spherical diameter is the diameter of a hypothetical sphere having a volume equal to that of the organism. Gray regions indicate the variability in the size-class boundaries used by different workers. Megafauna are those organisms that are visible in photographs of the seabed taken at more than about one meter off the bottom. Modified from Jumars (1993). Copyright 1993 by Oxford University Press, Inc. Used by permission of Oxford University Press, Inc.

Cameras

Cameras, mobile or stationary, are used to study the deep-sea-floor megafauna (Owen et al., 1967). Most deep-sea cameras use film, although video cameras and recorders are becoming more common. Because the deep sea is dark, a light source is paired with the camera. Circuitry to control the camera and light source and a source of power (batteries) complete the system. All components are housed in pressure-resistant cases.

Megafaunal organisms (e.g., demersal fishes, brittle stars) are sparse, and some are highly mobile and can avoid capture by mechanical sampling devices (see below). Because mobile cameras can be used to survey kilometer-scale transects relatively unobtrusively (but see Koslow et al., 1995), they have been crucial in estimating the abundance and biomass of such organisms and in discerning their distribution patterns (Hecker, 1994). For surveys, vertically oriented cameras have been suspended above the seabed from a ship's trawl wire to photograph the seabed as the ship moves (Rowe and Menzies, 1969; Huggett, 1987). Cameras have also been mounted obliquely on towed sleds (Thiel, 1970; Rice et al., 1982; Hecker, 1990) and on research submarines (Grassle et al., 1975).

Cameras have also been important in documenting the behavior of deep-sea megafauna, and in the discovery of rates of some deep-sea processes. For these purposes, cameras are mounted in frames (vertically or obliquely) and left for times ranging from hours to months, taking photographs at preset intervals (Paul et al., 1978). At the appropriate time, ballast weights are released, and the buoyant instrument package rises to the surface for recovery. This "free-vehicle" approach (Rowe and Sibuet, 1983) has been used, for example, to document the date of appearance of phytodetritus on the seafloor (Lampitt, 1985), the rates of mound-building by an echiurid (Smith et al., 1986), and megafaunal activity rates (Smith et al., 1993). Stationary cameras with bait placed in the field of view have been crucial to the discovery and study of food-parcel-attending species in the deep sea (Hessler et al., 1972).

Cameras cannot provide information about smaller epibenthic organisms or organisms of any size that are inconspicuous or evasive or that live below the sediment-water interface and make no conspicuous indications of their presence on the sediment surface. Further, cameras return no specimens, so they are not useful for work that requires biological material such as physiological or taxonomic studies (but see Lauerman et al., 1996).

Trawls, sledges, and sleds

Some devices (trawls and sledges) have been used to collect megafauna. They consist of a mesh collecting bag and a means of keeping the mouth of the bag open (Fig. 2.8). A sledge has runners upon which the device rides; a trawl does not. Both are pulled along the seabed, collecting megafaunal invertebrates and fishes living on or very near the seabed. Smaller organisms are lost through the openings in the mesh. For some purposes, these devices have an advantage over cameras because they collect specimens, but they sample much less area per unit time than cameras and fail to collect agile species that detect the approach of the device and escape. Much effort has been expended toward improving these samplers (Rice et al., 1982; Christiansen and Nuppenau, 1997), but the best that has been achieved is a device that collects all individuals of a few species, a constant proportion of others, and none or a varying proportion of others. The simultaneous use of camera and trawl or sledge surveys may be the best approach to quantification of the megafauna.

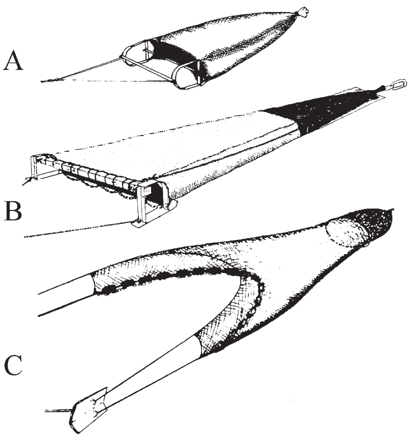

Fig. 2.8. Some deep-sea trawls (drawn roughly to scale). A, 3-m-wide Agassiz trawl; B, 6-m-wide beam trawl; C, a semiballoon otter trawl. Modified from Gage and Tyler (1991). Copyright: Cambridge University Press 1991. Reprinted with the permission of Cambridge University Press.

The epibenthic sled (Hessler and Sanders, 1967) is a type of sledge designed to collect macrofauna from the sediment surface and from the top few centimeters of seabed (Fig. 2.9). The collecting bag has a smaller mesh than that used in a trawl or sledge. As a sled is towed along the seabed, an (adjustable) cutting blade slices under the upper layer of sediment,

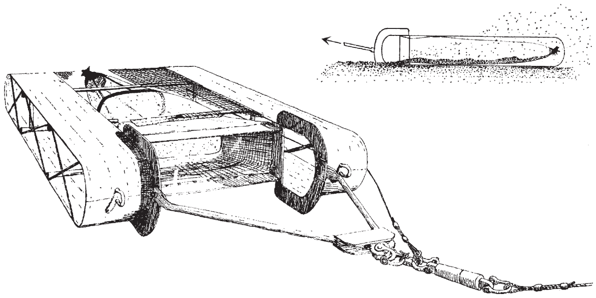

Fig. 2.9. The epibenthic sled used to collect large, non-quantitative samples of deep-sea infauna and epifauna. For scale, each runner is 2.3 m long by 0.3 m wide. The right-hand figure illustrates the operation of the sled. Modified from Hessler and Sanders (1967). Copyright: Elsevier Science.

which moves into the collecting bag. Sleds collect macrofauna in large numbers, supplying specimens for research in which properties of each individual must be determined – for example, studies of reproductive biology, biomass distribution, and taxonomy. Sleds do not collect every individual in their path in the layer to be sampled because the mouth of the bag clogs with sediment as the sled moves along the seabed (Gage, 1975), so sleds are inappropriate for quantitative studies. They can also damage delicate specimens (e.g., the legs of isopods tend to be broken off) and cannot sample macrofauna living at greater depths than 1–2 cm.

The deep-sea-floor ecosystem extends into the near-bottom water because some animals living in or on the seabed make excursions into the near-bottom water, and some animals living in the water just above the seabed interact with the seafloor. Hyperbenthic sledges (see also Rice et al., 1982) have been developed to sample the near-bottom water. Such sledges consist of runners and a frame supporting a vertical array of opening–closing nets (Dauvin et al., 1995; Fig. 2.10).

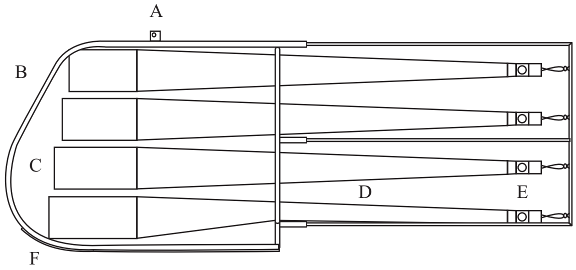

Fig. 2.10. The hyperbenthic sled, a device for collecting deep-sea animals in the waters just above the seabed. The device is 1.51 m tall. A, Attachment point for the cable to the ship; B, frame; C, mouth of a sampler; D, net; E, sample container; F, runner. Modified from Dauvin et al. (1995). Copyright: Elsevier Science.

The usual limitations of plankton nets apply to these samplers (e.g., bias in collections owing to differences in avoidance behavior among species, variable filtering efficiency resulting from net clogging). In addition, the frame may put animals from the seabed into suspension and thus cause them to be caught, particularly in the lowest net. Despite their limitations, these samplers provide access to an understudied component of the deep-sea fauna (see also Wishner, 1980).

Despite their limitations, most of the taxonomic, systematic, and biogeographic research on the deep-sea fauna has been based on the large collections that trawls, sledges, and sleds provide (Hessler, 1970). This research has resulted in discoveries regarding, for example, the high diversity of the deep-sea-floor fauna (Hessler and Sanders, 1967) and the systematics and phylogeny of major invertebrate groups (Wilson, 1987). Also, such samples taken repeatedly from the same area have provided information on temporal phenomena, in particular reproductive periodicity in the deep sea (Rokop, 1974; Tyler et al., 1982).

Corers

Corers are used to sample macrofauna, meiofauna, and microbiota. Two types are presently in common use. Box corers, in particular the USNEL-Sandia 0.25-m^2 box corer (Hessler and Jumars, 1974; Fig. 2.11), are lowered on a ship's trawl wire. About 100 m above bottom, the rate of descent is slowed to 15 m min^{-1} until the corer penetrates the bottom. This relatively high entry speed is necessary to minimize multiple touches and pretripping. As the corer is pulled out of the seabed, the top and bottom of the sample box are closed. The advantages of a box corer are that it takes a sample of known area to a depth (>20 cm) that encompasses the bulk of the vertical distribution of deep-sea organisms.

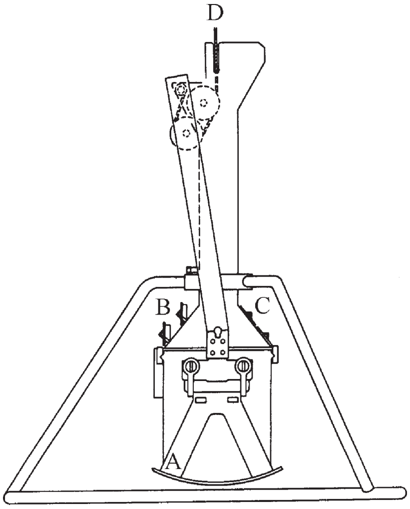

Fig. 2.11. An advanced version (Hessler–Sandia) of the USNEL box corer (shown in the closed position), a device for collecting quantitative samples of deep-sea macrofauna. The width of the sample box is 0.5 m. A, The detachable spade; B, vent flaps in the open position for descent; C, vent flaps in the closed position for ascent; D, cable to the ship. Some details omitted. Modified from Fleeger et al. (1988).

Box corers are not strictly quantitative. They occasionally collect megafaunal individuals, but megafauna are too rare to be effectively sampled. Further, the pressure wave that precedes the corer (even in the most advanced designs only about 50% of the area above the sample box is open) displaces material of low mass (e.g., the flocculent layer, phytodetritus; Jumars, 1975; Smith et al., 1996), if any is present (Thistle and Sherman, 1985). Therefore, box-corer samples usually underestimate abundances of organisms that live at the sediment surface or in the upper millimeters. The bias becomes worse as animals decrease in size and mass (see Bett et al., 1994).

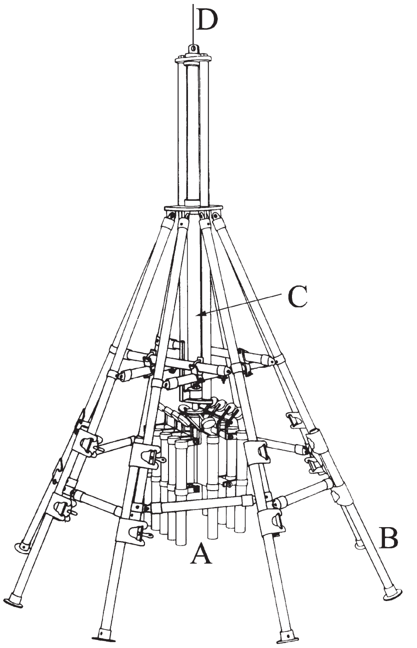

Fig. 2.12. Scottish Marine Biological Laboratory multiple corer, a device for collecting quantitative samples of deep-sea meiofauna, phytodetritus, and other materials that would be displaced by the pressure wave preceding a box corer. A, Sampling tubes; B, supporting frame; C, hydraulic damper; D, cable to the ship. Some details omitted. Modified from Barnett et al. (1984). Copyright: Elsevier Science.

Deliberate corers (Craib, 1965; Fig. 2.12) are alternatives to box corers. These devices consist of a frame, one or more samplers carried on a weighted coring head hanging from a water-filled hydraulic damper, and mechanisms to close the top and bottom of the sampler(s) during recovery (Soutar and Crill, 1977; Barnett et al., 1984). The corer is lowered on the ship's trawl wire. At the seabed, the frame takes the weight of the coring head. When the wire slackens, the hydraulic damper allows the coring head to descend slowly, which forces the sampler(s) into the seabed. As a consequence, the pressure wave is minimal. When the trawl wire begins to wind in, the coring head rises, allowing the top and bottom closures to seal the sampler(s).

The advantage of deliberate corers is that they can sample quantitatively material that would be displaced by the bow wave of a box corer (Barnett et al., 1984). The disadvantage is that the surface area sampled tends to be smaller; also, stiff sediments are not penetrated as well as when box corers are used. Thus, despite the superior sampling properties of deliberate corers (Bett et al., 1994; Shirayama and Fukushima, 1995), box corers are still used because, for some taxa (e.g., polychaetes) in some environments (e.g., areas of the abyss with low standing stocks), deliberate corers collect too few individuals to be useful.

Corers have also been developed for use with research submarines and remotely operated vehicles (ROVs). Tube corers are plastic cylinders (~34 cm^2 in cross section), each fitted with a removable head that carries a flapper valve and a handle by which the sampler is gripped. To sample, the mechanical arm of the research submarine or ROV presses the corer into the seabed. The corer is then removed from the seabed and transferred to a carrier that seals its bottom. With this method of coring, samples can be taken from precisely predetermined locations, allowing the sampling of particular features or previously emplaced experimental treatments (Thistle and Eckman, 1990). Even though these corers enter the seabed slowly, the water in the corer tube must be displaced for the sediment to enter, so that there is a bow wave, but its effect has not yet been measured. Also, because the bottom of the corer is not sealed during the transfer to the carrier, these cores can only be used in deposits where the subsurface sediment seals the corer, i.e., cohesive muds.

Modified Ekman corers are also commonly used by research submarines and ROVs. These corers consist of a metal box of surface area typically between 225 cm^2 and 400 cm^2, with a handle for a mechanical arm to grasp and with mechanisms to close the top and bottom after a sample has been taken. These corers have the advantages that they can be deliberately positioned; they take larger samples than do tube corers; and, because they are sealed at the bottom as the sample is taken, they can be used in fluid muds or in sands. A disadvantage is that they sample a much smaller area than a box corer because of handling and payload constraints on their size. Also, despite the low speed at which they are inserted into the seabed, light surface material can be displaced from the periphery of the sample (Eckman and Thistle, 1988).

A variety of corers have been used historically to sample macrofauna, meiofauna, and microbiota (gravity corers, Smith–McIntyre grabs). The sampling properties of these devices were not as good as those of the box corer, deliberate corers, or submarine/ROV samplers (see below). In particular, the bow wave was more severe. Therefore, the data obtained with such samplers must be interpreted with caution. Finally, the collection of subsurface megafauna remains an unsolved problem, but acoustical approaches (Jumars et al., 1996) seem likely to be useful for some types of measurements.

Research submarines and remotely operated vehicles (ROVs)

A research submarine is comparable in size to a delivery truck. Those in service typically carry a pilot and one or two scientists in a pressure sphere about 2 m in diameter. Surrounding the sphere is equipment for life support, propulsion, ascent and descent, and scientific purposes (manipulator arms, cameras, specialized payload in a carrying basket) (Heirtzler and Grassle, 1976). Research submarines bring the ecologist into the deep sea and thereby confer large benefits by correcting the tunnel vision that deep-sea scientists acquire from the study of deep-sea photographs. Further, research submarines permit a wide range of ecological experiments. For example, trays of defaunated sediment have been placed on the seabed for study of colonization rates (Snelgrove et al., 1992), and dyed sediment has been spread and subsequently sampled for estimates of sediment mixing rates (Levin et al., 1994).

Research submarines have limitations. For example, positioning the vehicle and then removing the device to be used (e.g., a corer) from its carrier, performing the task, and returning the device to its carrier require a substantial amount of time, so relatively few tasks can be done during a dive. Also, because the vehicle is large, maneuvering can be awkward, and experiments are occasionally run over and ruined. Because of their cost, few research submarines are in service, so dives are rare. Much more research needs to be done than can be accommodated.

Remotely operated vehicles (ROVs) are self-propelled instrument packages. Some operate at the end of a cable that provides power and hosts a two-way communications link; others are untethered, carrying their own power and recording images and data. The instrument package consists of a propulsion unit, sensors (particularly television), and, in some cases, manipulator arms. Some ROVs are designed to "fly" over the seabed. These ROVs tend to be used for large-scale surveys, but some can be maneuvered with precision and can inspect or sample centimeter-scale targets (e.g., the MBARI ROV: Etchemendy and Davis, 1991). Other ROVs are bottom crawlers (e.g., the Remote Underwater Manipulator: Thiel and Hessler, 1974) and are more suitable for seabed sampling and experimentation.

The great advantage that ROVs have over research submarines is endurance. Because the investigators are on the support ship rather than in the vehicle, the ROV does not have to be recovered each day to change crew as does a research submarine. The time savings result in far more ROV bottom time than research submarine bottom time for each day at sea. Limitations of ROVs include slow sampling and cumbersome maneuvering. Also, there are substantial benefits to allowing deep-sea scientists to come as close as possible to experiencing the deep-sea environment. Scientists who have made dives relate how their conception of the deep sea was substantially changed by the experience, improving their science.

Sensors

Knowledge of the chemical milieu in which deep-sea-floor organisms live has increased markedly since the introduction of microelectrode sensors. These devices measure chemical parameters (oxygen, pH) with a vertical resolution measured in millimeters. Early measurements were made on recovered cores, but free-vehicle technologies have been developed so that measurements can be made *in situ* (see Reimers, 1987).

Other technologies

The devices discussed above are those that are in common use. Many other devices have resulted in important work but have not become common (see Rowe and Sibuet, 1983). It is beyond the scope of this chapter to present all these devices, but two are conspicuous. The free-vehicle respirometer (Smith et al., 1976), which measures oxygen utilization by the benthic community, has been important in studies of deep-sea community energetics, which have implications for global carbon cycling. Free-vehicle traps have been crucial to the study of food-parcel-attending species in the deep sea (Hessler et al., 1978).

Costs and benefits

Good techniques are available with which to sample, and reasonable techniques are available with which to do experiments in the deep sea, but the expense is substantial. Both sampling and experimentation require the use of large, and therefore expensive, ships. Research submarines and ROV's add additional costs. For soft bottoms, separating the animals from the sediment and identifying the diverse fauna (Grassle and Maciolek, 1992) are time-consuming, so sample processing is costly. These expenses are among the reasons why relatively few data have been collected from this vast ecosystem and why few ecological experiments have been performed.

Despite these costs, scientists persist in the study of the deep sea, and their research provides a variety benefits for society. For example, research on hydrothermal-vent animals led to the discovery of DNA polymerases that work at high temperatures, which are crucial tools in pure and applied molecular biology. Safe repositories for human waste, such as dredge spoils, sewage sludge, industrial waste, and radioactive materials, are needed. Ongoing ecological work will help determine whether wastes dumped in the deep sea make their way back into contact with humans, and the effects of these wastes on the functioning of natural ecosystems in the ocean (Van Dover et al., 1992). The deep-sea floor contains mineral resources; for example, economically important amounts of cobalt and nickel occur in manganese nodules. The work of deep-sea ecologists is helping to determine the environmental consequences of deep-ocean mining (Ozturgut et al., 1981). More generally, the deep-sea benthos provides critical ecological services (e.g., recycling of organic matter to nutrients: Snelgrove et al., 1997).

THE SOFT-BOTTOM FAUNA OF THE DEEP-SEA FLOOR

Taxonomic composition

At high taxonomic levels (i.e., phylum, class, and order), the soft-bottom, deep-sea fauna is similar to that of shallow-water soft bottoms (Hessler, 1974; Gage, 1978). For example, the megafauna consists primarily of demersal fishes, sea cucumbers, star fishes, brittle stars, and sea anemones. The macrofauna consists primarily of polychaetes, bivalve mollusks, and isopod, amphipod, and tanaid crustaceans. The meiofauna consists of primarily of foraminifers, nematodes, and harpacticoid copepods. At lower taxonomic levels (family and below), however, the similarities disappear. In particular, the species that live in the deep sea are not, in general, found in shallow water. Gage and Tyler (1991) have reviewed the natural history of deep-sea taxa.

Many taxa that have large numbers of species in shallow water have a few members that penetrate into the deep sea. For example, of 300 stomatopod (mantis shrimp) species, only 14 occur below 300 m (Manning and Struhsaker, 1976). The decapod crustacean fauna in shallow water (<200 m) consists of more than 200 species, predominantly brachyuran crabs. Below a depth of 1500 m, there are fewer than 40 species of decapods, and brachyurans make up ~10% of this total. The proportion of the bivalve mollusks that are eulamellibranchs decreases as well (Sanders et al., 1965). In contrast, the proportion of isopod species that are asellotes (Hessler and Wilson, 1983) and of bivalve mollusk species that are protobranchs increases with depth. Finally, some taxa inhabit the deep sea exclusively; for instance, the protist group of xenophyophores have not been found above ~500 m (Tendal, 1996).

Variation of biomass and numbers with depth

The general pattern of the distribution of the biomass of organisms on the deep-sea floor is known (Fig. 2.13) and appears to be controlled by the rate at which food is supplied to the seabed (Rowe, 1971). The basic pattern is set by the productivity of the surface waters. For example, primary productivity is highest nearest the continents, and the deep-sea floor near continents tends to have the highest biomass. The depth of the overlying water modifies this pattern. As food particles sink, a portion of each particle is lost to decay, and some particles are consumed by mid-water organisms. The deeper the water, the longer it takes particles to reach the seabed, and the greater the loss from these processes. Given two regions with identical primary productivities in the overlying water, the deeper location will have the lesser food input

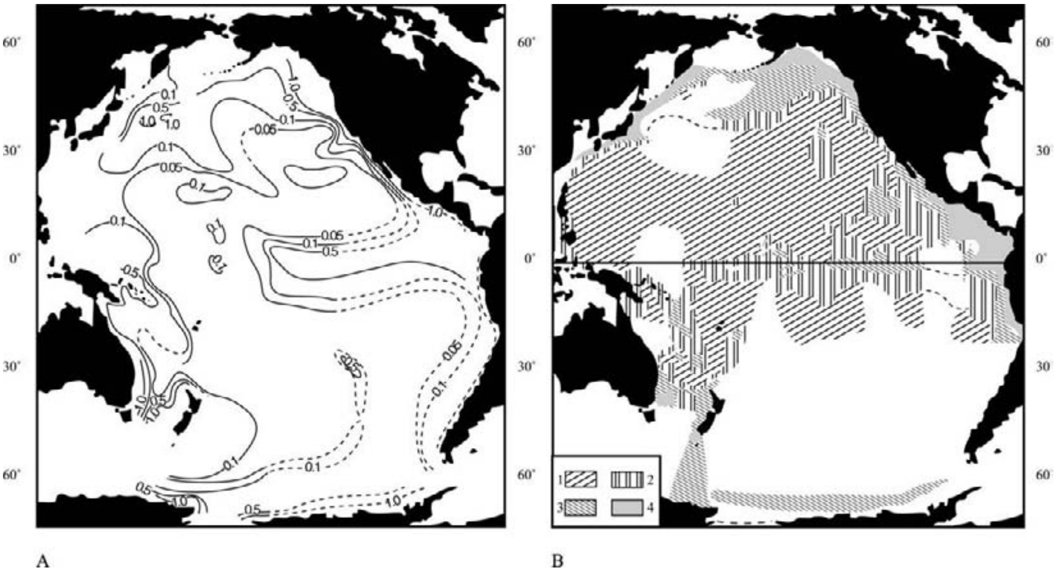

Fig. 2.13. The correspondence between water-column primary production and deep-sea benthic biomass. A, Distribution of benthic biomass (g wet weight m^{-2}) in the Pacific; B, zones of primary productivity in the Pacific. Values 1–4 are <100, 100–150, 150–250, and 250–650 mg C m^{-2} d^{-1}, respectively. Modified from Hessler (1974). Reproduced by permission of the Oregon State University Press.

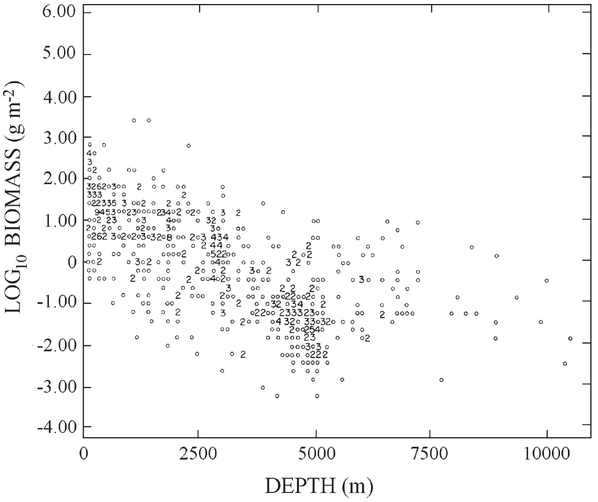

Fig. 2.14. Biomass from 709 deep-sea quantitative samples plotted against depth showing the logarithmic decline in biomass with increasing depth. Modified from Rowe (1983), who gives the sources of the data. Numerals in the figure indicate the number of co-occurring points. Copyright: 1983, John Wiley and Sons. Reprinted by permission of John Wiley and Sons, Inc.

and, therefore, the smaller benthic biomass. Food is also supplied to the deep-sea benthos as organic debris (e.g., pieces of seagrass and macroalgae) that moves across the seabed from shallow to deep water (Carey, 1981). This phenomenon appears to explain why those trenches that are near continents have higher biomasses than would be expected for their depths (Belyaev, 1989). The trench traps and concentrates the organic debris that would otherwise be spread over a wider area (Rowe, 1983).

Because shallow water is adjacent to the continents in most regions, higher productivity, shorter food-particle settling times, and larger seabed fluxes of organic debris are all correlated, resulting in the generalization that the abundance of life in the deep sea decreases with depth and distance from a major land mass (Murray, 1895). More simply, the biomasses of megafauna (Lampitt et al., 1986), macrofauna (Rowe, 1983; Fig. 2.14), and meiofauna (Shirayama, 1984; Tietjen, 1992) decrease as depth increases.

The number of animals per unit area of sea floor also decreases with depth (Hessler, 1974; Thiel, 1979). For example, macrofaunal abundance decreases significantly with depth in the Gulf of Mexico (Rowe and Menzel, 1971) and in the northwest Atlantic (Rowe et al., 1982), as does that of meiofauna in the western Pacific (Shirayama, 1984) and Mediterranean (de Bovée et al., 1990; see also Thiel, 1979).

Trophic composition of the deep-sea-floor fauna

Ecologists often find it useful to combine species into groups whose members are similar in selected attributes, to facilitate the search for generalizations

(Jumars and Fauchald, 1977; Sokolova, 1997). Deep-sea workers have frequently grouped species by feeding mode. This approach has led to interesting results, but few direct observations of the feeding of deep-sea species have been made. Although some gut-content studies have been done (Sokolova, 1994), most inferences about how a deep-sea species feeds have been based on knowledge of the feeding of its shallow-water relatives.

Deposit feeders

A deposit feeder ingests sediment. During gut passage, the animal converts a portion of the organic material contained in the sediment into a form that can be assimilated. Deposit feeding is the dominant feeding mode in the deep sea (Thiel, 1979). For example, at an oligotrophic site in the abyssal Pacific, 93% of the macrofauna were deposit feeders (Hessler and Jumars, 1974; see also Flach and Heip, 1996). The dominance of deposit feeding may arise because the rain of organic material into the deep sea consists primarily of small particles of little food value. Deposit feeders apparently can collect and process this material profitably despite the costs of manipulating the mineral grains that they simultaneously ingest.

Adaptations to deep-sea deposit feeding include an increase in gut volume (Allen and Sanders, 1966). The larger volume is thought to allow the rate of sediment processing to increase without a decrease in gut residence time or to allow gut residence time to increase without a decrease in the rate of sediment processing (Jumars and Wheatcroft, 1989). Either adjustment would increase the rate of food assimilation by organisms feeding on the relatively food-poor deep-sea sediment as compared with that which could be achieved with the gut morphology of a closely related shallow-water species.

Deposit feeders can be grouped by the sediment horizon at which they feed and by their mobility (Jumars and Fauchald, 1977). Sessile surface-deposit feeders remain in a fixed location and feed from the sediment surface. Discretely motile surface-deposit feeders move infrequently but must be stationary to feed efficiently (echiuran worms: Ohta, 1984; Bett and Rice, 1993). Both sessile and discretely motile surface deposit feeders extend structures (a proboscis, palps, tentacles) over the sediment surface to collect material. Motile surface-deposit feeders (holothurians such as *Scotoplanes globosa*) ingest sediment as they move over the sediment surface. Subsurface deposit feeders tend to be motile and feed as they burrow through the sediment.

Among deposit feeders, some ecologically interesting patterns have been observed. The decrease in the average size of macrofaunal deposit feeders as depth increases (and the rate at which food reaches the deep-sea floor decreases) was described above. In addition, as depth increases from about 400 m to that of the abyss, the proportion of sessile forms among deposit-feeding polychaetes decreases (Jumars and Fauchald, 1977; see also Rowe et al., 1982). Jumars and Fauchald (1977) suggested that this pattern could arise if the maximum feeding radius of sessile surface-deposit feeders were fixed (e.g., because of mechanical limitations to the length of polychaete tentacles). Therefore, as food flux decreases, fewer sessile deposit feeders are able to reach a large enough area to survive. Because the foraging areas of motile polychaete deposit feeders do not have such mechanical limits, they would not be as much affected by the decrease in food flux.

The rules can be different in areas that experience strong near-bottom flows. For example, at such a site at a depth at which sessile deposit-feeding polychaetes should be rare, the dominant polychaete is a sessile deposit feeder (Thistle et al., 1985). This species digs a pit around itself approximately 1 cm deep and 4 cm in diameter. As the near-bottom flow encounters the pit, the streamlines of the flow expand and its speed decreases (by the principle of continuity: Vogel, 1981). When the speed of the flow decreases, its capacity to transport particles (including food particles) is reduced, which increases the flux of food particles to the bed. The worm harvests these particles (Nowell et al., 1984) and thus can occur in large numbers at a depth where sessile feeding on deposits would not be expected to function well.

Exploiters of large food parcels

Not all of the food that enters the deep sea does so as small particles of little food value. For example, the carcasses of fishes and whales reach the sea floor. These high-quality food parcels are rare (Smith et al., 1989) but attract a subset of the fauna. These “parcel-attending species” include necrophages, which consume the carcass directly, and species that benefit indirectly from the food fall. The parcel attenders include certain species of demersal fishes (Dayton and Hessler, 1972; Smith, 1985), amphipods of the family Lysianassidae (Hessler et al., 1978; Thurston, 1979), decapod shrimps (Thurston et al., 1995), gastropods (Tamburri and Barry, 1999), and brittle stars (Smith, 1985). Whether any species depends exclusively on carcasses has not yet been shown (Jumars and Gallagher, 1982; Ingram and Hessler, 1983), but some omnivorous species include carcasses adventitiously in their diets (Smith, 1985; Priede et al., 1991).

The response of the parcel attenders to carcasses placed on the seafloor has revealed much about their ecology. Minutes to hours after a bait parcel is placed on the seafloor, swimming parcel attenders begin to arrive; nonswimmers arrive more slowly. Both approach predominantly from down current (Dayton and Hessler, 1972; Thurston, 1979; Smith, 1985), attracted by a current-borne cue, probably odor (Sainte-Marie, 1992). These animals feed voraciously until their guts are full. Satiated individuals leave the carcass but remain in the vicinity, perhaps to optimize digestive efficiency (Smith and Baldwin, 1982) or to return to the carcass after the gut is partially emptied (Smith, 1985). At peak abundance around a fish carcass, tens of fishes, hundreds of amphipods, and hundreds of brittle stars may be present (although these peaks are not simultaneous) (Smith, 1985). These abundances are many times greater than abundances in the background community, so carcasses cause local concentrations of individuals. As the amount of flesh decreases, the parcel attenders disperse. Some species depart while some flesh remains; others remain weeks after the flesh has been consumed (Smith, 1985). Dispersal distances may be a few meters for walkers, such as brittle stars; but Priede et al. (1990) have shown that food-parcel-attending fishes disperse more than 500 m. Of the parcel attenders, amphipods are best known biologically (but see Tamburri and Barry, 1999, for other taxa). According to Smith and Baldwin (1982), these crustaceans survive the long periods between food parcels by greatly reducing their metabolic rate while retaining an acute sensitivity to the arrival of carcasses at the seafloor. When they detect the odor from a carcass, they rapidly increase their metabolic rate and begin a period of sustained swimming toward the bait. To maximize consumption at the food parcel, they feed rapidly, filling their extensible guts. At satiation, the gut fills most of the exoskeleton, which can be greatly distended (Shulenberger and Hessler, 1974; Dahl, 1979). The ingested material is rapidly digested (95% in 1–10 days), making space in the gut for more food and increasing the flexibility of the body for swimming (Hargrave et al., 1995). Younger stages need to feed more frequently than adults, but all can survive for months between meals (Hargrave et al., 1994).

Differences in behavior and morphology suggest that groups of parcel attenders have different strategies. For example, some parcel-attending amphipods have shearing mandibles. They consume bait rapidly and probably combine scavenging and carnivory in their feeding strategy. Other parcel-attending amphipods have triturating mandibles and combine scavenging with detritivory (Sainte-Marie, 1992). Jones et al. (1998) have reported that the former arrive first at the carcass and are replaced by the latter over time. Ingram and Hessler (1983) found that the populations of three species of small-bodied, parcel-attending amphipods were concentrated about 1 m above the bottom and that the population of a larger-bodied species was concentrated about 50 m above the bottom. Turbulent mixing in the bottom boundary layer causes the chemical signal from a carcass to widen and to increase in vertical extent with increasing distance from a carcass, while it simultaneously decreases in concentration. Ingram and Hessler (1983) therefore suggested that the two groups of species exploited the carcass resource differently. The high-hovering species surveys a wide area and detects primarily large carcasses. The low-hovering species detect the full range of carcass sizes but from a smaller area. These ideas are suggestive, but depend on the untested assumptions that carcasses produce chemical signals in proportion to their sizes, and that the threshold concentrations at which a signal can be detected are approximately the same for the two guilds (Jumars and Gallagher, 1982). Also, differences between guilds in swimming speed and ability to sequester food are likely to be necessary to explain why the optimal foraging height for the small-bodied species is lower than that for the large-bodied species (see also Sainte-Marie, 1992).

After leaving the carcass, necrophages transfer calories and nutrients to other deep-sea soft-bottom organisms by defecating (Dayton and Hessler, 1972). Smith (1985) estimated that about 3% of the energy required by a bathyal benthic community can be provided in this way (see also Stockton and DeLaca, 1982).

The concentration of potential prey that a carcass attracts may itself be a resource. Jones et al. (1998) reported that none of the fish species attending cetacean carcasses that they placed in the abyssal Atlantic consumed the carcass. Rather, they preyed on the parcel-attending amphipods.

Suspension feeders

Suspension feeders (Fig. 2.15) feed on material they collect from the water column, intercepting epibenthic plankton, particles raining from above, and particles that have been resuspended from the seabed. The food particles captured vary in size from microns to millimeters, depending on the suspension feeder. The smaller particles include bacteria, pieces of organic matter, microalgae, and silt- and clay-sized sediment particles with microbial colonies. Larger particles include invertebrate larvae and the organic aggregates known as "marine snow" (Shimeta and Jumars, 1991). Examples of suspension feeders on deep-sea soft bottoms are sea anemones (Aldred et al., 1979), sea pens (Rice et al., 1992), sponges (Rice et al., 1990), and stalked barnacles (personal observation).

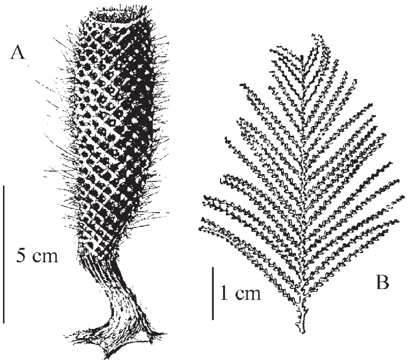

Fig. 2.15. Representative suspension feeders. A, Glass sponge; B, horny coral. Modified from Gage and Tyler (1991). Cambridge University Press 1991. Reprinted with the permission of Cambridge University Press.

Particles can be collected from seawater in five basic ways (Levinton, 1982). In mucous-sheet feeding, an animal secretes a mucous sheet that particles encounter and stick to, which the animal (e.g., members of the polychaete genus *Chaetopterus*) collects and consumes. In ciliary-mucus feeding, the feeding current passes over rows of mucus-covered cilia. The mucus and the embedded particles are moved by the cilia to the mouth. This approach to suspension feeding is used by ascidians (Monniot, 1979), sabellid polychaetes, brachiopods, bryozoans, and some bivalve mollusks (Levinton, 1982). In setose suspension feeding, a limb is drawn through the water, and suspended particles are captured by setae on the limb. The collected particles are scraped from the limb and transferred to the mouth. Suspension-feeding crustaceans feed in this manner, in particular barnacles and suspension-feeding amphipods. In sponges, water enters through pores and is drawn along internal canals to flagellated chambers by the pumping action of the flagellated cells. The entrained particles encounter the collars of the flagellated cells. Particles that are retained are phagocytized or transferred to phagocytic amebocytes, where digestion also occurs (Barnes, 1987). In suspension-feeding by foraminifers (e.g., *Rupertina stabilis*: Lutze and Altenbach, 1988), suspended particles encounter and stick to pseudopodia extended into the near-bottom water.

Active suspension feeders expend energy to cause water to flow over their feeding structures; for example, barnacles move their cirri through the water, and sponges pump water over the collars of their flagellated cells. Passive suspension feeders – for example, some foraminifers, crinoids, some ophiuroids, some holothurians, some octocorals, and some ascidians – depend on external flows to move water over their feeding structures. For both active and passive suspension feeders, the rate of particle capture (and to a first approximation their rate of energy acquisition) depends on the product of the flow rate over their feeding apparatus and the concentration of food particles in the filtered water (= the particle flux). Passive suspension feeders depend on the local particle flux, whereas active suspension feeders depend only on the local particle concentration because they control the speed of the flow over their feeding apparatus (Cahalan et al., 1989).

For a passive suspension feeder to survive at a location, the particle flux must be sufficient to meet its metabolic requirements; thus, not all locations in the deep sea are suitable. Rather, the interaction of local flow with topography will create a finite number of appropriate sites. Because both average particle concentration and average flow velocity decrease with depth, the number of sites suitable for passive suspension feeders decreases with depth. Similarly, suspended particle concentration varies locally, so only a finite number of sites will be suitable for active suspension feeders, and this number will decrease with depth as the suspended-particle concentration decreases. For passive suspension feeders, the minimum particle concentration for survival can be lower than for active suspension feeders because the animal expends no energy filtering; and, up to some limit, more rapid ambient flow can increase the effective concentration for passive but not for active suspension feeders. Therefore, the number of suitable locations (and therefore abundance) should decrease more rapidly with depth for active suspension feeders than for passive suspension feeders. This pattern has been observed (Jumars and Gallagher, 1982).

Given the low suspended-particle concentrations in the deep sea, maximizing the particle-capture rate may be particularly important. In particular, passive suspension feeders should orient their collecting surfaces to maximize the flux of particles that they intercept. Data from the deep sea with which to test this prediction are sparse, but some types of behavior are suggestive. For example, the sea anemone *Sicyonis tuberculata* bends its body in such a way that its feeding surface faces into the current as the current direction rotates with the tide (Lampitt and Paterson, 1987). Also, under the West-African upwelling, the vertical flux of food particles is large and near-bottom currents are slow, so the vertical flux of food particles greatly exceeds the horizontal flux. There, the passive suspension-feeding sea anemone *Actinoscyphia aurelia* orients its collector upwards, as expected (Aldred et al., 1979).

Some passive suspension feeders increase particle capture rates by exploiting the increase in horizontal speed of the near-bottom water as distance from the seabed increases. For example, the deep-sea foraminifer *Miliolinella subrotunda* builds a pedestal 1–6 mm tall on which it perches to suspension-feed (Altenbach et al., 1993). Other passive suspension feeders occur on topographic features or the stalks of other organisms, such as glass sponges, thus placing their feeding apparatus in regions of more rapid flow. A sea anemone moved ~30 cm up the side of an experimental cage in ~5 days to perch at the highest point (personal observation).

Some shallow-water polychaetes can switch feeding modes (Taghon et al., 1980; Dauer et al., 1981). When the flux of suspended particles is large enough, these species suspension-feed. When it is not, they deposit-feed. Many deep-sea polychaetes are thought to have this capability (G. Paterson, personal communication, 1997).

Carnivores/predators

Carnivores select and consume living prey. For example, in the deep sea, kinorhynchs have been found with their heads embedded in the sides of nematodes (personal observation). Such direct evidence of feeding on live prey is difficult to obtain from the deep sea. Gut-content analysis, both by visual inspection (Langer et al., 1995) and by immunological methods (Feller et al., 1985), has been used; but this approach cannot always distinguish carnivores from scavengers. As a result, feeding mode is often inferred from the feeding patterns of similar, shallow-water species. For example, a group of deep-sea nematodes with teeth in their buccal cavities (Fig. 2.16) are thought to be carnivores because shallow-water species with such armature are carnivorous (Jensen, 1992). The proportion of the deep-sea fauna that is carnivorous is not well known. Jumars and Gallagher (1982) estimated that carnivores constituted between 2% and 13% of the polychaetes at four Pacific sites. Tselepides and Eleftheriou (1992) reported that 49–52% of the polychaetes between 700 and 1000 m depth off Crete were carnivorous.

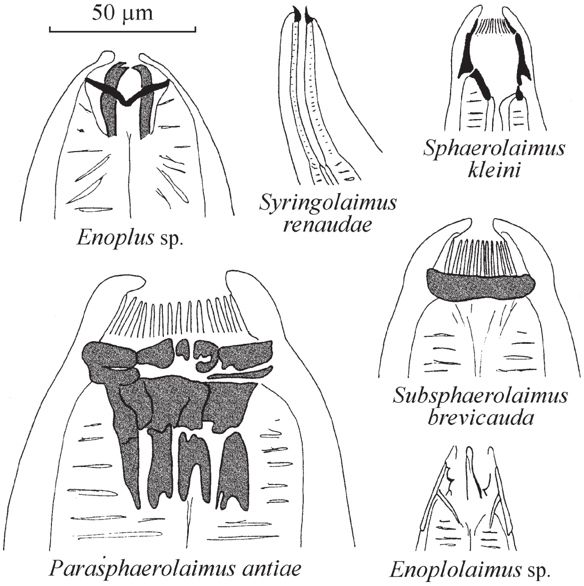

Fig. 2.16. Examples of deep-sea nematodes that are thought to be carnivores because their buccal cavities have teeth as do carnivorous nematodes in shallow water. Only the anterior portion of each worm is shown. Modified from Jensen (1992). Reproduced by permission of the Station Biologique de Roscoff.

In the food-poor deep sea, prey are rare, so the time between encounters with prey will be long compared to that needed to subdue and ingest a prey item once encountered. Under these circumstances, optimal-foraging theory predicts that diets should be generalized to shorten the time between prey encounters, increasing the food-acquisition rate (MacArthur, 1972). The step from feeding on live prey to including carrion in the diet is a small one, so organisms that might be predators in shallow water are likely to consume both

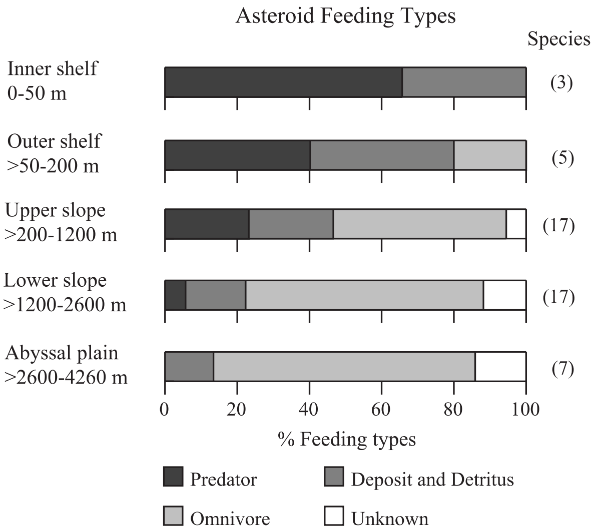

Fig. 2.17. The proportion of asteroid feeding types at increasing depth, showing the shift to omnivory as depth increases. Modified from Carey (1972). Reproduced by permission of Ophelia Publications.

living and dead material in the deep sea. For example, Carey (1972) reports a trend for the proportion of predaceous asteroids to decrease and the proportion of omnivorous asteroids to increase with increasing depth in the deep sea (Fig. 2.17).

Although prey are rare, they may be more detectable in the deep sea than in shallow water. Flow in the benthic boundary layer is slower and more orderly in the deep sea than in shallow water, so chemical gradients should be more persistent and provide better information for prey location. Also, pressure waves produced by prey (Ockelmann and Vahl, 1970) should be more easily detected in the deep-sea benthic boundary layer because of its lower turbulence. Background acoustic noise is also lower in the deep sea, making weak acoustic signals produced by prey relatively easy to detect. These physical attributes of the deep sea also facilitate the transmission of information to the prey about the approach of a predator, so that sensory capabilities of the prey may be evolving in parallel with those of the predators (Jumars and Gallagher, 1982).

The general decrease in food input with increasing depth in the deep sea appears to affect predators disproportionately. For example, Rex et al. (1990) found that abundance of predaceous gastropods decreased at a greater rate with depth than did that of deposit-feeding gastropods (Fig. 2.18). One possible explanation for this pattern is that, as the distances between prey increase with depth, the energy spent in searching increases, but the energetic return per prey item found remains the same. Therefore, as depth increases, fewer gastropod species (and perhaps fewer species of other taxa) can make an energetic profit as predators.

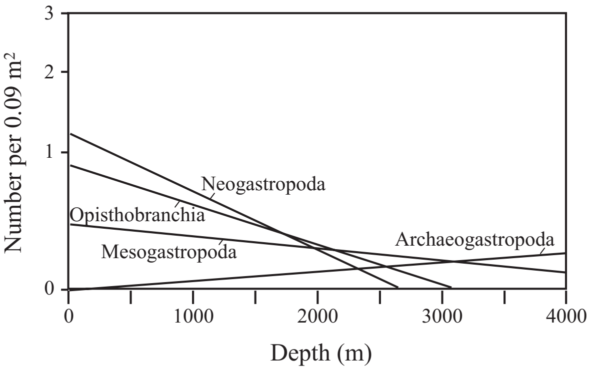

Fig. 2.18. Logarithm of abundance of major taxonomic groups of gastropods at different depths in the North Atlantic, showing that predators decline more rapidly than do deposit feeders. Neogastropoda and Opisthobranchia are predators. Modified from Rex et al. (1990). Copyright: Elsevier Science.

Croppers

In the food-poor deep sea, there should be strong selection to digest and assimilate any organic material encountered, living or dead. Dayton and Hessler (1972) proposed the term "cropper" for an animal that ingests live prey, whether exclusively or in combination with dead prey or inorganic materials. Deep-sea croppers include species of holothurians, echinoids, ophiuroids, asteroids, cephalopods, and some polychaetes, decapods, and demersal fishes. Most deposit feeders in the deep sea are croppers because they feed on living and dead material. Given the large proportion of deposit feeders among deep-sea-floor animals, much of the living prey may be consumed by deposit feeders (Dayton and Hessler, 1972).

There are several corollaries of this view. Deposit feeders vary in size from fishes to nematodes. Given that food is in short supply, the size of the prey ingested should be limited only by the size of the deposit feeder's mouth. Therefore, the smaller the prey organism, the greater its predation risk because the number of mouths large enough to ingest it increases as its size decreases. Thus larvae, juveniles, and meiofauna of all life stages should experience more intense predation than do macrofaunal and megafaunal adults. This increase in predation pressure with decreasing size should decrease the probability of competitive exclusion among smaller animals, and allow larger overlaps in their utilization of resources. In particular, as an animal's size decreases, its diet should become increasingly broad (Dayton and Hessler, 1972).

Finally, the environment of the deep sea is less physically variable than that in shallow water and is likely to impose less mortality on deep-sea organisms than the physical environment of shallow water imposes on shallow-water organisms. As a consequence, the mortality imposed by croppers may be crucial to the organization of deep-sea communities (Jumars and Gallagher, 1982).

Size structure

The size of the average macrofaunal individual decreases with increasing depth in the deep sea (Fig. 2.19).

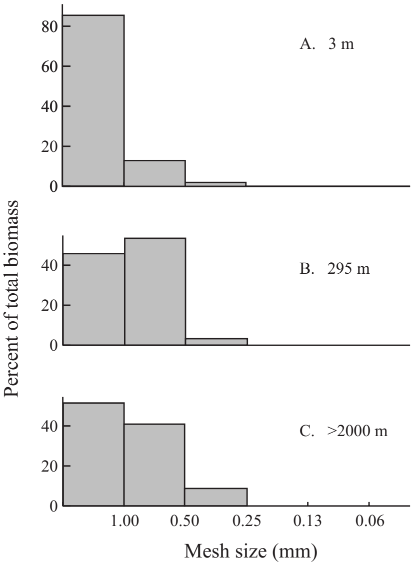

Fig. 2.19. Macrofaunal biomass of different size groups in three depth zones, showing the decrease in average size with depth. Note that size decreases from left to right. Modified from Shirayama and Horikoshi (1989). Reproduced with the permission of Wiley-VCH Verlag.

An early indication of this pattern was that workers who wished to retain the individuals of macrofaunal taxa from deep-sea samples quantitatively had to use sieves with smaller mesh openings than would be necessary to collect those taxa in shallow water (Sanders et al., 1965; see Table II in Rowe, 1983). More formally, Rowe and Menzel (1971) showed that the proportional decrease in macrofaunal biomass with depth was greater than the proportional decrease in macrofaunal numbers in the Gulf of Mexico, a result that has been found in other areas (Shirayama and Horikoshi, 1989; but see Polloni et al., 1979) and for the meiofauna (Soetaert and Heip, 1989). Direct measurements of animal sizes along depth gradients reinforce these conclusions. For example, Soltwedel et al. (1996) reported that the length of nematodes declined with depth; Vanaverbeke et al. (1997) found that nematode biomass per individual decreased with depth. For macrofauna, the miniaturization appears to occur by species replacement rather than by decreases in the average body size within species (Gage, 1978).

Hessler and Jumars (1974) have presented a hypothesis to explain the decrease in the size of macrofauna with depth (see also Thiel, 1975; Gage, 1977). Food arrives at the deep-sea floor from above. As food supply decreases with increasing depth, fewer animals are present per unit area, so food should not be mixed as deeply by bioturbation. Therefore, the layer in which the food is concentrated at the sediment surface becomes increasingly thin. For organisms that feed by ingesting sediment, Hessler and Jumars (1974) argued that those with small mouths should be best at restricting their ingestion to the food-rich layer, minimizing the costs of feeding by reducing the amount of food-poor sediment inadvertently ingested. On the assumption that mouth size and body size are correlated, the size of successful deposit feeders should decrease as food supply decreases with depth. Because the bulk of the macrofauna in the deep sea are deposit feeders, this explanation could account for the decrease in their average size.

Suspension feeders also decrease in size with increasing depth. Ascidians (sea squirts) decrease from >1 cm to <2.5 mm in size and by a factor of 25 in mass from the upper slope to the abyssal plain (Monniot, 1979). Monniot (1979) argued that the dwarfing of these active suspension feeders is an adaptation to the decrease in food for suspension feeders with increasing depth. That is, an individual ascidian uses energy to pump water through its filtering apparatus and gains energy by ingesting the particles it collects. The energy harvested must exceed the energetic costs of the pumping and the energetic costs of maintaining the individual. The amount of energy harvested decreases as food-particle concentration decreases with depth, but the energetic costs of pumping a unit of water remain constant. As a consequence, Monniot (1979) suggested that the maximum mass that can be supported decreases with depth, resulting in dwarfing.

In contrast to the trend toward miniaturization, gigantism (= species many times the size of their near relatives) occurs in the deep sea. Among the giants are species of scavenging amphipods (Hessler et al., 1972), surface-deposit-feeding holothurians (Gage and Tyler, 1991), and isopods (Wolff, 1956). The giants are not closely related evolutionarily and have different life styles, so it is unlikely that gigantism arises for a single reason.

Some abyssal ascidians are three to ten times larger than other abyssal members of their families. These giants have greatly modified filtering structures and appear to have abandoned active suspension feeding for passive suspension feeding. Monniot (1979) argued that the elimination of the energetic costs of pumping allowed individuals of greater mass to be supported from a given concentration of suspended particles than could be supported by active suspension feeding; but these giants can occur only in locations where the flux of food particles is relatively high.

The changes in size with depth reported above were for entities that contained many species, such as macrofauna and nematodes. Rex and Etter (1998) argued that such patterns should be investigated within individual species, because only within species will it be possible to understand the ecological and evolutionary forces that created the patterns. When they did so for several gastropod species, they found that the trend was for individuals to increase rather than decrease in size with depth (see also Wilson, 1983, and Macpherson and Duarte, 1991).

Biogeography

Introduction

Geographical patterns in the distribution of species (or higher taxa) and the causes of those patterns are not well known for animals of the deep-sea floor. This situation arises, in part, because of the great mismatch between the vastness of the habitat and the small amount of sampling that has been done. In addition, large numbers of species are present in the deep sea, most of which are undescribed. Further, the number of specialists who can provide identifications or taxonomic descriptions is small and is decreasing.

The shape of the ocean floor sets the stage for deep-sea biogeography. Briefly, within major ocean basins at slope depths, the habitat is more or less continuous along isobaths, interrupted by relatively small features, such as submarine canyons. The major oceans and most of the secondary seas are connected at these depths. Below about 2500 m, the mid-ocean ridges and submarine mountain ranges divide the major oceans into regions, for instance, the eastern Atlantic. Below about 3500 m, the deep-sea floor consists of isolated basins (Fig. 2.20).

Fig. 2.20. The Atlantic Ocean showing the location of the deep-ocean (>3500 m) basins (black) and the mid-Atlantic Ridge (dashes). Modified from Allen and Sanders (1996). Copyright: Elsevier Science.

Patterns along isobaths

The distribution of higher taxa is unusually homogeneous in the deep sea. For example, of the 143 genera of asellote isopods known from the World Ocean, all but nine are found in the Atlantic. This level of similarity is much greater than expected on the basis of shallow-water isopods (Hessler and Wilson, 1983).

Some deep-sea species are widespread, but many more have restricted distributions. For example, along 180 km of the 2100-m isobath off the northeastern coast of the United States, 10 abundant macrofaunal species occurred at all stations (Grassle and Maciolek, 1992), but 43% of the peracarid crustacean species, 34% of the polychaete species, and 21% of the bivalve species occurred at only one. The constraints (ecological or historical) that cause large numbers of species to be endemics in this environment are unknown, but the differences among higher taxa in the proportion of species with localized distributions may provide a point of departure for further research. Because the widespread species constitute the bulk of the individuals at each station, the faunas at either end of the 180-km transect are relatively similar (of the species expected in a random sample of 200 individuals at each of the two localities, 79% were shared) (Grassle and Maciolek, 1992). Despite this similarity, the endemics are a source of faunal heterogeneity among stations.

The pattern of a few widespread species and many endemics also occurs in the ocean basins. For example, at the scale of the Atlantic, 11 of 109 species and subspecies of protobranch bivalves have been found in six or more of the 15 deep basins, but 48 have been found in only one, and the remaining species tend to occur in two adjacent basins (Allen and Sanders, 1996). At least for protobranchs, the distributions of most species tend to be much smaller than pan-Atlantic, and the protobranch faunas of adjacent basins tend to be similar – for instance, the Sierra Leone and Angola Basins share 20 of a total of 40 species. The Norwegian Basin is an exception. It shares no protobranch species with any other Atlantic basin. The reason for this difference is not known, but the Norwegian Basin became anoxic during the last glaciation (Schnitker, 1979) and lost most of its metazoan fauna. It is unclear why some species occur in several basins and others occur in only one, but ecological differences among the basins, dispersal limitations, and history are all likely to play a role.

Patterns with depth

The faunal break at the shelf/slope transition has been confirmed repeatedly (Sanders and Hessler, 1969; Haedrich et al., 1975; Rex, 1977; Carney and Carey, 1982). Below that depth, regions of relatively slow faunal change (= zones) are separated by bands of more rapid faunal change. The depths of zone boundaries vary among taxa and locations, but in the North Atlantic appear to be at about 0.5, 1, 1.5, and 2 km (Gage and Tyler, 1991). Below 2 km, the rate of change of the fauna slows, and zonation does not appear to be as marked, perhaps in part because of the smaller sampling effort at these depths.

Although the depth range of an individual species does not often extend from 200 m into the trenches or even from 200 m to the abyssal plain, some species have extensive ranges. For example, the brittle star *Ophiomusium lymani* off North Carolina has been found from 1372 to 3987 m (Grassle et al., 1975). Species are not equally abundant throughout their ranges, tending to be rare at the extremes as expected, if conditions become less suitable as their range boundaries are approached (Grassle et al.: their table 6). The depth range of a species may vary along isobaths. For example, in contrast to its depth range off North Carolina, *O. lymani* was found only between 1705 and 2170 m on a transect from Massachusetts to Bermuda (Schoener, 1969). Many species appear to have very small depth ranges, having been collected at only one station along a transect. Because many transects have had stations at depth increments of a few hundreds of meters, the depth ranges of such species must be less.

Contrary to expectation, representatives of deep-sea taxa are found on the shelf in the Arctic, Antarctic, and Mediterranean seas and in Scandinavian fjords. For example, species of asellote isopods of deep-sea genera have been found at shelf depths in the Bay of Naples (Schiecke and Fresi, 1969) and off Sweden (Hessler and Strömberg, 1989); foraminifer species of deep-sea genera have been found at SCUBA-diving depths in Antarctica (Gooday et al., 1996); and a sponge from a bathyal–abyssal subphylum has been found in a cave at 18 m in the Mediterranean Sea (Vacelet et al., 1994). This pattern could arise if representatives of taxa that had evolved in the deep sea entered shallow water. Alternatively, the shallow-water representatives of these taxa could be relics in the original environment of groups that invaded the deep sea. At least for the shelf representatives of asellote isopods, the former appears to be the case (Hessler and Thistle, 1975). The environments where representatives of deep-sea taxa are found in shallow water have deep-sea temperatures at shelf depths (cold at the poles but warm in the Mediterranean), suggesting that ordinarily the temperature gradient (or a correlate) separates the deep-sea fauna from that of the shelf.

Combined along- and across-isobath patterns

Relatively few deep-sea studies have had sample coverage adequate to address along- and across-isobath patterns in the distribution of species. For protobranchs at the scale of the Atlantic, Allen and Sanders (1996) found that the similarity of the fauna among stations was much greater along isobaths than across isobaths. In particular, the faunas of stations separated by 16 500 km along an isobath were as similar as those of stations separated by 0.8 km across isobaths. The pattern of greater similarity along than across isobaths has also been found at the 100-km, within-ocean-basin scale (Carney et al., 1983; Grassle and Maciolek, 1992). At the 100-km scale, recent work on benthic decapods from the Mediterranean slope has revealed discrete regions of high abundance within the range of a species which extend both along and across isobaths (Maynou et al., 1996). Therefore, the distribution of a species within its depth range may be a series of patches (see Blake and Hilbig, 1994).

These results have been based on the distribution of macrofauna. Theory suggests (Fenchel, 1993) that animals of smaller size (meiofauna, microfauna) may have larger species ranges, so many species may be cosmopolitan. Relatively little information is available with which to evaluate this idea in the deep sea, but many common deep-sea formaminiferal species appear to be cosmopolitan (Gooday et al., 1998).

Finally, deep-sea biogeography is based almost entirely on morphological species, which is not surprising given the difficulty of working in this environment. Substantial genetic variation has been discovered within some nominal species (Etter et al., 1999), raising the possibility that some morphological species may be complexes of cryptic species, a situation that would make deep-sea biogeography even more difficult.

Factors controlling the depth range of a species

The physiological limits of a species set the ultimate bounds of its range; shallow-water species could therefore be excluded from the deep sea and vice versa, and the ranges of deep-sea species restricted. For example, mitosis is inhibited when shallow-water sea urchins are exposed to deep-sea pressures (Marsland, 1938, 1950). Also, larvae of a bathyal sea urchin require bathyal temperatures to develop properly, setting a physiological limit to the minimum and maximum depths at which the larvae can develop (Young and Cameron, 1989). Similarly, when eggs of an asteroid that lives between 1000 and 2500 m were exposed to pressures corresponding to 0 and 3000 m, virtually no normal development occurred (Young et al., 1996).

Ecological limitations could be imposed in a variety of ways. As depth increases, sediment composition can change. Because some species are restricted to particular sediment types, sediment changes can limit their ranges. For example, on a depth transect off North Carolina, sands give way to sandy silts and then to clayey silts. Nematode species were restricted to these sediment-defined depth bands – 17, 5, and 49 species, respectively (Tietjen, 1976). The depth distribution of a species may also be controlled by food availability. For example, the decrease in suspended food concentration with depth limits the penetration of certain suspension-feeding species into the deep sea (see above, pp. 20–21). In contrast, on the Carolina slope unusual conditions occur such that food is supplied to the slope at rates comparable to those on the shelf, and some species ordinarily confined to the shelf are present on the slope in large numbers (Blake and Hilbig, 1994). Examples of other environmental variables that can affect the ranges of species include low oxygen concentration in the near-bottom water (Wishner et al., 1990), strong near-bottom flows (Rice et al., 1990; Paterson and Lambshead, 1995), and correlates of the permanent thermocline (Gage, 1986).

The depth distribution of a species may also be controlled by ecological interactions with other species. For example, Rex (1977) found that groups made up largely of croppers and predators such as the epibenthic macrofauna and gastropods had smaller species ranges on average than did infaunal deposit feeders. To explain the difference, he noted that the former were at a higher trophic level than the latter and that studies in other environments have found that the higher the trophic level the greater the competitive interactions among species. He suggested that the increased probability of competition among species of epibenthic macrofauna and gastropods resulted in lower average range sizes than in the infauna, whose populations were much less likely to interact competitively because of the intense predation upon them (but see Carney et al., 1983).

THE HARD-BOTTOM HABITAT

Examples of deep-sea hard-bottom habitats include the exposed portions of rocks and manganese nodules, mollusk shells, new oceanic crust, regions of steep topography where sediment does not accumulate, and locations where the sediment has been washed away by currents (e.g., portions of some seamounts). Despite this variety, two generalizations can be made. The hard-bottom fauna differs in taxonomic composition and life-style from that of deep-sea soft bottoms (Table 2.2), and near-bottom flow tends to be more important to this fauna than to that of the deep-sea soft bottoms.

The fauna

Soft bottoms are three-dimensional, and although the sediment surface has great ecological importance to many of the species present, few animals live on it. Hard bottoms are two-dimensional. Most of the animals live on the surface of the substratum, and infaunal

Table 2.2
Comparison of soft-bottom and hard-bottom faunas in the deep sea

Feature	Soft-bottom habitat	Manganese-nodule habitat	Other hard-bottom habitats
Dominant taxa	polychaetes, nematodes	foraminifers	sponges, black corals, horny corals
Dominant size	macrofaunal and meiofaunal	macrofaunal and meiofaunal	megafaunal
Dominant mobility mode	mobile	sessile	sessile
Dominant feeding mode	deposit	suspension and surface deposit	suspension

organisms are essentially absent. One exception to this generalization is "cauliflower"-type manganese nodules, where sediment accumulates in the crevices and harbors a more or less conventional infauna (Thiel et al., 1993).

The dominant taxa of deep-sea soft bottoms are polychaetes, nematodes, and foraminifers. The dominant taxon on manganese nodules is the agglutinating foraminifers (Mullineaux, 1987). On other hard bottoms, sponges, horny corals (gorgonians), and black corals (antipatharians) dominate (Genin et al., 1986, 1992; Tyler and Zibrowius, 1992), and xenophyophores may be present (Levin and Thomas, 1988). Soft bottoms are dominated by macrofauna and meiofauna. The dominant hard-bottom taxa on manganese nodules and mollusk shells are macrofauna and meiofauna, but on other hard bottoms megafauna appear to dominate. Soft-bottom animals tend to be mobile and to deposit-feed; whereas on manganese nodules and mollusk shells, most organisms are sessile (Mullineaux, 1987; Voight and Walker, 1995). They suspension-feed or collect particles from the surface of the substratum (Mullineaux, 1987, 1989), a process analogous to surface-deposit feeding in soft bottoms. On other hard-bottom habitats, the dominant animals are sessile or sedentary, and they suspension-feed (Genin et al., 1986, 1992; Tyler and Zibrowius, 1992).

Distribution

Regularities in the distribution of hard-bottom organisms are apparent at several scales. For example, on the Bahamian slope, sponges occur in greater numbers on vertically oriented surfaces than on horizontal surfaces, creating marked patchiness on scales of meters. The difference in exposure to siltation, which adversely affects sponges, may underlie the difference (Maldonado and Young, 1996).

At scales of hundreds of meters along a depth transect, there are changes in species composition, and there may be changes in the general characteristics of the fauna. For example, sponge species diversity is high on the shelf and upper slope of the Bahamas. As depth increases, the diversity decreases as the species of the lower reefs disappear. Deeper on the slope, deep-sea sponges occur, resulting in a secondary peak in diversity and abundance. Branched erect sponges are common in shallow but not in deep water, so there is also a change in the morphological composition of the fauna with depth (Maldonado and Young, 1996).

The importance of near-bottom flow

The hard-bottom fauna includes many sessile suspension feeders. These animals depend on near-bottom flow to transport their propagules to settlement sites. To a first approximation, the flux (flow velocity x propagule concentration) of propagules determines the initial distribution of these species. These animals also depend on the near-bottom flow to supply them with food. To a first approximation, the flux of food determines survivorship.

Evidence of such effects on the hard-bottom fauna has been found at several scales. For example, on a wide peak on the summit of Jaspar Seamount (Pacific Ocean), individuals of a species of black coral are more abundant on the edges of the peak than in the center. This pattern matches that of variation in the velocity field (Genin et al., 1986). Also, where the Western Boundary Undercurrent encounters the Blake Spur (Atlantic Ocean), the cliffs are bathed by flows of $\geqslant 30\,\mathrm{cm\,s^{-1}}$ (much faster than the $3\,\mathrm{cm\,s^{-1}}$ of typical deep-sea flows). There, massive sponges and horny corals are unusually abundant (Genin et al., 1992).

In these examples, Genin et al. assumed that the concentration of propagules (or food) was the same in the water that impinged on the high- and low-flow environments. This assumption may not always be valid, particularly near the seabed. For example, Mullineaux (1988) compared the settlement rate of sessile organisms (predominantly foraminifers) on manganese nodules suspended 20 cm above the seabed to the rate on nodules at the seabed. She found that the rate of settlement was significantly greater on the lower nodules despite their exposure to much slower flows. A complete understanding of such flow effects will require simultaneous measurements of velocity and the concentration of propagules (or food).

Flow effects also arise because of the vertical gradient in horizontal velocity adjacent to the seabed (Fig. 2.21). At the seabed, the horizontal velocity is zero (Vogel, 1981). In the layer immediately above the seabed, molecular viscosity suppresses turbulent motions, and horizontal velocity increases slowly and linearly with height. In the deep sea, this region of slow flow (the viscous sublayer) may be a centimeter thick (Jumars and Gallagher, 1982). Above the viscous sublayer, turbulence is present and horizontal velocity increases logarithmically with height. This "log" layer can be 1–10 m thick in the deep sea (Jumars and Gallagher, 1982). As the horizontal velocity in the log layer increases, the viscous sublayer becomes thinner, and turbulent eddies collide with the seabed more frequently, disrupting or destroying the viscous sublayer.

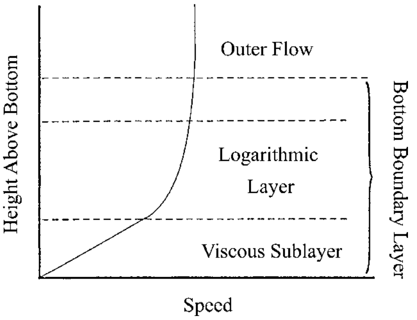

Fig. 2.21. An illustration of the decrease in horizontal speed in the bottom boundary layer as the seabed is approached.

This vertical gradient in horizontal velocity can be expected to influence the settlement location of sessile suspension feeders, because most hard-bottom suspension feeders extend a collecting apparatus into the flow and depend on water motion to bring particles to it. Assuming that there is no vertical gradient in food concentration, the flux of food increases with height above the bottom (and the rate of increase rises rapidly with height as the viscous sublayer gives way to the log layer). Therefore, there should be strong selection for passive suspension feeders on hard bottoms to extend their feeding apparatus as far from the seabed as possible, and there is a large premium on extension above the viscous sublayer. Accordingly, the propagules of passive suspension feeders that are small as adults may be expected to settle at locations where the local horizontal velocity is great enough to disrupt the viscous sublayer or reduce its thickness (Jumars and Gallagher, 1982). For example, a variety of foraminifers attach in such a way that they are millimeters to centimeters above the seabed (Lutze and Altenbach, 1988; Lutze and Thiel, 1989). This selection pressure should also apply to passive suspension feeders that are large as adults, because their juveniles should benefit from extending out of the viscous sublayer (Jumars and Gallagher, 1982). For example, passive suspension feeders tend to be found on the edges of rocks, where the flow can be expected to be locally accelerated and the viscous sublayer thinned. Also, the feeding polyps of horny corals (gorgonians) and sea pens (pennatularians) are absent near the base of the animal, where the flow is slowest, and feather stars (comatulid crinoids) perch on other animals well above the seabed (Tyler and Zibrowius, 1992). Although the flux of propagules and the flux of food may increase monotonically with increasing velocity, the rate of larval settlement and the rate of food capture by a suspension feeder may not. In particular, as near-bottom velocity (more correctly, the vertical gradient of horizontal velocity) increases, the shear (horizontal) force exerted on the seabed increases. To settle, a larva must attach with sufficient strength to resist that force. At some velocity, the frequency of successful settlement will begin to decrease, raising the possibility that settlement success could be greatest at intermediate-velocity locations (Crisp, 1955). Also, when velocity exceeds some limit, the feeding rate of some suspension feeders will begin to decline because their feeding apparatus will be deformed by the flow (Koehl, 1977) and become less effective. The distribution of suspension feeders (predominantly sessile foraminifers) on manganese nodules may reflect such effects. They were more abundant in a band below the summits of manganese nodules than on the tops of the nodules, where the velocity (and shear stress) was greatest (Mullineaux, 1989; see also Mullineaux and Butman, 1990).

Flow is not the only variable that influences the settlement location of propagules on hard substrata. Mullineaux and Butman (1990) found that some species would settle on plates coated with ferromanganese but would not settle on smooth control plates, indicating that some propagules seek specific substrata or textures (see also Mullineaux, 1988; Bertram and Cowen, 1994, 1999).

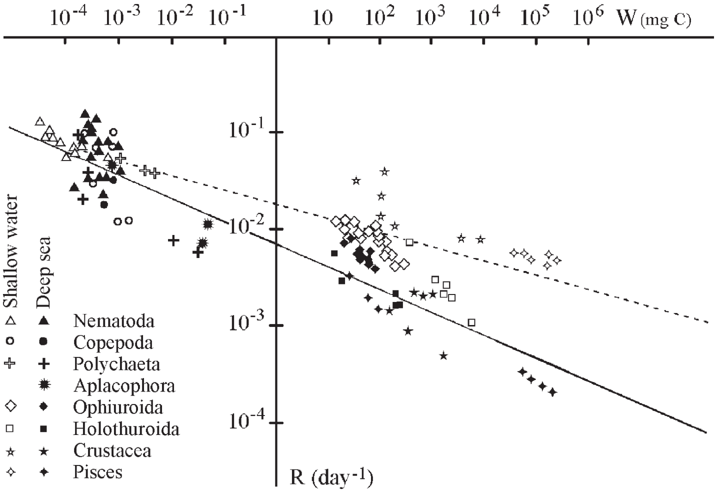

Fig. 2.22. Weight-specific respiration rate of benthopelagic organisms living in shallow water (dashed regression line) and in the deep sea (solid regression line) as a function of individual organic carbon weight (W), illustrating the lower metabolic rates in the deep sea. Modified from Mahaut et al. (1995). Copyright: Elsevier Science.

THE PACE OF LIFE IN THE DEEP SEA

Because the rate of input of food to the deep sea is small, it has been assumed that energy-conserving strategies (low movement rates, low metabolic rates, long life, late maturity, and small reproductive output) have been selected for, giving rise to the expectation that the pace of life is slower in the deep sea than in shallow water. The results of some early deep-sea rate measurements (Jannasch et al., 1971; Smith and Hessler, 1974; Turekian et al., 1975) reinforced this impression, but some rates in the deep sea may be similar to or only marginally lower than rates in shallow water (Gage, 1991).

Locomotion

Movement rates of epibenthic megafauna and demersal fishes have been measured, but comparable shallow-water data are not always available. Most individuals most of the time are stationary or are moving slowly. For example, demersal deep-sea fishes swam slowly ($8\,\mathrm{cm\,s^{-1}}$) over the seabed in a nomadic search for food (Bagley and Priede, 1997). Deep-sea brittle stars moved at 1–3 $\mathrm{cm\,min^{-1}}$ (LaFond, 1967), whereas shallow-water brittle stars moved at 15–45 $\mathrm{cm\,min^{-1}}$ (Broom, 1975). Deep-sea holothurians moved at 1–2 $\mathrm{cm\,min^{-1}}$ (Gage, 1991), whereas shallow-water holothurians moved at $7\,\mathrm{cm\,min^{-1}}$ (Parker, 1921).

Although ordinary movement is slow, when stimulated, many deep-sea animals can move at rates comparable to those of similar shallow-water animals. For example, when approached by a research submarine, demersal fishes swam away rapidly enough to stir up a cloud of sediment (Grassle et al., 1975). Brittle stars are ordinarily still, and parcel-attending amphipods are still or drift with the currents. When these animals detect a food parcel, they move rapidly toward it (Smith, 1985). Speeds of $7\,\mathrm{cm\,s^{-1}}$ have been measured for amphipods, which are comparable to speeds measured on shallow-water confamilials (Laver et al., 1985).

Metabolic rates

To investigate the relative metabolic rates of deep-sea and shallow-water animals, Mahaut et al. (1995) calculated regression lines of metabolic rate (as weight-specific respiration) against mass from published data (Fig. 2.22). The regression line for deep-sea animals fell below that for shallow-water animals, so on the average, weight-specific metabolic rates are lower in the deep sea. The difference decreased with the size of the animal, suggesting that rates for macrofauna and meiofauna in the deep sea are lower but not markedly lower than in shallow water (see also Gage, 1991). The data for the larger deep-sea animals came from measurements on fishes. The metabolism of demersal fishes, even those that swim constantly, appears to be slower than that of shallow-water species. For example, the resting oxygen consumptions for individuals of two fish species from 1230 m were significantly lower than rates measured on similar shallow-water, low-temperature fishes (Smith and Hessler, 1974). These low rates appear to be necessary because of low food availability and are achieved by minimization of locomotion and accompanying economies at the cellular level, e.g., lower enzyme concentrations in muscles than in comparable, shallow-water species (Siebenaller and Somero, 1982). In contrast, the weight-specific oxygen consumption of bathyal brittle stars (three species) and a bathyal holothuroid (*Scotoplanes globosa*) were similar to those in shallow water (Smith, 1983).

The collective metabolism of the organisms (bacteria, protozoa, meiofauna, and macrofauna) resident in the sediment has been estimated by measurements of sediment-community oxygen consumption (SCOC) per unit area. Smith and Teal (1973) found that the SCOC at a station at 1850 m was two orders of magnitude less than that at several shallow-water stations. Further work (Smith, 1987) has shown that SCOC decreases with increasing depth in the deep sea. On a unit-biomass basis, the 1850-m station had a tenth the SCOC of the shallow-water stations (Smith and Teal, 1973). In contrast, there was no trend in SCOC per unit biomass with depth among the deep-sea stations (Smith and Hinga, 1983; Smith, 1987). If one assumes that the relative metabolic rate among the component groups of organisms does not change markedly as depth increases, these results imply that the metabolic rate of the sediment-dwelling organisms is lower in the deep sea than in shallow water, but within the deep sea, there is no trend with depth.

Bioturbation

Bioturbation occurs when organisms (primarily the infauna) move sediment. Bioturbation rates decrease with increasing depth in the deep sea, but when bioturbation rates are normalized by the number of animals per unit area, which also decreases with increasing depth, the rate does not change with depth (Gage, 1991). Individual deep-sea animals mix the sediment at about the same rate as shallow-water animals, suggesting that movement rates and metabolic rates of infauna may not be too dissimilar to such rates in shallow water.

Growth

The growth of demersal fishes appears to be slow in the deep sea (Beamish and Chilton, 1982; Merrett, 1989), as might be expected from their low metabolic rate. The rate of growth of the deep-sea infauna is less clear. Turekian et al. (1975) used a radioisotope technique to study the growth rate of a deep-sea clam. Their best estimate was that the largest size class (8 mm) was about 100 years old and that reproductive maturity was reached in 50–60 years. Although the confidence limits around these estimates were large, the report has been very influential because it supported preconceptions that growth rates would be low and life spans long in the deep sea.

The disparity between the results of Turekian et al. (1975) and those from shallow water are not as great as originally thought. For example, the growth rates of some deep-sea bivalve species are comparable to those of shallow-water bivalves (Gage, 1991). Following the work of Turekian et al. (1975), the growth rates of deep-sea benthic organisms have been estimated by other indirect methods. If the assumptions made are correct, the growth rates of deep-sea invertebrates are lower than, but not markedly different from, growth rates of shallow-water species (Gage, 1991). Direct measurements from time-lapse photographs have shown that the growth of a deep-sea hard-bottom barnacle was almost as rapid as that of similar, shallow-water barnacles (Lampitt, 1990) and that the volume of three xenophyophore individuals increased by a factor of 3–10 in 8 months; during these 8 months, periods of rapid growth were interspersed with periods of no growth (Gooday et al., 1993) (Fig. 2.23). Colonization studies suggest that an aplacophoran mollusk can reach adult size in two months (Scheltema, 1987).

Food availability appears to be a leading variable in the control of the growth rate of deep-sea animals; where food is abundant, growth is rapid compared to that where food is scarce. For example, food is abundant for tube worms (Vestimentifera) at hydrothermal vents, and their length can increase by tens of centimeters per year (Lutz et al., 1994). Similarly, pieces of wood (e.g., tree trunks) that wash offshore and sink are a rich source of food for wood-boring bivalves (Xylophaginidae), which reach adult size within months of settlement (Turner, 1973). The growth rate of a gooseneck barnacle increased several-fold when phytodetritus, a likely source of food for this suspension feeder, was present (Lampitt, 1990). It appears that growth rates in the deep sea are limited, not by the physiological challenges of the physical

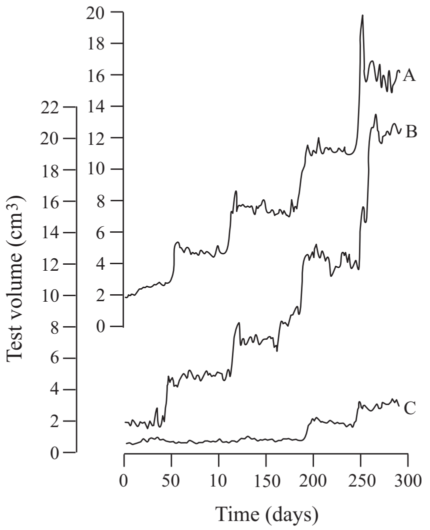

Fig. 2.23. Growth (as test volume) of three abyssal xenophyophore individuals illustrating that growth can be rapid for deep-sea organisms. Outer scale refers to individuals B and C. Inner scale refers to individual A. Modified from Gooday et al. (1993). Copyright: Elsevier Science.

environment (high pressure, low temperature), but by the meager supply of food.

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Chapter 3

THE PELAGIC ENVIRONMENT OF THE OPEN OCEAN

Martin V. ANGEL

INTRODUCTION

The waters of the ocean provide the most voluminous habitat on the planet, since 71% of the Earth's surface is covered by sea to an average depth of 3800 m. The water in the oceans is estimated to have a volume of 1.368×10^9 km^3, and to be equivalent to about 0.24% of the Earth's total mass. The shelf seas 0–200 m deep, that fringe the continental landmasses, extend over about 5% of the Earth's area. At the outer edge of most shelf seas is the shelf-break where the seabed falls quite steeply to depths of around 3000 m, forming the continental slope and rise; these continental margins account for a further 13% of the Earth's area. Beyond that, abyssal depths 3000 to 6000 m deep cover about 51% of the Earth's surface, and the deepest or hadal depths (including many of the ocean trenches) where depths are >6000 m cover less than 2%. The volume of the living space provided by the water of the oceans is 168 times that of terrestrial habitats (Cohen, 1994; see Table 3.1). The oceans have a major influence on climate, since they transfer substantial amounts of heat from equatorial zones to the polar regions. Beneath the clearest of oceanic waters sunlight is detectable only to depths of 1000 to 1250 m. In consequence, the major part of this, the most extensive environment on Earth, is virtually completely dark, lit only by brief flashes of bioluminescence, the light the animals themselves produce. It is a very cool environment; the waters at depths of 1000 m and below have temperatures that range mostly between –0.9º and 5ºC. Their physical and chemical environments hardly vary, and the very limited variation is at scales that are much coarser than those of terrestrial and freshwater habitats. Since uniformity of habitat is unfavourable for the evolution of new species, the total inventory of species inhabiting the waters of the oceans is surprisingly small considering their vast volume. Certainly there are generally far fewer pelagic species in the oceans than occur in terrestrial environments, but estimates of the numbers of benthic species, based on very meagre sampling, range from 0.5 to 2000 million depending on the assumptions made.

Table 3.1
Biophysical characteristics of oceans compared to those of continents[1]

	Oceans	Continents
Surface area (10^8 km^2)	3.6	1.5
Surface area as % Earth's surface	71%	29%
Mean depth of life zone (km)	3.8	0.05
Volume of life zone (10^9 km^3)	1.37	0.0075
Volume % of total	99.5	0.5
Standing crop of plants (10^{27} kg C)[1]	~2	560
Biomass per unit area (10^3 kg C km^{-2})	5.6	3700
Biomass per unit volume (10^3 kg C km^{-3})	1.5	75.000
Dead matter (10^{15} kg C)	~2	1.5
Dead organic matter per unit area (10^6 kg C km^2)	5.5	10
Net primary productivity (NPP) y^{-1}	25–44	~50[1]
NPP per unit area (10^3 kg C km^{-2} y^{-1})	69	330
Carbon residence time in living biomass (years)[2]	0.08	11.2

[1] Adapted from Cohen (1994).
[2] Based on Harte (1988).

Despite the relative uniformity of the chemical and physical conditions, the oceanic water column is an environment that is physiologically highly challenging to life because of resource limitations. However, before discussing the oceanic water column as a habitat, some consideration needs to be given to the exceptional characteristics of water as a medium.

THE NATURE OF WATER

Water is a compound with many unique physicochemical properties. Its boiling and freezing points are considerably higher than might be predicted from the characteristics of other oxides of elements of low molecular weight, which lie close to hydrogen in the periodic table. Carbon dioxide, for example, is a gas with a much lower boiling point than that of water. Moreover its solid phase, or dry ice, is heavier than its liquid phase. The unusual properties of liquid water result from the molecules loosely associating into groups of five. This effectively increases its molecular weight fivefold, which greatly modifies its physical characteristics. Ice, the solid phase of water, is equally unusual, in that it floats; its lower density results from the "looser" packing of the molecules within the solid crystal structure.

Water has also an unusually high heat capacity. This serves to dampen the impact of variations in heating and cooling, and enables ocean currents to transfer copious amounts of heat from low latitudes to high latitudes; hence, they play a major role in modifying global climate. Its latent heats are the highest known for any liquid. The latent heat of ice formation is 80 calories per gram, so that when 1 g of ice melts it lowers the temperature of 80 g of liquid water by 1ºC. Even more important from an oceanographic point of view: the latent heat of evaporation is 537 calories per gram. Thus, when water evaporates from the sea's surface, it cools the skin temperature considerably. Both ice formation and evaporative losses are very important processes in the determination of "water mass" characteristics (see below).

Chemically, water is amphoteric (i.e. it can function either as a base or as an acid). Thus, although pure water has a neutral pH (i.e. pH 7), when it dissociates it can equally well act either as a provider of hydrogen or of hydroxyl ions. Hence it is a good solvent for many inorganic compounds, and for those organic compounds with radicals that can dissociate. Organic compounds without such radicals tend to be insoluble in water, and these include compounds that are important structural components of cells and membranes. Since water is the major chemical constituent of the internal and external milieu of organisms at all levels of organization – from cells to tissues and whole bodies – an understanding of its physicochemical characteristics (Dorsey, 1940) is fundamental to understanding the physiology and ecology of living organisms and communities.

Chemical constituents of ocean water

Nearly all 92 of the naturally occurring elements have been detected dissolved in sea water, although the majority of them occur only in trace amounts (Open University, 1989). "Salinity" is the term used to quantify the total amounts of dissolved salts in seawater. In most oceanic water it ranges between 33 and 37, averaging about 35[1]. Most constituents of seawater are conservative, so that their concentrations vary in direct proportion to the salinity. This is particularly true for the major constituents (i.e. those occurring at concentrations >1 ppm) which together contribute 99.9% of the salinity value (Table 3.2). Most are in steady state – that is, their chemical budgets are in balance, although their turnover times (i.e., the ratio of the total mass of the substance in the oceans

Table 3.2
Mean concentrations and estimated total content of the major constituents of sea-water

Element	Mean conc. g. ℓ^{-1}	Total in 10^{12} tonnes
Chlorine	1.95×10^4	2.57×10^4
Sodium	1.08×10^4	1.42×10^4
Magnesium	1.29×10^3	1.71×10^3
Sulphur	905	1.20×10^3
Calcium	412	545
Potassium	380	502
Bromine	67	88.6
Carbon	28	37
Nitrogen[1]	11.5	15
Strontium	8	10.6
Oxygen[1]	6	7.93
Boron	4.4	5.82
Silicon	2	2.64
Fluorine	1.3	1.72

[1] Elemental oxygen and nitrogen are not normally considered to be major constituents of sea-water because they are dissolved gases.

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[1] See Glossary, p. 477, for an explanation of the way in which salinity is expressed.

to the rate at which it is being supplied or removed) can vary considerably. The mean ocean mixing time is of the order of 500 years (Stuiver et al., 1983), so any substance whose turn-over takes 10^5 years or more is uniformly distributed, except very close to major point sources or sinks. However, there are many substances whose concentrations fluctuate widely, notably those that play a role in biological systems – oxygen, carbon, and plant nutrients. Many higher organisms regulate their internal ionic concentrations; for example, potassium and calcium are concentrated in the blood of fish, whereas sodium is excreted. Some of the rarer elements are essential in trace concentrations; for example, vanadium is a constituent of the oxygen-carrying compound in the blood of salps, and copper is a constituent of haemocyanin, the blood pigment in crustaceans. However, elements that are essential in trace concentrations become toxic if their concentrations rise too much in the ambient seawater. Emissions from hydrothermal vents (Parson et al., 1995) result in the occurrence of high local concentrations of heavy metals such as manganese, cobalt and mercury. To survive, the organisms that inhabit the vicinity of vents must either avoid the discharge plumes, or be capable of tolerating the presence of the heavy metals in some way. Some detoxify them and store them; others control the concentrations in their blood and tissues by ionic regulation and excretion. Hydrothermal vents may have played and still be playing a significant evolutionary role by creating chemical variability in the otherwise monotonous pelagic environment of the deep ocean.

The density of sea water

The density of sea water plays a key, but indirect, role in ecological processes, through its control of the stability of the upper water column and its contribution to ocean circulation. Three factors, temperature, salinity and hydrostatic pressure, determine its density. Generally water density increases with depth. However, wherever and whenever the density is uniform with depth, the water readily mixes vertically. However, only quite small increases in density can inhibit vertical mixing and the water becomes stratified. Typically in the upper few tens of metres and also close to the sea floor, the density of the water is almost always uniform. Near the surface it is the action of the winds in the atmosphere that keeps the upper part of the "water column" well mixed and uniform. This layer of uniform water is called the wind-mixed layer. The other uniform layer immediately overlying the interface between the water and the seabed, which is again created by frictional forces but this time between the water currents and the seabed, is termed the "benthic boundary layer". This layer is important to those pelagic animal species that live close to the seabed in deep water, but it is even more important to the ecology of the benthic organisms that inhabit the sea floor. Between these two extremes, quite small differences in density between contiguous layers of water inhibit vertical mixing and the water is horizontally layered. This layering is so stable that even quite large perturbations (caused by tides or the seamounts) may not disrupt it, but instead generate internal waves. Internal waves are analogous to the waves at the surface, but they can have amplitudes of tens or even hundreds of metres, and wave lengths (i.e., the distance from crest to crest) that are very long. Under the right conditions they can break, just as surface waves approaching a shoreline break. Generally horizontal gradients in oceanic waters are extremely weak, whereas vertical gradients are often steep; an animal migrating 50 m vertically across the thermocline may experience a greater change in water temperature than if it swims 1000 km horizontally. Thus, patterns of distribution (of both physicochemical and biological characteristics) within the water column are often clearly defined vertically, but weakly defined horizontally.

At the base of the wind-mixed layer there is often a sharp increase in density, which is usually associated with a rapid decline in water temperature. This zone of transition is described as the "seasonal thermocline", and is a very important ecological feature (see p. 49). In the tropical and sub-tropical zones the seasonal thermocline is present throughout the year except in regions where upwelling occurs (see pp. 67–68). In temperate to tropical latitudes there is another deeper temperature discontinuity, which is described as the permanent thermocline. This marks the transition between the warm waters and the cool deep waters, and this transition outcrops at the surface along the Polar Fronts at high latitudes. Thus the oceans can be regarded as comprising a "cold-water sphere" which extends from the polar seas and across low latitudes at depths of *c.* 800 to 1000 m, and a "warm-water sphere" that fills the shallower depths at low and middle latitudes.

Hydrostatic pressure is almost entirely a function of depth. The pressure (p) at any depth (z) results from the weight ($g\sigma$) of the overlying water per unit area (where g is the gravitational constant and σ is the density of the sea water). In the open ocean the local effects of variations in atmospheric pressure are small, but at larger scales they can play a key role in some of the large-scale physical processes, such as the generation of El Niño Southern Ocean Oscillation (ENSO) events (see below, p. 65). In shallow inshore waters, fluctuations in atmospheric pressure can generate storm surges, which can result in catastrophic flooding when sea level rises quite suddenly by several metres. During hurricanes in coastal areas more people are drowned in the floods caused by the storm surges than are killed by the high winds. Water is only very slightly compressible, so that there are only slight increases in *in situ* density with increasing depth. If sea water at a temperature of 0ºC, with a density of 1028.1 kg m^{-3} at the surface, is lowered to a depth of 100 m and its temperature is kept constant, its density will increase to 1028.6. Lowering it further to 1000 m will increase its density to 1032.8, and at 4000 m its density will be 1046.4. If a sample of seawater is collected at depth and brought back to the surface in a fully insulated container, it cools down because its volume expands slightly. Ecologically and physiologically, the effects of pressure tend to be relatively small compared to those of other environmental factors such as temperature. However, it has a strong influence on the dissolution of calcium carbonate, and on those organisms that use gas-bladders or gas-filled vacuoles to regulate their buoyancy.

There are marked geographical variations in the density of sea water at the surface of the oceans. These are generated by variations in solar heating, and by the balance between water being lost from the surface by evaporation (which cools the surface and increases the salinity) and inputs of fresh water from rainfall (which can either cool or warm the surface, but also reduces surface salinity). Where additions of fresh water from rainfall are higher than the losses through evaporation, the density of the surface water in the upper wind-mixed layer decreases, so that it becomes more buoyant and less likely to mix with the water below it – that is, it stabilizes the upper water column. Conversely where losses by evaporation exceed the inputs from rain, surface salinity increases and temperatures decrease, both factors increasing the density of the surface water. Once the surface water becomes denser than the water it overlies, it sinks into the interior of the ocean at convergences, sliding down along surfaces of equal density or isopycnals (e.g., McCartney, 1992), until it reaches the depth at which its density equals that of the surrounding water. Once there, because vertical mixing is limited the water retains its characteristic properties of temperature and salinity, and these bodies of water are known as “water masses”. These water masses can be tracked over extensive distances as they move within the deep circulation patterns of the ocean (e.g., Dickson et al., 1988), and specific communities of plankton and nekton tend to be associated with them. Finer details of the large-scale circulation are now being followed using natural chemical markers, such as ^{3}He emitted from hydrothermal vents, and anthropogenic chemical tracers such as chlorofluorocarbons or CFCs (Smethie, 1993) and radioactive isotopes (Schlosser et al., 1995). In a few regions large outflows of fresh riverine water play a significant role in reducing the density of surface seawater – notably in the Arctic, where the freshwater outflows of the large Russian rivers stabilize the upper water column, reducing the fertility of Arctic waters. Another example is the outflow of the Amazon, which has a strong influence on the circulation and ecology of the southern Caribbean and the equatorial Atlantic. Conversely, in the semi-enclosed Mediterranean (and the Red Sea) there is a significant excess of evaporation over the freshwater inputs from rain and riverine outflows (the latter have now been drastically reduced in the Eastern Mediterranean as a result of the construction of the Aswam Dam on the Nile), so that salinity is exceptionally high.

As fresh water is cooled its density increases to a maximum at 4ºC, but then it decreases as the temperature is further cooled towards freezing point. In contrast, the density of sea water continues to increase until it reaches its freezing point at about −1.9ºC (it may be noted that salinity affects the freezing point; the higher the salinity, the lower the freezing point). When sea water freezes the ice formed is almost free of salt, so that the water which remains unfrozen is not only saltier but also denser. This is the process that underlies the formation of Bottom Waters in the Weddell Sea (Southern Ocean) and off Greenland in the North-east Atlantic; this ensures not only that the deep ocean is cold but also that it is well ventilated with oxygen (see Chapter 2).

Dissolution of gases in sea water

Gases, such as oxygen, nitrogen and CFCs that do not react with water generally have low solubilities, whereas those that do, such as sulphur dioxide, nitrogen dioxide and ammonia, are highly soluble. Carbon dioxide reacts relatively slowly with water to form carbonic acid, and is usually considered to have a low solubility. However, its solubility is complicated by the chemical equilibria governing the dynamic balances between dissolved carbon dioxide and bicarbonate and carbonate ions. These interactions play an important ecological role in buffering sea water against changes in pH, which in sea water generally ranges from 7.7 to 8.2 (Brewer et al., 1995). The higher values occur where photosynthetic rates are high enough to result in a significant draw-down in dissolved carbon dioxide (i.e., the partial pressure of CO_2 in the surface waters falls well below that of the atmosphere). These interactions are also influenced by pressure, because like all gases carbon dioxide becomes more soluble with increasing pressure, and so carbonate also becomes more soluble with increasing depth. Thus, as depth increases, those animals which use calcium carbonate for their skeletons have to work progressively harder to secrete and maintain them.

Exchanges of gases across the sea–surface interface are rapid, especially in windy conditions when breaking waves inject suspended bubbles to depths of 10 m or more. Thus at the surface the partial pressures of the gases dissolved in the seawater rapidly equilibrate with those in the atmosphere (e.g., Thorpe, 1995), so that either the oceans are taking up gases or they are venting excess dissolved gases into the atmosphere. Since the partial pressures of gases increase as temperatures rise, their solubilities decrease – this is why water in a kettle bubbles long before it starts to boil (one may note that this is counter to the effect of temperature on the solubility of salts, which increases with increases in temperature). Thus, more oxygen and carbon dioxide can dissolve in the cold surface waters of polar seas than in warm surface waters of tropical seas. In consequence, the formation of bottom and deep water transfers surface waters with high concentrations of dissolved oxygen and carbon dioxide into the interior of the ocean. This enables animals and microbes to respire aerobically almost everywhere in the deep ocean (the exceptions will be discussed below), and has also been reducing the rate at which concentrations of carbon dioxide have been building up in the atmosphere as a result of the burning of fossil fuels. Even so, it has been estimated that anthropogenic emissions of carbon dioxide to the atmosphere have already resulted in a reduction of pH in the global ocean by 0.1 (Sarmiento et al., 1992), and further reductions are to be expected. These may begin to influence the depth of the lysocline (the depth at which calcium carbonate begins to dissolve) (see Chapter 13). When rates of primary production are high, as during seasonal bloom conditions at temperate latitudes, the partial pressure of carbon dioxide in the surface waters may be lowered well below that of the atmosphere, so that the ocean rapidly absorbs more from the atmosphere. Conversely, when cold deep water, enriched with dissolved carbon dioxide as a result of the breakdown of organic carbon by respiration, upwells to the surface, the excess carbon dioxide is vented back into the atmosphere, even though primary production may be stimulated by the high inputs of nutrients (see p. 50).

In the North Atlantic, the water is sinking along the Polar Front, which is similar in density to the water at the bottom – Antarctic Bottom Water. This water mass originates in the Weddell Sea and spreads northwards from the Southern Ocean along the bottom of the Atlantic. Being similar in density, these two types of water can mix freely, and they together form a new and highly characteristic water mass called North Atlantic Deep Water (NADW). North Atlantic Deep Water is important because it is rich in dissolved oxygen and pervades the deep waters of all the major oceans via the “Great Conveyor” – the term coined by Broecker (1992) to describe the general pathway of circulation throughout the global ocean. Its concentration of dissolved oxygen decreases as it ages (i.e., as the time since it was last at the surface increases). In the Atlantic the deep waters are well flushed with young waters, which contain high concentrations of dissolved oxygen ($>5.5\,\mathrm{ml}\,\ell^{-1}$), but in the several hundred years required for NADW to reach the Pacific and Indian Oceans its oxygen content has fallen to $<3\,\mathrm{ml}\,\ell^{-1}$.

Another sub-surface source of oxygen is photosynthesis. As plants combine carbon dioxide and water in the synthesis of carbohydrates using energy from the sun, a byproduct of the reaction is oxygen. Thus, when the rate at which photosynthesis is producing oxygen exceeds the rate at which it is being used up by the respiration of the pelagic organisms, oxygen concentrations build up. In some tropical seas the partial pressure of the oxygen dissolved in the water at depths of about 100 m exceeds its partial pressure in the atmosphere; the water is then described as being supersaturated with oxygen. However, vertical profiles of oxygen concentrations generally show a steady decline to a minimum at the permanent thermocline, and then a slight increase in the deeper water of the "cold-water sphere". In upwelling regions (see pp. 67–68), such as the Arabian Sea and the Eastern Tropical Pacific, surface productivity is exceptionally high, so that an unusually high supply of organic carbon sediments down to subthermocline depths. These high organic inputs stimulate microbial respiration to such an extent that virtually all the dissolved oxygen in the water is used up. In the Eastern Tropical Pacific there is a permanent zone of oxygen depletion at depths of 200 to 1000 m (Wishner et al., 1995); in the Arabian Sea an oxygen-depleted zone develops during the upwelling season while the south-west monsoon is blowing. Within these oxygen minimum zones, both the organic flux regime and the water chemistry are drastically altered. Most pelagic species depend on aerobic respiration, they are excluded from the depleted zones, but a few that can tolerate the low oxygen conditions flourish. In a few localities, such as the Black Sea and the Cariaco Trench (off Venezuela), there is never any oxygen available in the deep water below 100 to 200 m.

As the hydrostatic pressure increases, the partial pressures of the dissolved gases decrease and so their solubilities increase. Thus the energy required to extract gases from the water – oxygen for respiration, carbon dioxide for incorporation into skeletal calcium carbonate, and other gases to inflate swim-bladders – increases substantially with depth. Moreover, because gases are so much more compressible than water, their effectiveness in regulating buoyancy declines with depth, because their densities increase more rapidly than that of the surrounding medium. However, the acoustic characteristics of gases are maintained, so, even at abyssal depths there are examples of animals retaining gas bubbles for the detection of sound.

Transmission of light through water

Light is one of the major ecological factors influencing distributions of organisms in the upper 1000 m. At depths greater than this its influence wanes, despite the almost universal use of bioluminescence by pelagic organisms for inter- and intra-specific signalling (Herring et al., 1990). In the euphotic zone light is one of the key factors, together with nutrient availability and vertical stability, that regulate rates of primary production and hence the supply of organic material to the deep-living communities. Water is translucent rather than transparent. It selectively absorbs and scatters light of different wavelengths (Sathyendranath and Platt, 1990). The red wavelengths ($\lambda = 650$–700 nm) are most rapidly absorbed (except when turbidity is very high), and even in the clearest oceanic waters all red light has been absorbed once a depth of 30 m has been reached. Blue-green light ($\lambda = 475$–485 nm) penetrates to the greatest depths and is detectable at depths of 1 km beneath the clearest oligotrophic water that underlies the subtropical gyres. Pure water scatters light, but this scattering is greatly enhanced by suspended particles. Hence, as productivity increases and phytoplankton becomes more abundant, the more rapidly is light attenuated with depth. Profiles of light intensity and the proportional changes in its colour composition play an important role in determining the zonation of the communities in the upper kilometre of the ocean, through determining the optimal strategies for detecting prey and countering visual predation.

Below 250 m, the brightest light comes from directly overhead and, regardless of the elevation of the sun, there is a symmetrical fall-off in intensity with increasing angle to the vertical, the dimmest light being backscattered from the depths (Denton, 1970). Many of the fish species living at depths of 250–600 m during the day have elaborate arrangements of photophores (light-producing organs) along their undersides. Their function appears to be to break up the silhouette of a fish when it is viewed from directly underneath. Below depths of 600–700 m, the downwelling light becomes so dim that the silhouette ceases to be a problem; then the ventral photophores no longer confer any advantage, and they become less elaborate or are totally lost. As the value of visual cues for detecting prey dwindles with depth, so chemoreception plays an increasingly important role in both intra- and interspecific communication. Chemical plumes spread more readily along isopycnals (i.e., surfaces of constant density) than vertically across them. Many deep-sea organisms have highly elaborate chemical receptors [see Marshall (1971) and Bone et al. (1995) for examples in fish], and probably have specialized behavioural adaptations linked to the detection of these chemical cues. These adaptations are also reflected in the morphology of the brains of many deep-living fish, those regions involved in chemosensory perception being well developed, but those involved in vision are reduced.

Animals that produce light (bioluminescence) may rely on their own luciferin/luciferinase system, or "culture" luminescent bacteria within their light organs (or photophores), or even in a few exceptional species derive the light-producing system from the food they eat. Bioluminescence is an almost universal characteristic of oceanic species, particularly of those inhabiting depths below the photic zone (Herring, 1990). As the intensity of daylight declines with depth, coloration ceases to play a major role in animal communication and/or camouflage, and bioluminescence takes over many of its functions in inter- and intra-specific signalling.

Transmission of sound through water

Water is much more "transparent" to sound than it is to light. But as frequencies increase (and wavelengths shorten) attenuation increases, especially as the wavelengths approach the acoustic diameter of suspended particles. Particles (or bodies) whose sizes exceed the wavelength of the sound will tend to backscatter it, but dense concentrations of finer particles also attenuate the sound through Tyndall scattering. Thus sound with a frequency of 10 kHz can generally penetrate to full ocean depths, being backscattered only by the larger fishes, whereas sound of frequency 150 kHz penetrates to a maximum depth of 400 m and is backscattered by high concentrations of zooplankton (e.g., Urick, 1975). Thus, sound is used by oceanographers for observing some of the ocean's physical characteristics, such as its depth, density distribution and particle concentration, and also for locating and communicating with devices deployed in deep water to make measurements. It is also quite widely used by fishes and marine mammals as a means of intra-specific communication and echolocation.

CHARACTERISTICS OF OCEAN BASINS

Knowledge of how the morphology of ocean basins and circulation patterns in the global ocean have changed over geological time is constantly improving (Parish and Curtis, 1982) (Fig. 3.1). Imprints of past ocean circulation patterns, which have resulted from changes in the gross distribution of continents over geological time, have been identified in present-day distributions (Van der Spoel et al., 1990; White, 1994). These changes continue to have an influence on current distributions of species and on their diversity (see p. 60–64).

The continents are asymmetrically distributed across the Earth's surface; in consequence, there are significant disparities between the environmental characteristics of the major oceans and basins. In the Northern Hemisphere 60.7% of the area is covered with ocean, compared with 80.9% in the Southern Hemisphere. Consequently sea-surface temperatures range more widely at temperate latitudes in the Northern Hemisphere than in the Southern Hemisphere (Fig. 3.2). The boundaries of four of the major oceans are largely determined by the distribution of the continental landmasses.

The largest and oldest ocean by far is the Pacific. It has a total area of around 165.38×10^6 km^2, a mean depth of 4200 m and a maximum depth of 11 524 m in the Mindanao Trench. Its total volume is about 695×10^6 km^3. It is fully open to the Southern Ocean, but has only a shallow connection with the Arctic Ocean via the Bering Strait. At present, it is connected to the Atlantic only by the Drake Passage to the south of Cape Horn at the tip of South America. However, as recently as 5 million years ago, there was a shallow-water connection through the Panama Isthmus; consequently, there is close similarity between the shallow-living tropical water faunas of the two oceans, but marked differences between the deep-living faunas. Faunal exchanges would also have been possible between mesopelagic species whose life histories include a shallow-living larval phase of sufficient duration for them to be carried by currents through the connecting channel. There are connections between the Pacific and the Indian Ocean via the shallow sills to the north of Australasia between the islands of the Indonesian Archipelago (see Chapter 9), but connections at full ocean depths are only to the south of 44ºS. Many of the margins of the Pacific are tectonically active, bounded by deep trenches along the margins of the actively subducting plates. One important influence of the trenches is that they entrap turbidity flows, which otherwise would transport sediment from the continental slopes out over the abyssal plains.

The Atlantic is the second largest ocean, with an area of 82.22×10^6 km^2 (i.e., half that of the Pacific). The North Atlantic began to open up at the beginning of the Jurassic era about 200 million years ago when the supercontinent of Pangea began to fragment and the land mass of North America separated from Afro-Eurasia. The opening of the South Atlantic was initiated much later, about 100 million years ago. The Atlantic has an average depth of 3600 m, reflecting its relatively young age, and its volume is about

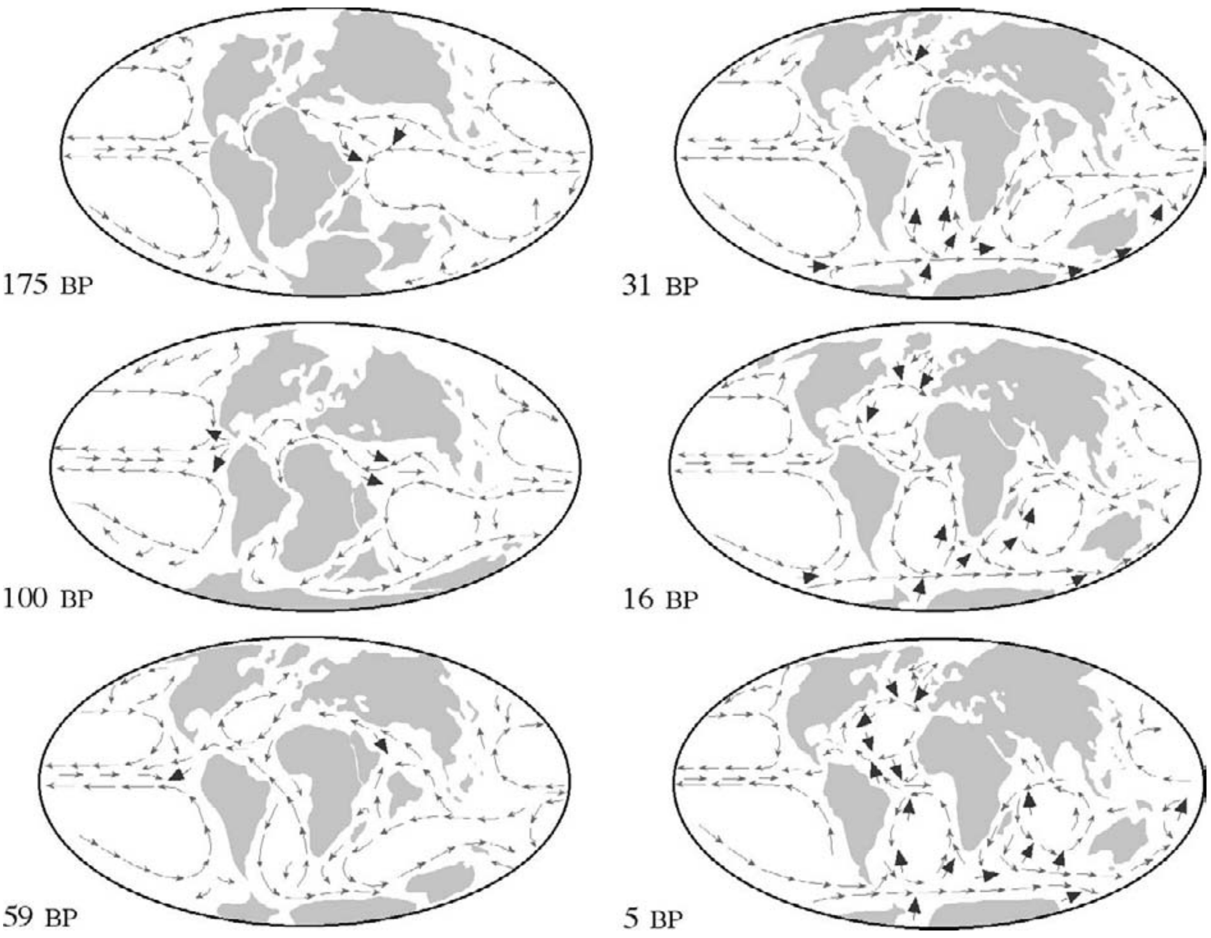

Fig. 3.1. The redistribution of the continental land masses as a result of continental drift at various intervals following the beginning of the fragmentation of the super-continent Pangea about 200 million years B.P. The arrows indicate the likely patterns of surface currents generated by the winds and influenced by the Earth's rotational effects. Redrawn from Parish and Curtis (1982).

296×10^6 km^3. Its maximum depth of 9560 m is in the Puerto Rico Trench. Otherwise its margins are tectonically passive, so that any slope failures result in extensive transport of turbidite[2] deposits far out across the abyssal plains.

The catastrophic events triggering the flows of water carrying the very high loads of suspended material that contribute most, if not all, of the material in each turbidite layer are highly intermittent, and are often set off by seismic events. On the other hand, the intervening layers between the turbidites are deposited over several millennia as a result of the slow continuous deposition of pelagic material. Hence there is a sharp contrast between the mineralogical content and character of the two types of deposit.

The Atlantic is the only ocean that has a deep-water connection with the Arctic Ocean. Warm Atlantic water flows north-eastwards into the Norwegian Sea and feeds the Spitsbergen Current; this outflow from the Atlantic has a major influence on the hydrography and ecology of the Arctic. These warm surface outflows from the Atlantic are balanced by cold inflows spilling over the ridges that lie between Greenland, Iceland, the Færøes and Scotland, and at the surface from the East Greenland Current, which carries southwards towards Nova Scotia icebergs spawned from the Greenland glaciers, such as the one which sank the *Titanic*. Atlantic hydrography is also greatly affected by the inflows from the Mediterranean and Caribbean (see Chapter 9). It also receives inputs from the Indian

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[2] See Glossary, p. 477.

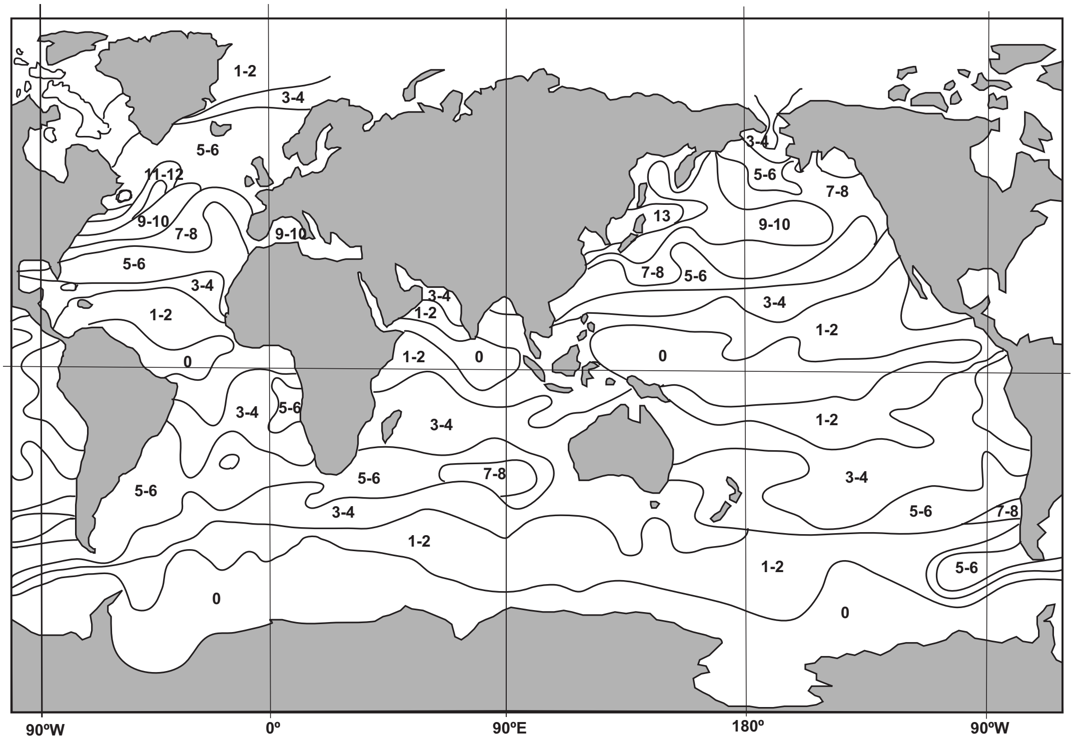

Fig. 3.2. Map of the seasonal ranges in sea-surface temperature in the global ocean. Redrawn from Van der Spoel and Heyman (1983). Note that the ranges tend to be greater in the Northern Hemisphere where the area of land is greater.

Ocean in the form of large eddies that pass around the southern tip of Africa. In the far south, the boundary between the Atlantic and the Southern Ocean is considered to be the Antarctic Convergence. However, this is a dynamic hydrographic feature which is not constrained to a precise geographical line, and whose position fluctuates seasonally and interannually. The various inflows into the Atlantic are balanced by the outflows of North Atlantic Deep Water to all the other major oceans (p. 43). This spread of NADW may provide a mechanism for gene flow between deep-living populations that otherwise appear to be widely separated geographically. For example, there is some molecular evidence that gene-flow may be occurring between the populations of the bathyal fish the orange roughy, *Hoplostethus atlanticus*, found both in the Northeast Atlantic and to the south of Australia (Elliot et al., 1994). However, so many deep oceanic species have such extensive distributional ranges that critical evaluation is needed to confirm whether each one is a single species, or is really a swarm of cryptic species, each one of which is genetically and possibly geographically isolated (Wilson and Hessler, 1987). At evolutionary time scales, the turnover of deep-ocean waters is relatively rapid (250 years for the Atlantic, 500 years for the Pacific and *c.* 1500 years for the global ocean). A few deep-living animals have been shown to have immense longevities: *Hoplostethus atlanticus,* for example, appears to live for up to 140 years (Smith et al., 1995). The large bathypelagic mysid *Gnathophausia ingens* has a life cycle lasting seven years (Childress and Price, 1978), so that over a few generations a population may circulate around a complete ocean system. However, Jumars and Gallagher (1982) have warned against regarding such extreme estimates of longevity as being generally characteristic of deep-sea faunas.

The Indian Ocean (area: *c.* 73.48×10^6 km^2, volume *c.* 282.9×10^6 km^3) is connected to only one of the polar oceans, the Southern Ocean; to the north it is bounded by continental Asia. As a result its climate is strongly modulated by the atmosphere's interactions with the landmasses to the north. These generate seasonal cycles of monsoon winds, which reverse in direction. As the direction of the winds reverses so do the surface currents, particularly to the north of the equator. As a result, in the Arabian Sea and to a lesser extent in the Bay of Bengal, surface conditions oscillate between being highly productive during the south-west monsoon, when off-shore winds result in coastal upwelling, and highly oligotrophic during the north-east monsoon, when normal subtropical/tropical conditions prevail. In the North-west Arabian Sea, this creates a unique cycle in deep-sea conditions, in which oxygen concentrations in subthermocline waters (down to depths of 1000 m) oscillate between being almost totally depleted towards the end of the south-west monsoon, and ranging between 2 and 3 $\mathrm{ml}\,\ell^{-1}$ during the north-east monsoon.

The Arctic Ocean is the only truly polar ocean, and is also a Mediterranean-type sea, being almost entirely enclosed by land (see Chapter 8). Nearly half of its total area of $14.06\times10^6\,\mathrm{km}^2$ consists of broad areas of shallow continental-shelf seas which are particularly extensive to the north of the Eurasian continental landmass. Its greatest depth of 4400 m occurs in the Fram Basin not far from the geographical North Pole. It has a narrow and shallow connection with the North Pacific via the Bering Strait, through which there are only limited exchanges of water. In contrast its connection with the North Atlantic is broad and deep, allowing much freer exchanges of water, which greatly influence the hydrography of both oceans. The inflow of relatively warm Atlantic Water (see above) pushes the southern boundary of the winter pack-ice far to the north. This inflow is largely balanced by the outflow of the East Greenland Current, which carries cold water, pack-ice and icebergs far to the south. Much of the Arctic Ocean remains covered throughout the year with multi-year (up to 5 years old) pack-ice, which ranges in thickness from 1.5 to 4 m. Recent evidence indicates that the Arctic pack-ice is thinning at a rate which will result in extensive areas becoming ice-free within a few decades. Normally during summer the area covered by pack-ice shrinks, but only by about 10%. Voluminous outflows of fresh water from the great Russian rivers create a stable haline stratification, which keeps productivity relatively low throughout much of the Arctic.

The Southern Ocean is very different. It is bounded polewards by the continent of Antarctica, so that a relatively small area lies to the south of the Antarctic Circle (see Chapter 8). To the north it is open to the other major oceans, and geographically cannot be readily separated from them. Hydrographically, its northern limit is the Antarctic Convergence (e.g., Foster, 1984). This is the major oceanic front at which Antarctic Intermediate Water forms and sinks as it spreads equatorwards, at its quasiequilibrium depth of 1000 m below the subtropical water mass. However, the exact position of the Convergence is not geographically restrained, and varies both seasonally and interannually (e.g., Peterson and Stramma, 1991). The major feature of the circulation in the Southern Ocean is the circumpolar current of the West Wind Drift. This current developed about 35 million years ago when circumpolar deep-water connections first opened up as the Antarctic and Australasian continents separated. The Antarctic Ice Cap developed only some 14 million years ago, but since then it has had a major influence on the development of Southern Ocean fauna, keeping the species sufficiently isolated for a high degree of endemicity to have evolved (Clarke, 1996). The extreme conditions have led to the evolution of some special adaptations. For example, some fishes have developed an antifreeze in their blood and tissues, without which their blood would turn to ice at temperatures below −1.5ºC. The establishment of the circumpolar current appears to have initiated a gradual cooling of the bottom waters throughout the global ocean from about 10ºC (during the Cretaceous) to the present 2º to 3ºC. The flow of the circumpolar current is constrained by the narrowness of the Drake Passage between the tip of South America and the Antarctic Peninsula, which has a profound influence on the general oceanic circulation.

The extent of pack-ice in the Southern Ocean fluctuates annually from about 20 million km^2 in the austral winter to 5 million km^2 in summer (Gloersen et al., 1992). Thus, in contrast to the Arctic, the areas of multi-year pack-ice are limited, and mostly occur in the Weddell Sea. It is in the Weddell Sea that bottom-water formation is most active. Large tabular icebergs are spawned from the broad ice-shelves of the Ross and Weddell Seas, where the continental shelf is unusually deep at 400–500 m, depressed isostatically by the weight of the ice.

Surface waters of the Southern Ocean to the south of the Convergence are always rich in plant nutrients (Levitus et al., 1993). The current theory to explain why the phytoplankton is never able to exhaust the supplies of nitrates (as occurs in the North Atlantic), is that there is insufficient iron available for the phytoplankton to achieve maximum growth rates (e.g., Martin et al., 1990; de Baar and Boyd, 2000). Other areas where this same phenomenon of high nutrient, low chlorophyll (HNLC) occurs include the North Pacific and Eastern Tropical Pacific. Another notable feature of the Southern Ocean is that there are exceptionally high sedimentation rates of silicate beneath the Antarctic Convergence (Shimmield et al., 1994).

There are a number of smaller seas separated from the main ocean basins, which have very different hydrological and ecological characteristics (see Chapter 9). The Mediterranean and Red Seas provide exceptional deep-sea environments, both pelagic and benthic. Shallow sills at the Strait of Gibraltar and Bab-el-Mandab prevent deep interchange with the neighbouring oceans. Both are situated at latitudes which are arid, so that freshwater inputs by precipitation and riverine run-off are much lower than the evaporative losses from the surface. This imbalance is compensated for by surface inflows through the Straits, but inside the Seas the surface salinities of these inflows increase, and there is localized formation of bottom water which creates uniquely warm, high-salinity deep water. In the Western Mediterranean deep-water temperatures and salinities are 12.6ºC and >36, respectively, in the Eastern Mediterranean 13.4ºC and >37, and in the Red Sea 21.6ºC and >38. At depths >300 m, both seas are almost isothermal, and the warm temperatures in the deep water enhance the rates of bacterial degradation of sedimenting particles, so that pelagic standing crops decline very much faster with depth than in the open oceans. Recent sampling from RRS *Discovery* in the Alboran Sea between Spain and Algeria confirmed that below 500–600 m there were almost no living copepods in the water column (c.f. Weikert and Koppelmann, 1996). Also, there is almost no bathypelagic community of species; instead, a few components of the mesopelagic fauna extend their bathymetric ranges to unusually great depths. The micronekton samples collected from depths >2000 m contained a small biomass consisting of a single species of caridean shrimp, *Acanthephyra eximia.* Little benthopelagic sampling has been carried out in either sea, but the deep communities appear to be supported either by fast-track large-package inputs or by downslope turbidity flows. Maybe these seas present conditions analogous to those that prevailed globally during the Mesozoic, when deep-water temperatures were generally very much warmer than today.

OCEAN GRADIENTS AND PRIMARY PRODUCTION

Many of the fundamental ecological processes are strongly influenced by the vertical structure of the water column, the most important of these processes being primary productivity. Rates of primary production are influenced by the availability of light and nutrients. In the open ocean the nutrient supply is strongly influenced by the degree to which vertical mixing occurs, and the resulting density structure of the upper water column. At low latitudes the density structure is predominantly determined by temperature, particularly by the depth of the thermocline, the zone of steepest temperature gradient. However, at high latitudes in the Arctic and Norwegian Sea, the range of water temperatures is small. Hence the density structure of the water is generated principally by the surface layer of low-salinity sea water resulting from the huge outflows of fresh water discharged into the Arctic by the big Siberian rivers and the Mackenzie River in North America.

The uppermost few tens of metres of the water column are kept well mixed by the turbulence generated by the wind. This uniform layer is called the “wind-mixed layer”. It is isothermal and isohaline, with similar nutrient concentrations throughout. In the North Atlantic at high latitudes during winter, the wind-mixed layer extends down to depths of several hundreds of metres, but in the North Pacific a strong salinity gradient maintains the stratification and restricts the wind-mixed layer to the uppermost 150 m or so. Phytoplankton cells have a very limited ability to regulate their depth, so that the turbulent mixing results in the cells spending most of the time at depths where the light is far too dim for photosynthesis. During springtime in the North Atlantic, the surface waters tend to become warmer as the strength and duration of the solar radiation increase. However, it is usually not until there have been a few calm days that the surface water eventually warms sufficiently for it to stratify thermally. The depth to which any turbulent mixing occurs is then limited to the top of the thermocline. The phytoplankton cells then are no longer being churned down into deep water but stay suspended at depths where there is ample sunlight for photosynthesis. The near-surface zone illuminated by enough sunlight to support photosynthesis is termed the “euphotic zone”. The phytoplankton population starts to grow rapidly. This rapid growth is maintained for as long as an adequate supply of nutrients (nitrate, phosphate, silicate and micronutrients like iron: e.g., de Baar, 1994) remains available in the surface waters. The biomass of plant cells continues to increase dramatically, forming a “spring bloom”. At sea level the sea looks green, and from space colour sensors mounted in satellites detect clear changes in ocean colour. However, the bloom is short-lived. Since the depth to which the wind-driven mixing is now restricted to above the thermocline, there is no longer any replenishment of the nutrients from below the thermocline. Once all the nutrients in the euphotic zone are used up, the bloom collapses almost as quickly as it develops. Much of the plant biomass sinks across the thermocline down into the ocean’s interior, generating a pulse of organic sedimentation that takes four to six weeks to reach the sea-bed at depths of 4000 m, fuelling both the midwater and the benthic communities. Most of this sedimentary pulse is either degraded by microbial activity or is intercepted during its descent by detritivorous pelagic species. About 10–20% of the carbon fixed by photosynthesis in the euphotic zone sinks into midwater, and only about 2–3% eventually reaches the benthic communities at abyssal depths.

In some oceans spring blooms do not occur. The build-up in plant biomass is either pegged back by the grazing of herbivorous zooplankton, or, in the high-nutrient, low-chlorophyll areas of the North and Central Pacific and in the Southern Ocean, an inadequate supply of iron appears to be the factor inhibiting the growth of the plant cells. It has been estimated that, if sufficient iron were present in these areas, primary production in the global ocean would nearly double.

In most of the tropics the upper water column is permanently stratified. Since the base of the euphotic zone lies at or above the thermocline and its associated nutriclines, the re-supply of nutrients by vertical mixing is limited year-round. The rate of photosynthesis is then limited to the amount that is supported by nutrients recycled (regenerated) within the wind-mixed layer, and relatively little organic material sinks into the deep water; these conditions are known as oligotrophic. In a few areas, such as along the equator, the depths of the isotherms become shallower (“shoal”) so that the thermocline comes to lie within the euphotic zone. Since the waters below the thermocline are rich in nutrients, much higher rates of primary production are stimulated, and much more organic material sediments out (is exported) into deep water.

A proportion of the organic material produced is respired and broken down while it is still in the wind-mixed layer. Some sinks into deep water, where its fate is also to be broken down either in midwater or on the seabed. The degradation releases the nitrogen and phosphorus content of the organic matter back into solution – a process known as “regeneration”. Hence the nutrients required for plant growth tend to accumulate in deep water. Following strong vertical mixing or upwelling (see pp. 67–68) nutrients are re-supplied into the euphotic zone and stimulate high rates of primary production. Primary production has two components – “old” and “new” production. “Old” production is the component that is supported by nutrients regenerated within the wind-mixed layer, whereas “new” production is supported by nutrients re-supplied from deep water by vertical mixing. The ratio between new and old production is the f-ratio (Eppley and Peterson, 1979). Low f-ratios occur when primary productivity is predominantly supported by regenerated nutrients and is dominated by the productivity of picoplankton, plant cells <2 μm in size. Since these cells are too small either to be extracted mechanically from the water by suspension-feeders or to sink under the influence of gravity, virtually all the organic material produced flows through the “microbial loop”. This is the component of the food web in which the grazers are either mucus-web feeders or exceedingly tiny themselves (mostly ciliates). Very little of the organic material flowing through the microbial loop is exported into deep water; most is respired within the euphotic zone, so that the nutrients it contains are also regenerated there.

Conversely, a very much higher proportion of the organic material resulting from new production is synthesized by larger phytoplankton cells, which are exploited by larger suspension-feeding zooplankton, and flows along pathways in the food-web that ultimately lead to carnivorous fishes, cephalopods and marine mammals. A much larger proportion of new production is exported into deep water via the “biological pump”; this is a significant mechanism whereby carbon dioxide is taken up into solution at the surface of the ocean and becomes transferred into deep water. The sedimentation of particulate organic matter (POM) under the influence of gravity is probably the most important component of this pump, and the quantity of organic matter thus removed from the upper ocean across the pycnocline into deep water is often described as “export production”. Export production is often correlated with the quantities of dissolved silicate available in the wind-mixed layer (Dugdale et al., 1995), and is closely linked to the growth and death of diatoms. Diatoms are a group of phytoplankton that have cell walls made out of two cylinders of silica that fit together like a pill-box. Their production dominates the spring bloom. But as the nutrients become depleted in the euphotic zone, they have the tendency to clump together into aggregations. These aggregations contribute to the formation of "marine snow" – aggregates that can range in size from 1 mm to 1 cm and which sink rapidly at speeds of several hundreds of metres per day (Lampitt and Antia, 1997). The term "marine snow" was coined to describe the large quantities of flocculent material first seen in the lights of the early submersibles. Seasonal pulses of sedimenting particles are a regular feature in many oceanic areas, and have been quantified using sediment traps. Sediment traps function like recording rain gauges, and are moored for up to six months at a range of depths in the ocean to quantify the fluxes of sinking particles (e.g., Honjo and Manganini, 1993). Time-lapse cameras deployed on the sea-bed have photographed the deposition of copious quantities of detrital material on to the sea-floor at abyssal depths in the North-east Atlantic within a few weeks of the collapse of the spring bloom at the surface (Lampitt, 1985; Thiel et al., 1988/89; Rice et al., 1994; Smith et al., 1996). Below the deepest range of vertical migration all organisms are dependent on the fluxes of organic matter that sink from the surface layers. The larger the particle or aggregate is, the faster it will sink, and so the less likely it is to be intercepted by detritivores on its journey down to the sea-bed. Also there will be less time for it to be degraded by microbial activity. Thus, the size range of the primary producers strongly influences the ultimate fate of the carbon fixed, and the quantities of organic material that reach the deep-living communities both within the water and on the sea-bed.

At low latitudes the re-supply of nutrients from subthermocline depths occurs either as a result of large-scale upwelling events (Summerhayes et al., 1995b) (see pp. 67–68), or smaller-scale vertical mixing that occurs around the meandering edges of eddies and along fronts (see pp. 65–67) as a result of the conservation of vorticity. (Vorticity is the mechanism used by skaters when they spin, either increasing their rotation by drawing their arms in and over their heads, or slowing it by throwing their arms out wide). There is also some resupply by vertical diffusion, but this is a very slow process. The biological response to vertical mixing and upwelling depends very much on the characteristics of the deep water being brought up to the surface. In the North Atlantic where the formation of deep water is actively going on, relatively little time has passed since the deep waters were at the surface, and they are described as being "young". The young waters that have been at the surface relatively recently contain plenty of dissolved oxygen (Mantyla and Reid, 1983), but relatively low concentrations of regenerated nutrients. This is clearly shown in Fig. 3.3, which illustrates the differences in the concentrations of nitrate between the deep waters of the various oceans (Levitus et al., 1993). Thus, in winter in the Bay of Biscay, although the water is mixed to very considerable depths (>500 m: Parsons, 1988), it does not boost the nutrient concentrations as much as it might in other oceans, because the deep water contains only moderate concentrations of nutrients. Consequently, phytoplankton production in the spring is not nearly as high in the North Atlantic as it is in the North Pacific, even though the vertical stirring is restricted to the uppermost 150 m. The subthermocline waters in the North Pacific are "older" and so contain richer quantities of regenerated nutrients (Fig. 3.3), but they also contain only about half the amount of dissolved oxygen.

Chemical profiles

The concentration profiles of dissolved substances vary according to the extent to which the substances are involved in biological processes. Thus, some metals and ions behave like the nutrients, and are controlled by biological activity, particularly in the euphotic zone (e.g., barium and cadmium). Typically these occur in low concentrations in the upper water column, because they are removed as part of the downward flux of organic material. In deep water their concentrations increase as chemical and microbial breakdown of the sinking organic matter releases them back into solution. Other substances are considered to be intermediate in their characteristics, because, although they are involved in biological processes, other dynamic processes are dominant in regulating their concentrations (e.g., copper). Oxygen concentrations are particularly interesting. As discussed, concentrations of dissolved oxygen generally reflect the age of the water – the length of time since the water was last at the surface – because the oxidation of the organic matter in midwater progressively uses up the available oxygen. The rate at which it is used up depends on how

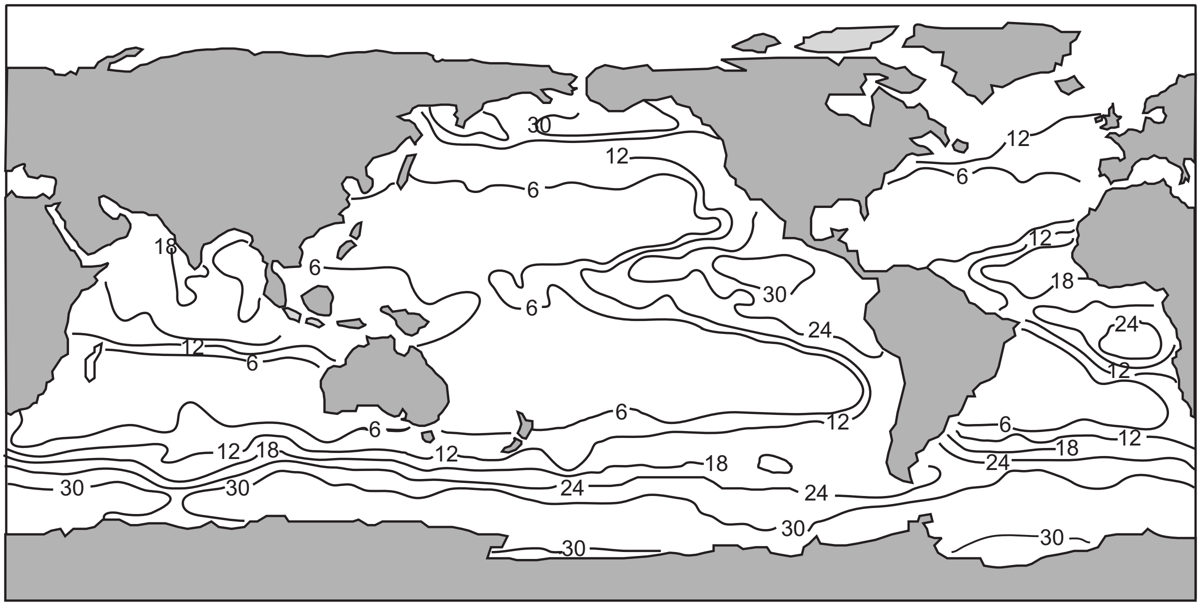

Fig. 3.3. Map of the mean concentrations of nitrate in the oceans at depths of 150 m, illustrating how nutrient concentrations match the gross patterns of the thermohaline circulation (from Levitus et al., 1993). Note how the highest concentrations of nitrate at these depths occur in the North Pacific, the Eastern Tropical Pacific and the Southern Ocean, all localities where it is postulated that availability of iron is limiting primary production.

much organic material is sinking out, and hence will vary according to productivity at the surface. Other substances like lead are inert, and their concentrations are indicative of where there are inputs and of the large-scale physical mixing processes. Thus, comparisons between the depth profiles of substances with differing responses to physical and biological processes can be useful indicators of the average rates at which key processes are taking place. Conversely, when the ratios of concentrations between ions with very similar responses are consistent, the measurement of one can be used as a proxy for the other. This is particularly useful in analysing the geological record; for example cadmium, which is preserved in sediment samples, can be used as a proxy indicator for the phosphate concentrations that prevailed at the time of deposition, and hence the past productivity.

Another example, uranium^{238}, which occurs in continental rocks, decays radioactively into radon. Radon is a radioactive gas and is emitted into the atmosphere. It decays into lead^{210}, which in the atmosphere becomes attached to dust particles. These dust particles are washed out of the atmosphere into the oceans in rain. Once in the ocean, the lead is inert and behaves predictably, settling slowly to the seabed. However, the lead^{210} also decays radioactively into yet another element, polonium, which, unlike the lead is reactive. It behaves very much like a nutrient since it is absorbed on to the surfaces of phytoplankton, and is removed from the euphotic zone by sedimentation. Hence the ratio between the concentrations of lead^{210} and polonium can be used as an indicator of the rate at which organic material is settling out from the euphotic zone (i.e., the organic flux rate).

Many detritivores inhabiting the deep water have been found to have quite high concentrations of polonium in their guts, which seems to be a useful indicator of their dominant feeding mode. Some individuals of the deep mesopelagic decapod *Gennadas valens* and the amphipod *Themisto compressa* have been found to contain such high natural levels of polonium in their hepatopancreas that they are receiving a radiation dosage which would be lethal to a man (Cherry and Heyraud, 1981). However, since these processes have been going on since the species evolved, they are probably well adapted to such radiation. Ratios between other radioactive isotopes have been used to estimate other rate processes; for example, the changing ratios of lead^{210}/radium^{226} in the otoliths (ear bones) of a deep-sea fish – (the orange roughy *Hoplostethus atlanticus*), have been used to estimate that the large fish may attain an age of 70–140 years (Fenton et al., 1991).

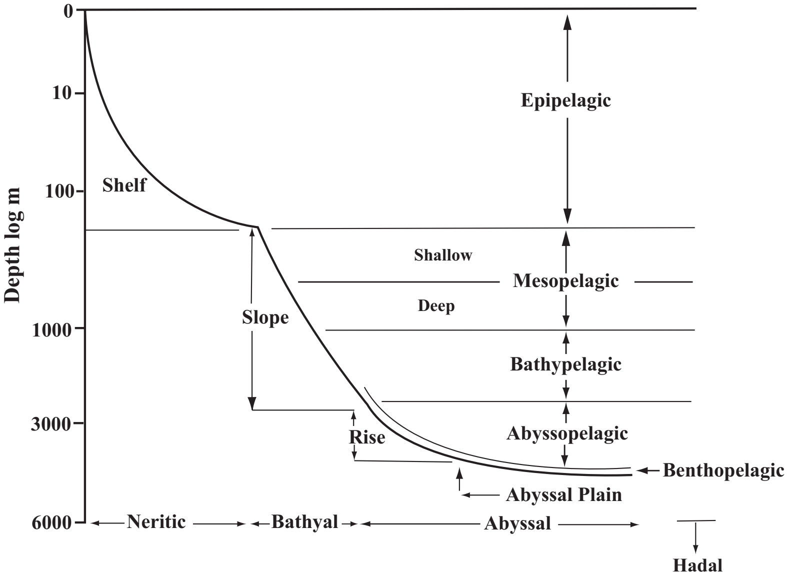

Fig. 3.4. Schematic representation of the pelagic and benthic zonation in the oceans. Note that the depth scale is plotted logarithmically, and that the interfaces between the zones are clinal rather than clearly defined boundaries. The depths of interfaces also show local and seasonal variations, and may also be obscured by dominant hydrographic features such as the edge of the Gulf Stream on the eastern seaboard of North America.

Biological profiles

The gradients of both chemical and physical characteristics have a strong influence on the distributions of pelagic organisms. This leads to the development and maintenance of strong vertical structuring or zonation in the pelagic assemblages (Fig. 3.4). However, even where the physical and chemical structuring is well-defined and contains sharp discontinuities, the biological discontinuities are usually quite fuzzy, so the biological interfaces tend to take the form of zones of rapid change (or clines) extending over several metres, rather than sharp boundaries. Moreover, these zones of change oscillate vertically in space and time in response to changes in light, physical features like eddies and fronts, and seasonality. Even so, the vertical distributions of pelagic communities have a generally consistent overall pattern of zonation that is common to most oceans (Fig. 3.4).

The distribution of biomass

By far the greatest part of primary production, the production of organic matter from carbon dioxide, is restricted to the upper sun-lit layers of the ocean which are sufficiently brightly illuminated for photosynthesis to occur (chemosynthesis at hydrothermal vents is thought to account for *c.* 0.3%). Thus, virtually all life in the ocean is based on primary production in the upper 100 m or so, some of which is subsequently exported into deep water. As discussed above, the sinking organic matter is progressively broken down by microbial activity and chemical oxidation, and consumed by deep-living pelagic organisms. Thus, as the depth increases, the supply of organic material dwindles. Between the euphotic zone and a depth of 1000 m the total pelagic standing crop (biomass) declines by about an order of magnitude (Fig. 3.5); and between 1000 m and 4000 m it declines by a further order of magnitude (i.e., to *c.* 1% of that in the euphotic zone) (Angel and Baker, 1982). These decreases reflect the proportions of primary production reaching the deep ocean as a result of sedimentation of particles and downward transport by migrating animals (see pp. 59–60). There are also shifts in average size of the populations. For example, profiles of ratios of the standing crops of macroplankton to micronekton was >10:1 in the euphotic zone in the vicinity of the Azores Front, but 1:1 at 1000 m depth (e.g., Angel, 1989b). Biomasses of benthic communities show similar exponential decreases with increasing depth (Rowe, 1983; Lampitt et al., 1986). However, the exponential decline with depth in the standing crop of pelagic communities is often obscured by day in

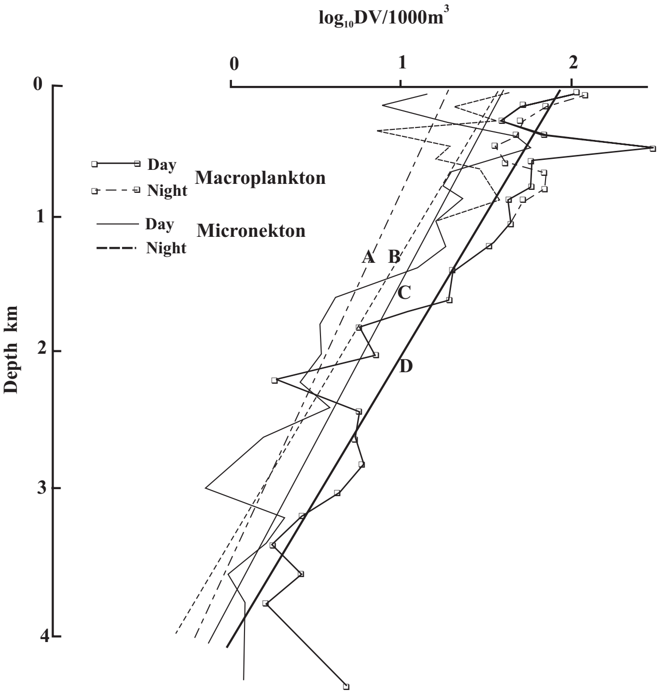

Fig. 3.5. Day and night profiles of macroplankton and micronekton biomass (expressed as $\log_{10}$ mls displacement volume per 1000 m^3) at 42ºN, 17ºW with their straight-line regressions superimposed (lines C and D). Also superimposed are straight-line regression for micronekton from two other stations in the Northeastern Atlantic: A, at 20ºN 21ºW; B, at 49º40′N 14ºW. The slopes of all the regressions lie between 0.004–0.005. Modified from Angel and Baker (1982).

the upper kilometre of the ocean by accumulations of vertical migrant species at depths of 300 to 500 m (see p. 55). The pattern is also disturbed in the benthopelagic zone, within about 100 m of the seabed, where the biomass increases towards the seabed (see p. 59). It is also lost during winter at high latitudes, after the majority of pelagic animals have vacated the upper ocean to overwinter in a state of diapause (an aquatic version of hibernation) at depths as deep as 2000 m.

Ecology of the epipelagic zone

This zone extends from the surface of the ocean to a depth of 200–250 m. Throughout the zone the light field tends to be asymmetrical vertically, so that the direction and elevation of the sun in the sky can still be detected. The epipelagic zone encompasses the euphotic zone and, where and when it occurs, the seasonal thermocline. This is the zone in which the primary production occurs that fuels virtually all other pelagic and benthic life. It is also the zone where, with the possible exception of winter conditions at high latitudes, that food is most abundant for herbivores and suspension-feeders. However, since most phytoplankton species are small, the majority of grazers either have to be small as well or have special mechanisms for extracting the plants cells out of the water. Cells >10 μm in diameter can be mechanically sieved from the water by suspension feeders such as euphausiids (krill). However, the smaller plant cells, the nanoplankton (10–2 μm) and picoplankton (<2 μm), are too small to be extracted from the water by means of the mechanical sieving available to the animals. In low-productivity areas and during the nutrient-limited phases of the production cycle at temperate latitudes, these small cells may be producing as much as 80% of the total primary production. To feed on such tiny cells the grazers either have to be almost as small themselves, so that they can handle the cells individually, or they have to use low-energy systems for collecting the cells, for example by trapping them on sticky sheets of mucus. Mucus-web feeding occurs in a wide range of planktonic groups, including pteropods, salps, larvaceans and the foraminifers. The mucus they secrete plays a role in another important process, the formation of “marine snow”. A loose sheet of mucus can act as a nucleus for the formation of a snow aggregate. Once formed, not only is the snow an important source of nutriment for larger zooplankton species, but it is also an important vehicle whereby particulate organic matter is exported by sedimentation to the deep ocean (Lampitt et al., 1993; Silver et al., 1998).

A rich assortment of animals inhabit the epipelagic zone. However, many of the species are not permanent residents, but are commuters from deeper water (see pp. 59–60). These commuting species include the diel vertical migrants, which each night swim up into the epipelagic zone to feed, and migrate down again at dawn; also, the eggs and early larval stages of species whose adults inhabit deeper depths; and even some benthic species. Some species invest little if any yolk in their eggs, so the early larvae have to feed if they are to grow and develop. For these larvae the invidious gamble is to risk a perilous existence in the well-lit waters where predators abound, but food is more abundant, rather than to starve deeper down where the dangers from predation are far less. Despite these migrations, both by day and by night the numerically dominant group of mesozooplankton (i.e., plankton caught in nets with meshes of 200 to 330 μm) are copepods; >75% of the organisms caught belong to this group of planktonic crustaceans.

Predators that hunt visually generate a strong selection pressure for the resident zooplankton inhabitants to minimize their visibility. This is achieved in just two ways: either by being very small (perforce many of the grazers have to be very small to feed on picoplankton) or by being highly transparent. Transparency (or translucence) is almost universal in the many gelatinous species – salps, siphonophores, medusae, foraminiferans and chaetognaths, and these groups tend to be the dominant components of the communities of larger organisms, by day often contributing >75% of the micronektonic biovolume (Angel and Pugh, 2000). Transparency is not an option that is widely adopted in fishes, but the *Leptocephalus* larvae of eels are notable for being almost totally transparent. More usually, fish are camouflaged by being counter-shaded. Their backs are dark, their bellies are pale, and their flanks are patterned with disruptive bars; this relatively simple colour pattern renders them surprisingly difficult to see underwater. Very close to the surface, however, they can be clearly seen by predators approaching from directly underneath, because they are silhouetted against a circular patch of bright water. This patch, called Snell’s circle, results from the refraction of light as it passes through the surface (Partridge, 1990).

Just after dusk, a vast array of planktonic and micronektonic commuters arrive. These are the diel vertical migrants. Their arrival often doubles the biomass of animals in the epipelagic zone, and also greatly extends the size range of the inhabitants. The migrants move up at dusk from daytime depths below the pycnocline and in many cases from the mesopelagic zone (see next section), and start on their way back down at around first light. Although the availability of food is far higher in the upper layers, the risk of predation, especially by visually-hunting predators, is greater. So, by moving up to feed under the cover of darkness the migrants optimize their chances of finding enough food, while minimizing the risks of predation. Since the migrants feed mostly at night, their movements provide another mechanism for the export of particulate organic matter out of the euphotic zone into deep water (see p. 50).

Ecology of the mesopelagic zone

Underlying the epipelagic zone and extending down to depths of about 1000 m is the mesopelagic zone. Although the dominant types of pelagic organisms do not change very much in the mesopelagic zone, there are marked changes in the species composition; also, the proportion of the smaller-sized individuals decreases (Fig. 3.6). Since there is an almost total absence of viable phytoplankton on which grazers can feed, the options for feeding become restricted to detritivory or carnivory. The mesozooplankton is still numerically dominated by copepods, but in the upper part of the zone the larger-sized organisms are predominantly gelatinous, particularly siphonophores. Many of these gelatinous forms are so fragile that they are impossible to sample with nets, so it was not until biologists began to dive in the open ocean that the abundance and importance of these fragile animals became recognized. Even now, knowledge of their role in pelagic processes is sparse; but they must be very important at depths of 200 to 400 m, where direct observations from submersibles have shown them to be extremely abundant. Many of the crustacean species inhabiting the upper mesopelagic zone are part transparent and part pigmented, usually tinged with red and orange carotenoid pigments. In the absence of red light at these depths, functionally these pigments are

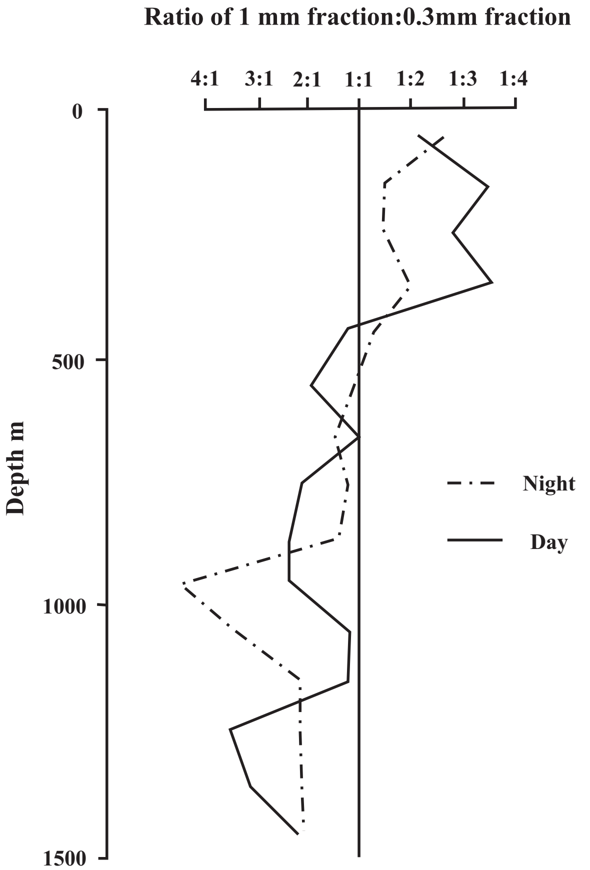

Fig. 3.6. Day and night bathymetric profiles of the ratios of biomass (displacement volumes) of size-fractions of macroplankton sieved *in situ* using concentric cod-ends of decreasing mesh sizes at 31º30′N, 25º30′W. The >1 mm fraction was filtered through an initial 4.5 mm mesh. The smaller size fraction passed through the 1 mm mesh and was retained on a 0.32 mm mesh, which was the same mesh as the body of the sampler. Note how during the day the biomass per unit volume of the smaller fraction was higher than the coarser fraction down to a depth of 400 m, but below that it tended to be exceeded by the larger faction. At night, diel vertical migration reduced, but did not eliminate, the dominance of the smaller fraction in the upper water column. From Angel (1997).

black. They also have maximum absorption of light at blue-green wavelengths, which is not only the colour of the residual daylight penetrating to these depths, but is also the colour of most bioluminescence – the light produced by the animals themselves. Carotenoids are plant pigments that cannot be synthesized by the animals, and so must be derived second- or third-hand from the content of their diets.

The characteristic morphology of fishes living at mesopelagic depths is exemplified by the myctophids (lantern fishes) and argyropelecids (hatchetfishes). They have black backs, flanks that are highly reflective and mirror-like and their undersides are lined with photophores (light organs). The silvering of the flanks is produced by regularly spaced platelets of a white pigment, guanine (Denton and Nicol, 1966); these function structurally as interference mirrors. When a fish is correctly orientated in the symmetrical light field, a predator approaching from the side will see, reflected from its mirror sides, light of exactly the same intensity as the background – a highly efficient form of camouflage. However, if the predator approaches from directly beneath, the fish will be silhouetted against the relatively bright light coming from directly overhead. Since many of the predators inhabiting these depths, including some of the species of hatchetfishes, have upward-looking tubular eyes and their mouths are also directed upwards, stalking prey from below by looking for their silhouettes appears to be a widespread hunting technique. The function of the light-organs arranged along the bellies of the fish is probably to reduce their vulnerability to this approach. Light emitted from their photophores will disrupt their silhouettes making them much harder to see. However, to be effective, the light emissions from the photophores must be the same intensity as the daylight coming from the surface. Some of the fishes have a light organ within each eye with which to compare the intensity of the light from the photophores with that of the ambient light; filters in the photophores can modify their output. In addition, the orientation of the mirrors along the fish's flanks needs to be kept vertical. Watching the behaviour of the hatchetfishes from submersibles has shown that they swim up and down by sculling with their pectoral fins. They keep their bodies correctly orientated to the light field and hence optimize the effectiveness of both of their mirror-sides and their ventral photophores as camouflage (Janssen et al., 1986).

Another characteristic of the photophores of many myctophids (lantern fish) is that the arrangement of the photophores that ornament their flanks is species-specific; a characteristic useful to taxonomists. It seems probable that this is not a coincidence, and the fish are also using these patterns to signal their specific identity to other individuals. There is also sexual dimorphism in the arrangement of some of the light organs in some species, males only having large dorsal and ventral light-organs at the base of the tail (i.e., on the caudal peduncle). Analyses of the stomach contents of large visually-hunting piscivorous fishes, such as tuna, show that they predominantly eat male rather than female lantern fish. In contrast, nets, which catch blindly, tend predominantly to sample females. Thus, there may be a sexual disparity in response to predatory attacks.

Such physiological characteristics, which enhance competitive fitness within a precise range of environmental conditions found within a specific depth range, may well limit an organism's ability to survive and compete elsewhere in the water column. Thus *Argyropelecus* species, which are so well adapted to the light conditions at daytime depths of 250 to 600 m, may become progressively more susceptible to visual predation the further they are displaced vertically, either deeper or shallower. Such high degrees of specialization have evolutionary implications (see p. 61).

The mesopelagic zone can usually be subdivided faunistically at about 600 to 700 m into a shallow and a deep sub-zone. During the day, fishes inhabiting the upper mesopelagic zone are predominantly mirror-sided with ventral photophores, and the decapod crustaceans (e.g., *Oplophorus spinosus, Sergestes* spp. and *Systellaspis debilis*) are mostly half red and half transparent. In the deeper zone, on the other hand, fishes with mirrorlike sides are replaced with species with non-reflective sides; the advantage of mirror-sides, it would appear, diminishes quite rapidly with increasing depth. Presumably in the dimmer light conditions below 600 m any fish with mirror-sides would tend to be lit up by any nearby flashes of bioluminescence; consequently, the selective advantage swings towards species with uniformly dark, non-reflective coloration. However, many deep mesopelagic fishes still have small, simple ventral photophores. The decapod species are totally red (e.g., *Acanthephyra* spp. and *Sergia* spp.).

At dusk, most of the diel migrants, that move up from daytime depths in the shallow mesopelagic zone, readily migrate up through the pycnocline into the wind-mixed layer, whereas those that migrate up from the deep mesopelagic zone (mostly micronekton) tend to halt at the base of the thermocline. The majority of macroplanktonic organisms inhabiting the deep mesopelagic depths are non-migrants.

Ecology of the bathypelagic zone

At about 1000 m, the maximum depth to which detectable daylight penetrates in all but the clearest oligotrophic waters, the mesopelagic zone gives way to the bathypelagic zone. This depth also marks the lower limit to the range of diel migration by most micronekton at temperate latitudes. In the temperate Atlantic, it also approximates to the deep oxygen minimum and the base of the permanent thermocline (Angel, 1989a), although at equatorial latitudes these features are displaced closer to the surface (domed). It is also the depth at which the greatest variety of pelagic species are caught (see p. 62), despite pelagic biomass having fallen to about one-tenth of that found near the surface (see p. 54).

As the availability of food diminishes both quantitatively and qualitatively with increasing depth, the cost/benefit balance of various physiological adaptations to the pelagic mode of life shifts (see pp. 72–75). Marshall (1971) compared the characteristics of two congeneric fish species *Gonostoma denudatum* and *G. bathyphilum,* which are mesopelagic and bathypelagic, respectively (Fig. 3.7). *Gonostoma denudatum,* the mesopelagic species, is a dark-backed, silvery-sided fish with prominent ventral photophores, and

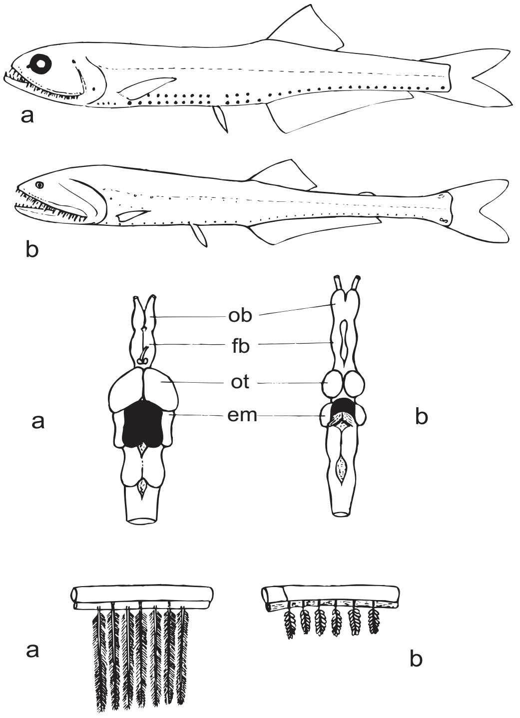

Fig. 3.7. Comparison between a) the mesopelagic fish *Gonostoma denudatum* and b) the bathypelagic species *G. bathyphilum,* illustrating the relatively small eyes and photophores in the bathypelagic species. Also shown are their brains drawn to the same scale, again showing marked differences in the sizes of the olfactory bulb (ob), the forebrain (fb), the optic tectum (ot), the eminetia granularis (em) and the corpus cerebellum (in black) between the two species, and also the relative sizes of the gills on the first gill arch. Redrawn from Marshall (1971).

undertakes diel vertical migrations. Its eyes, olfactory organs and muscles are well developed; it has a well-calcified skeleton and a gas-filled swimbladder with which to regulate its buoyancy. In contrast, *G. bathyphilum* is a non-migratory species and is totally black with poorly developed ventral photophores. Its eyes are half the size of those in *G. denudatum* and in adults have probably regressed and become non-functional. Its mouth is relatively large and capable of engulfing much larger prey. Its skeleton is weakly calcified, and it lacks a swim bladder. The reductions in physiological demands resulting from these reductions in size of its organs also leads to the bathypelagic species having evolved with smaller and less elaborate gills, smaller heart and kidneys, and a less elaborate brain (Table 3.3).

Table 3.3
Comparison of the morphological organization of mesopelagic and bathypelagic fishes [1]

Features	Mesopelagic sp.	Bathypelagic sp.
Colour	many silvery sided	black
Photophores	numerous well developed	small, regressed except for lures
Jaws	relatively short	relatively long
Eyes	relatively large	usually small and regressed
Olfactory organs	moderately developed in both sexes	small or regressed except in males of some species
Central nervous system	well developed throughout	weakly developed except for acoustico-lateralis centres
Myotomes	well developed	weakly developed
Skeletons	well ossified, including scales	poorly ossified; scales often absent
Swimbladder	present in most species	either lacking, or invested with fat
Gills	numerous filaments with many lamellae	few filaments with reduced lamellar surfaces
Kidneys	large with numerous tubules	small with few tubules
Heart	large	small

[1] After Marshall (1971).

Many bathypelagic species have bizarre life cycles. For example, ceratioid anglerfish are strikingly sexually dimorphic. The females are relatively large and inactive fish with tiny eyes, large luminous lures and mouths with enormous gapes. The males are small, highly mobile, with large eyes and chemical receptors. Each male probably has a relatively short time in which to seek out a female before it "burns out". The male probably locates a female by detecting chemical attractants (pheromones) which she releases, and sighting the characteristic flashing of her lure (see below). Once a male has located a female, he has to avoid being eaten by her, and attaches himself to her flank. Once safely attached he thereafter lives as an ectoparasite, fertilizing her eggs as she releases them. In several other species the adults undergo sex changes; in *Cyclothone microdon,* for example, the changes are protandrous: initially after maturation individuals are male, and later change to become female.

In the permanent darkness below 1000 to 1250 m, bioluminescence is used for many functions. Copious discharges of luminescing secretions can act either as smoke screens within which the animals hide, or as decoy targets to distract an attacker while an escape is made. I have already mentioned an example of intra-specific recognition and sexual displays. Several fish species have large cheek light-organs which probably function like headlights emitting a bright blue-green light, used when the fish is making its final strike on its prey. In a very few species of the genera *Aristostomias, Malacosteus,* and *Pachystomias*, the fish have suborbital photophores that emit light in the far-red ($\lambda = 708$ nm), instead of the more normal blue-green. Normally the retinal pigments of deep-sea fishes are sensitive only to blue-green light, but in these species with the red-emitting photophores the retinal pigments are specialized by being sensitive to red light (Bowmaker et al., 1988). This would seem to be an ideal specialization for feeding on the red macroplankton and micronekton, because it enables the prey to be illuminated without being able to detect the threat. However, these fishes are quite scarce, which implies that their success must be limited by some other factors. Many species have luminous lures presumably to entice potential prey within striking distance. The stalked lure, or esca, on the head of female ceratioid anglerfish, contains luminescent bacteria. The fish controls the flashing of the bacteria by regulating the supply of blood to the esca. Stomiatoid fishes have luminous chin barbels on their lower jaws; some of these barbels have elaborate shapes that are likely to be mimics of planktonic species.

Ecology of the abyssopelagic zone

A further subtle change occurs in the pelagic assemblages at depths of about 2500–2700 m. At 42ºN 17ºW in the Northeast Atlantic, Angel (1983) recorded a sudden decline in abundance of fish at 2700 m, so that they ceased to be the dominant component of the micronekton biomass. Initially they were replaced by decapod crustaceans, which in turn, at even greater depths, were replaced by mysids. This depth of 2700 m may be critical for physiological reasons. In some rather crude preliminary field trials, Menzies and Wilson (1961) compared the survival of benthic specimens brought up to the surface, and of littoral species lowered to depth. For both sets of species there was a critical boundary for survival at 2500 to 2700 m; all the deep-living animals retrieved from greater depths succumbed to the change in hydrostatic pressure, whereas the shallow-living species all survived being lowered to 2400 m, but succumbed if lowered deeper. The abyssopelagic zone extends down either to hadal depths (i.e., depths >6000 m) or to the benthopelagic zone within *c.* 100 m of the sea floor.

Ecology of the benthopelagic zone

The benthopelagic zone usually coincides with the benthic boundary layer (BBL) – the layer of isothermal and isohaline water contiguous to the sea floor. However, in regions where there is high mesoscale eddy activity (e.g., in regions of western boundary currents such as the Gulf Stream), benthic storms are frequent and create isohaline and isothermal conditions extending as much as 1000 m above the bottom (Weatherly and Kelley, 1985). Wishner (1980) first noted that the standing crop of plankton increases very close to the bottom, and may more than double within the benthopelagic zone. In addition, the rather special conditions result in many of the species found there being endemic to the zone (Angel, 1990).

The general reversal of the gradient of pelagic biomass close to the seabed implies that the declining gradient in food availability seen higher in the water column is reversed in close proximity to the seabed. Above the BBL, the organisms in the water have only the flux of sedimentary particles as the basic source of food, and this flux is very patchy and intermittent in time and space. However, once these particles are deposited on the seabed, they remain available until they are either consumed or microbially degraded. Whenever the current at the bottom exceeds a critical velocity the particles are resuspended, once again becoming available to organisms in the water. Any organism that scavenges on the bottom reduces the scale of the problem of finding food from three-dimensional in the body of the water to two-dimensional on the surface of the sediment.

This reversal of the gradient in standing stock also tends to reverse the gradient of predation pressure. A pelagic organism becomes safer from the risks of predation the higher above the bottom it is swimming, so that the water column above the BBL may be used as a refuge. Conversely species that feed on the bottom can find a more dynamic hydrographic regime by swimming up into the water column, and become better able to pick up scent plumes from food packages such as whale carcasses (Smith et al., 1998), or even potential mates. Baited traps deployed at various heights above the seabed catch large numbers of these amphipod scavengers close to the bottom, but their abundance dwindles almost to zero >50 m above the bottom (Thurston, 1979; Wickens, 1983; Christiansen, 1996). Occasionally these amphipods have been caught in trawls several hundreds of metres above the bottom; the reasons for these extensive migrations are not clear.

The benthopelagic zone is also used by the pelagic larvae and post-larvae of benthic species. Several holothurian species, normally considered to be megabenthos, have the ability to float up off the seabed and have been caught several hundreds of metres above the bottom (Billett et al., 1985; Billett, 1991). Several deep-sea benthic gastropod species have been found to have fully pelagic larvae, which undergo extensive development near the surface and then descend into deep water on maturation (Bouchet and Warén, 1985). The dispersion of such larvae within the deep-water column may result in the establishment of pseudopopulations of adults of species in areas which have environmental characteristics unsuitable for their reproduction (Bouchet and Taviani, 1992).

Vertical migrations

There are three basic types of vertical migrations: diurnal (or diel), ontogenetic, and seasonal. In terms of ecological processes, diel vertical migrations, the behaviour of many pelagic species in swimming up towards the surface at dusk and returning back down again at dawn, is by far the most significant. There is an increasing amount of evidence that these migrations contribute to the downward fluxes of organic matter from the surface (Longhurst and Harrison, 1988; Dam et al., 1995; Zhang and Dam, 1998; Steinberg et al., 2000; Angel and Pugh, 2000). The majority of planktonic and micronektonic animals which perform diel vertical migrations only feed during the shallow phase of their migrations, where and when food is more available. They migrate down with full stomachs, and when they return the following dusk their guts are empty. Thus, any organic material they do not retain after ingestion but defaecate contributes to a downward flux. Since most of what they consume comes from shallow depths, anything they excrete at depth, be it carbon dioxide, ammonia, or dissolved organic matter, will have been derived from near the surface. If they moult, die or are eaten, there is a downward flux of material. Recent data from the equatorial Pacific show that diel migrant mesozooplankton were exporting 0.6 and 1.1 mmol $\mathrm{C\,m^{-2}\,d^{-1}}$ in the two seasons of observations, respectively, contributing 31% and 44% to the sedimentary flux (Zhang and Dam, 1998). To this estimate must be added the export by migrating micronekton, whose biomass is roughly about half that of the mesozooplankton (Angel and Pugh, 2000), but whose migrations extend over much greater vertical distances. These values imply that the active flux by migrants may amount to about half that resulting from particle sedimentation.

Diel migrations are generally restricted to the upper kilometre of the water column (i.e., they involve exchanges between the epipelagic and the deep and shallow mesopelagic zones), but in the central oligotrophic gyres pelagic decapods (Domanski, 1986) and some myctophid fish migrate even deeper. The myctophid fish *Ceratoscopelus warmingeri* was found to be migrating to depths of 1600–1700 m in the region of the Azores Front (Angel, 1989b).

Ontogenetic migrations are carried out by species that change their depth ranges during their life cycles. Many deep-living species produce buoyant eggs, which float up to the surface so that the larvae hatch and feed in the euphotic zone. As they reach the stage when they are ready to metamorphose into the adult form they sink back down into deep water. Euphausiids of the genus *Euphausia* show the reverse pattern of development. They lay yolk-rich eggs that are heavier than water. These eggs sink to depths of 1000–2000 m, where they hatch into non-feeding larvae. These larvae begin the long swim back up towards the surface, their early development being fuelled by the yolk. As they near the surface their development has progressed to their first feeding stage as they exhaust their yolk supplies. Presumably this strategy ensures that the return of the high investment of resources in providing each egg with so much yolk is optimized by the larvae spending so much time at depths where predation is relatively low. A special example is seen in the copepod *Calanoides carinatus*, which abounds in newly upwelled water in coastal upwelling regions such as the Somali Current (Smith, 1984) and the Benguela Region (Verheye, 1991) (see pp. 67–68). Its ontogenetic migrations enable the species to stay within the cell of circulation associated with the upwelling, so that it seeds the newly upwelled water with larvae which can then exploit the phytoplankton bloom which follows an upwelling event.

Seasonal migrations are particularly common at high latitudes, where the season of high productivity is too brief for many of the species to be able to complete their life cycles within a year. In late summer/autumn they migrate down into deep water and overwinter, very often in a state of diapause during which the gut regresses and they do not feed. In spring they migrate back to the surface to mature, breed, and start the cycle again. In the North Atlantic, the dominant high-latitude large copepod species *Calanus finmarchicus* overwinters as a diapausing Stage v copepodite, at depths as deep as 2000 m, and it needs to complete a further instar before it matures and can breed. On the other hand, in the North Pacific, the dominant copepods belong to the genus *Neocalanus,* some of which diapause as Stage vi copepodites and mature as soon as they come out of diapause and return to the upper layers. There are also some smaller species which undergo an alternation of generations. Their growth rates are fast enough for them to have a short-lived summer generation, which is then followed by a longer-lived winter generation which spends several months in deep water. However, in terms of gross fluxes these seasonal migrations result in trivial transfers of organic material.

Diversity in pelagic communities

The diversity that one sees today is the result of a dynamic interaction between speciation, whereby the global inventory of species has evolved, and the subsequent dispersion of the species, and the currently prevailing environmental conditions which maintain the assemblages. Some knowledge of how ocean basins and their water masses developed over geological time is a basic need for understanding how the current composition of pelagic assemblages came into existence. Imprints of the circulation patterns in ancient oceans (Fig. 3.1) are still detectable in the zoogeographical distributions of some of the more ancient lineages. Superimposed on these patterns are the effects of one-off geophysical or vicariance events, such as the opening and closing of the Panama Isthmus, the Messinian salinity crisis in the Mediterranean, and to a lesser extent, the impacts of fluctuating sea levels during the glacial cycles. All these events led either to the creation or to the removal of land barriers to the dispersion of the species. If, as the result of such an event, a population of a species became fragmented into two or more isolated metapopulations, then over time each metapopulation will have tended to diverge as a result of genetic drift and adaptation to the local environmental conditions. In time they may have diverged sufficiently to have evolved into separate species. If these barriers are subsequently removed, once again restoring the potential for gene flow between the metapopulations, there are several possible outcomes. The simplest is if the extent of differentiation has been only slight, and the metapopulations remerge into being a single, albeit rather variable, species. However, if interbreeding is no longer possible because of either genetic or behavioural shifts, then the two types may directly compete with one another as they intermix. If one population proves to be competitively more successful throughout the total range, it may replace the other driving it to extinction. Alternatively if each population is competitively more successful in different areas or zones within the ranges, they may co-exist, partitioning the available resources (and habitats) either in time or in space, and emerging as distinct, albeit closely related species. This process appears to have been the way in which the richly diverse communities of inshore copepods found in the waters around the East Indies evolved. In this case, the succession of Quaternary glacial and inter-glacial eras resulted in sea-levels fluctuating by nearly 100 m, so that during the glacial episodes some of the deep basins became isolated, but were re-connected during the subsequent interglacial period (Fleminger, 1986). The seas around the East Indies are a hot spot for species richness in a wide range of shallow-living marine groups.

A similar process may currently be taking place in the Mediterranean, where during the last glaciation some temperate/boreal species gained access from the North Atlantic and have persisted as “glacial relicts”, although they are now experiencing very much warmer water temperatures particularly below 300 m. These stocks are now isolated from their parental stocks in the North Atlantic. The marked contrast between the environmental conditions inside the Mediterranean and outside in the North Atlantic will probably be imposing contrasting selective pressures. Thus, the relict populations of the euphausiid *Meganyctiphanes norvegica* and the myctophid fish *Benthosema glaciale* can be expected to have been diverging from their original genetic stocks and from the other isolated populations of these species which occur in the cool waters in the coastal upwelling region off Northwest Africa. Whether the period of 18 000 to 20 000 years that has elapsed since the end of the last glaciation has been long enough for them to have become separate species is yet to be examined. Studies on the biodiversity of pelagic marine communities have focused predominantly on the processes that are currently maintaining the community structure, rather than on those that led to their origins (White, 1994; Angel, 1997).

Speciation rates vary. An interesting trait that has emerged from the study of fossil molluscs is that taxa that are highly specialized speciate more readily, but are also more susceptible to extinction than more generalist, adaptable taxa (Taylor, 1997). However, the unchanging physical characteristics of the oceanic water column over evolutionary time appears to have favoured the evolution of those highly specialized organisms whose biology has become very finely tuned to conditions in the water column. In the absence of change, these specialized taxa appear to be able to out-compete new, less highly adapted, immigrants (Maynard Smith, 1989).

There are two distinct aspects to biodiversity, which are confusing and often confused. Moreover, both aspects give different values of diversity according to the time and spatial scales of sampling. The first and simplest aspect to understand is species richness. This is the number of species in an inventory, which of course varies from global, to regional, to local, and even between replicated samples. Estimating the numbers of species in an assemblage has to be based on sampling, but each individual sample contains only a subset (and often a small one) of the total inventory. Hence the larger the sample taken and the more samples, the more representative becomes the species list. Even so, the inventory of species for a region may only approach completion after several years of thorough and systematic sampling at all depths and at all seasons. Estimates of species richness are strongly influenced by the sampling methods and procedures, and also by chance events that may result in the exceptional occurrence of species in an area.

The second aspect of biodiversity is described as dominance or conversely evenness, and is dependent on the proportional representation of individuals of the component species in a community or sample. Populations dominated by many individuals of a very few species are considered to be of low diversity, whereas a population in which all the species are represented by similar numbers of individuals are considered to be of high diversity. A samples containing 100 specimens of two species divided 50:50 is considered to be richer than another also containing 100 specimens but with three species divided up 98:1:1.

Studies of diversity in pelagic communities have revealed some consistent trends related to depth and latitude. The number of pelagic species present in the total water column increases from high to low latitudes. The number of species present also increases to a maximum at a depth of around 1000 m (Fig. 3.8) and slowly declines at greater depths (Angel, 1997). The relatively species-poor pelagic assemblages that occur at high latitudes tend to be dominated by a very few species. As one moves towards lower latitudes the number of species increases but the dominance decreases (or alternatively the evenness increases). The same trend occurs with increasing depth, at least to a depth of 1000 m. However, these patterns run counter to the trends on productivity. Where productivity is higher – for example, where there is strong seasonality, upwelling or eutrophication – the assemblages become less species-rich and the dominance by a few species increases.

The latitudinal trends are exemplified by data from collections of copepods from 44ºN, 13ºW (Roe, 1984), from the Western Mediterranean (Scotto di Carlo et al., 1991) and from the Canary Islands (Roe, 1972) (Fig. 3.9). The sampling procedures were not the same, so that the results are not strictly comparable; but the differences in the results are striking. They also serve to highlight another general characteristic of pelagic assemblages – namely, that they contain large numbers of infrequent and apparently rare species. However, rarity in such samples may arise for a number of reasons:

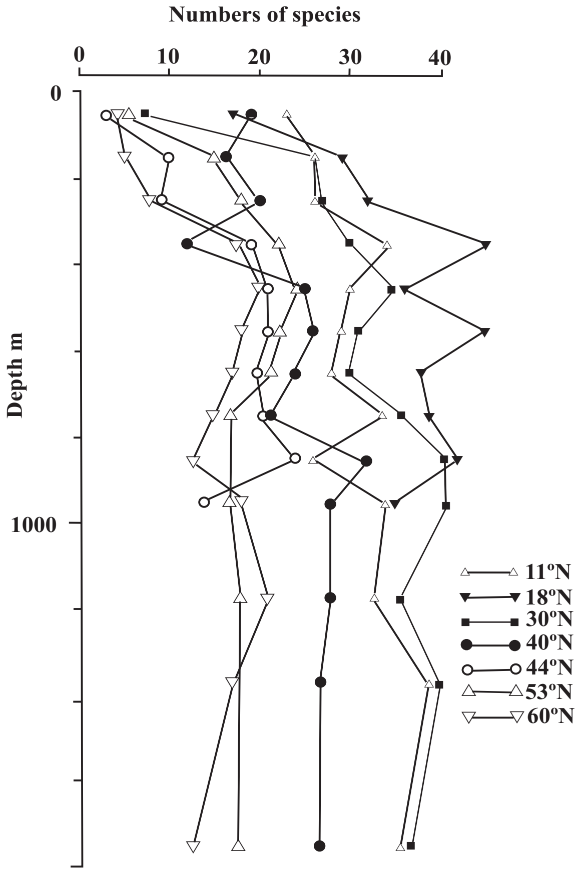

Fig. 3.8. Profiles of the numbers of planktonic ostracod species throughout the surface 2000 m along 20ºW in the N.E. Atlantic, showing how at latitudes lower than 40ºN there are more species at all depths than at higher latitudes. The change in average species richness appears to occur at the southern boundary of seasonal turnover in the near-surface waters and the regions where there is a springtime peak in phytoplankton production (Angel, 1997).

(1) The sampling range may not have extended over the normal range of that particular species, so the specimens caught were outliers.
(2) The mesh size may be too large to retain most specimens.
(3) The species may normally be active enough to avoid the sampler in use.
(4) The analysts may have overlooked many of the specimens, especially those species that are either very fragile or very similar to other abundant species.
(5) At the time of sampling most specimens of the species may have been at a life-history stage that was either not sampled or unidentifiable.

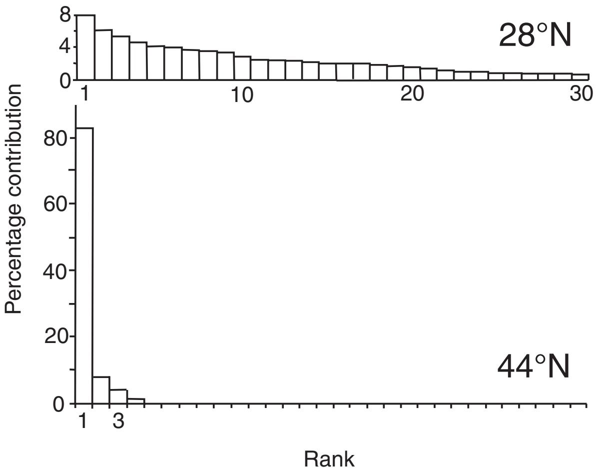

Fig. 3.9. Relative abundances of the 30 most abundant copepod species in multiple samples collected from the Canary Islands (Roe, 1972) and 44ºN, 13ºW (Roe, 1984). Note that at this scale only four of the species at 44ºN, 13ºW provided >1% of the total number sampled and so the other data points do not show up.

Table 3.4A

Copepod species and their relative abundances at two stations in the north-east Atlantic and in the Mediterranean. Numbers of species contributing given percentages of the total sample in a combined data set from four sampling depths[1] at 44ºN 13ºW

Range of % contribution of individual species to total sample	Number of species	% contribution of category to the total population
>1%	3	95.0%
<1 to >0.1%	15	4.1%
<0.1 to >0.01%	26	0.79%
<0.01 to >0.001%	35	0.12%
<0.001%	27	0.01%

[1] 100, 250, 450 and 600 m; the total number of specimens identified was 520 115 and the total number of species was 106 (Roe, 1984).

(6) The patchiness of pelagic distributions may have led by chance to the species being under-represented in the samples.
(7) These may be expatriate species carried in by currents from far beyond their normal distributional ranges.
(8) Finally, the species may indeed be rare.

Scotto di Carlo's Mediterranean data also illustrate how the composition of the assemblages can change substantially with season. Seasonality is usually more pronounced at higher latitudes, but it also occurs in some subtropical and tropical areas, notably in the Northwest Indian Ocean where the reversal of the monsoon winds results in major readjustments to the large-scale circulation and seasonal upwelling (Tables 3.4 A,B,C).

In benthic ecosystems, species richness is often estimated from rarefaction curves and generally attains a maximum at depths of 2–3 km (Rex, 1983; see also Chapter 10), although both the actual numbers of species and of specimens observed decline at depths below 1–2 km. For example, data for benthic polychaetes in the Rockall Trough reported by Paterson and Lambshead (1995) showed that there were 80 species present at a mean total population density of 1828 individuals m^{-2} at 1000 m, compared with 44 species at a mean total density of 960 individuals m^{-2} at 2875 m depth. Paterson and Lambshead concluded, based on the rarefaction curves, that maximum polychaete diversity occurred at depths of >2000 m (see Chapter 10). Analysis of repeated samples of macroplankton at 1000 m at 44ºN 13ºW showed, for several of the groups analysed, that there was a steady exponential increase in the numbers of species caught as the sampling effort increased (Angel et al., 1982). However, in several of the groups the total number of species known from the region had been collected and no further additions to the species lists were to be expected. For the planktonic ostracods, all the known species from the region had been collected once 10^5 specimens had been collected, and no further species were found despite further sampling effort increasing the numbers of specimens to over 15×10^5 (Angel, 1984). This casts considerable doubt on the effectiveness of the rarefaction method for estimating the size of the total inventory of species in an assemblage. In the pelagic environment there must be a minimum abundance that must be exceeded if a species is to be able to survive, otherwise sexual reproduction would not be possible. Even for phytoplankton different assumptions about the scaling of species ranges and distributions have been used to estimate global diversity of phytoplankton species to be about 5000 (Tett and Barton, 1995). The application of rarefaction to estimations of total species richness assumes that spatial and temporal scaling of species ranges and distributions is consistent; this is certainly not the case in pelagic environments.

Another factor that may be influencing the biogeography of deeper-living species, and hence the composition of the communities, is that some of the deeper-living benthic species have longevities

Table 3.4B
Copepod species and their relative abundances at two stations in the north-east Atlantic and in the Mediterranean. Numbers of species contributing given percentages of the total sample in seasonal samples collected in the Bay of Naples (Scotto di Carlo et al., 1991)

Month	Total numbers	Total species	>10%	<10 to 1%	<1 to 0.1%	<0.1 to 0.01%	<0.01%
February	15 065	102	1	26	32	19	24
April	19 860	103	0	28	39	19	17
May	14 395	98	1	27	27	32	12
June-1	22 084	101	2	22	36	33	18
June-2	22 036	96	1	25	34	28	8
July-1	11 915	98	1	27	36	29	5
July-2	11 635	97	2	26	36	23	10
October	22 123	115	0	29	33	27	26
TOTAL	139 113	140	0	31	33	39	37

Table 3.4C
Copepod species and their relative abundances at two stations in the north-east Atlantic and in the Mediterranean. Numbers of species contributing given percentages of the total sample in samples collected off Fuerteventura I, Canary Islands (Roe, 1972); the percentage of the total sample contributed by each group of species is also indicated

	Total number	Total species	>1%	<1 to 0.1%	<0.1 to 0.01%	<0.01%
Day	109 808	205	26 (76.9%)	52 (19.5%)	82 (3.3%)	45 (0.23%)
Night	69 840	176	25 (72.3%)	57 (24.3%)	67 (3.1%)	27 (0.29%)
Total	179 648	223	24	58	80	61

in excess of a hundred years. Thus, within ten to twenty generations such a long-lived species can be dispersed throughout all oceans, especially in the deep oceans where environmental boundaries are almost non-existent and the ranges of variation for abiotic parameters are very limited. For example, the bathyal fish, *Hoplostethus atlanticus*, lives for 70–140–years (Smith et al., 1995) and it has been suggested that there is significant gene-flow between populations in the North Atlantic and off South Australia (see above). The ages of deep-living species have only been estimated for a few commercial fishes, so one cannot be certain whether or not these considerable longevities are characteristic of deep-living pelagic species. But if they are, then in the absence of major barriers to lateral dispersion in the deep ocean, and rates of advection being rapid relative to the generation times of many species, many deep-living pelagic species may well prove to have ranges that are cosmopolitan. However, Palumbi (1992) has pointed out that, theoretically, speciation may occur in wide-ranging species if rates of dispersion are slow. Thus, it remains unresolved as to whether apparently cosmopolitan abyssopelagic species, such as the planktonic ostracods *Archiconchoecia simula* and *Proceroecia vitjazi* recorded from the Southern Ocean, the North-east Pacific and the North-east Atlantic (Angel, 1993), are indeed single species, or are complexes of cryptic species which cannot be distinguished on the basis of their morphology. Molecular biological techniques now provide the means to establish whether gene flow is indeed occurring throughout their full range.

THE ECOLOGICAL ROLE OF OCEAN CIRCULATION

Large-scale features

The large-scale ocean circulation is driven by latitudinal variations in heating and cooling by solar radiation, the balance between inputs of fresh water by rainfall and by rivers, losses by evaporation, the transfer of frictional energy across the ocean surface by winds, and planetary forcing, particularly that resulting from the rotation of the Earth. The pattern

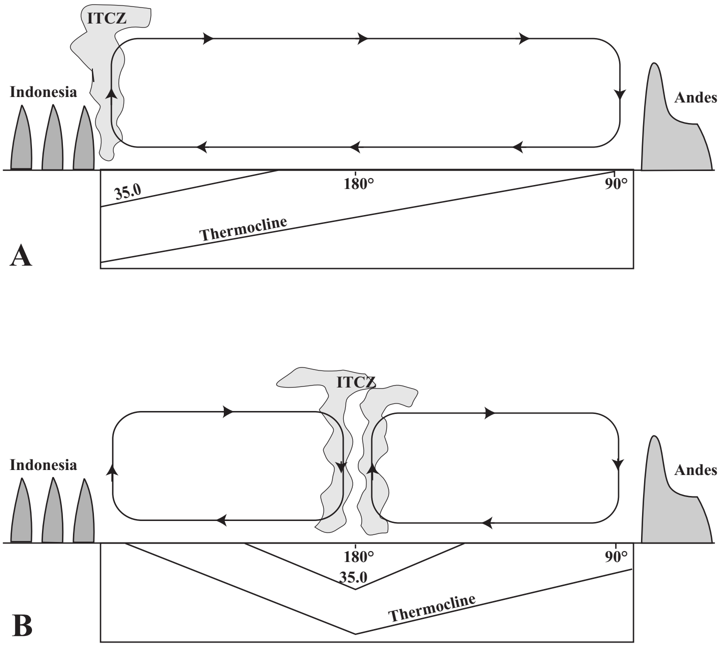

Fig. 3.10. Cartoon illustrating how shifts in the position of the Intertropical Convergence Zone (ITCZ) between the Western and Central Pacific, by tilting and depressing the thermocline, and, through locally lowering surface salinity via the effects of the heavy rainfall associated with the ITCZ, play a major role in ENSO events in the Pacific. (A) shows the usual position of the ITCZ off Indonesia, with the thermocline and the depth of the 35 isotherm tilting up towards the east. This means that the thermocline outcrops near the coast of South America, so that sea surface temperatures are cool and any upwelling brings nutrient-rich waters to the surface. (B) shows what happens when the ITCZ shifts eastwards towards the dateline at 180º longitude, as occurs during ENSO events. The depths of the thermocline and the 35 isohaline become shallower in mid-ocean, but deeper off both Indonesia and South America at 90ºW. Off South America, sea surface temperatures become anomalously warm and there is heavy rainfall and flooding in many regions. Upwelling still occurs, but the water that comes to the surface comes from above the thermocline and so is relatively warm and devoid of nutrients. Adapted from Donguy (1994).

of trade winds that drive many of the surface flows are determined by the development of Hadley cells in the atmosphere and the development of polar high pressure systems, and the influence of the Intertropical Convergence Zones (ITCZ). Longitudinal instabilities in the ITCZ in the Western Pacific (Fig. 3.10) play an important role in the generation of El Niño Southern Oscillation (ENSO) events (Donguy, 1994). These cause substantial fluctuations in sea-surface temperatures, ocean productivity and weather patterns, which are transmitted via planetary waves eastwards along the equator and then polewards along the western margins of the continents. Under normal conditions the trade winds generate major gyral circulation features bounded by major frontal systems, such as the polar fronts and the subtropical convergences. These fronts not only coincide with the boundaries of water masses, but are also major biogeographical boundaries for pelagic communities (Fig. 3.11). However, relatively few species have geographical ranges that are exactly confined within these fronts. Changes in environmental conditions across the fronts are subtle in comparison with the physiological tolerances of the individual species, so that many species can survive being advected across them, albeit with reduced viability.

Smaller-scale features

At smaller scales (10–100 km) the major source of variability in the pelagic ecosystem are mesoscale eddies and rings. The subsurface temperatures in the centres of the eddies may either be cooler (cold core) or warmer (warm core) than the general surroundings (Joyce and Wiebe, 1992). Eddies of these scales are commonplace throughout the ocean, and are akin to the weather systems in the atmosphere. However, a cyclonic feature in the atmosphere typically has a diameter of *c.* 1000 km, and a height of 10 km, whereas oceanic eddies are smaller, being 10–200 km across and 5 km deep. However, seawater is a much denser medium, so, although they are smaller, ocean eddies

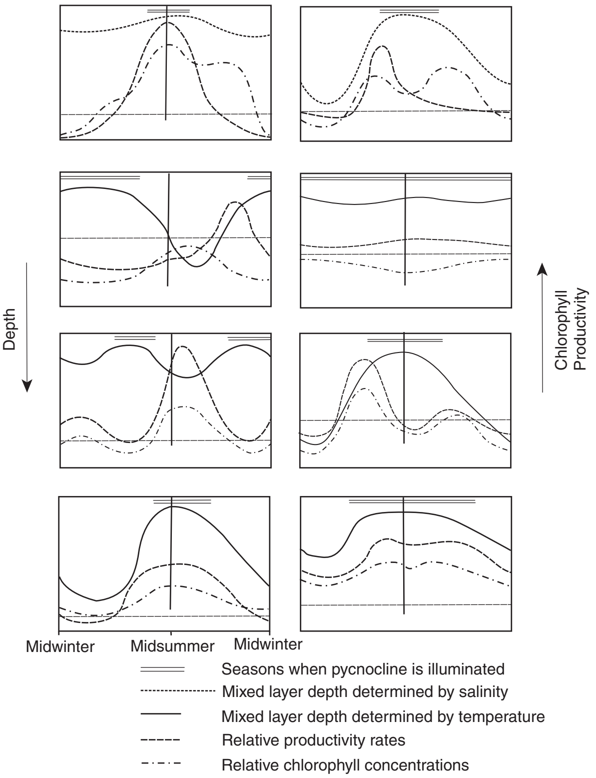

Fig. 3.11. Schematic illustrations of the general features of eight basic types of annual production cycle identified by Longhurst (1995). The relative depth below the surface (the upper line of each cartoon) of the mixed layer is determined either by temperature (t) or salinity (d). Fluctuations in relative chlorophyll concentrations (c) and rates of primary productivity (p) are shown (with zero being the base of each cartoon) about the time of midsummer (the vertical line). The seasons when the pycnocline is illuminated are indicated by the double horizontal lines. The relative proportion of the annual production that occurs above and within the deep chlorophyll maximum is indicated by the dashed line. Redrawn from Longhurst (1995).

contain about thousand times more dynamic energy than their atmospheric counterparts. Moreover, some persist for up to 1–2 years, compared with the week or so that most atmospheric eddies last.

Mesoscale eddies can often be seen clearly in satellite images of sea-surface temperature and ocean colour. They also show up in altimeter data, since sea level in the centres of cold-core eddies is lower, and in the centres of warm-core eddies higher than the surroundings. The most striking images come from the regions of the eastern boundary current, for example, along the margins of the Gulf Stream. Here meanders often pinch off to form ring structures. Along its in-shore margin, anticyclonic warm-core rings are formed which have a core of warm Sargasso Sea water wrapped around with a belt of cooler Gulf Stream water, and they move across the shelf where they are surrounded by even cooler Shelf Water (Joyce and Wiebe, 1992). Conversely, along the off-shore boundary, cold-core cyclonic rings are formed with a central core of relatively cold Shelf Water wrapped around by Gulf Stream Water, which move through the even warmer Sargasso Sea water. The eddies themselves move at speeds of 5–10 km d^{-1}, but their internal currents are up to ten times faster, reaching speeds in excess of 1 m s^{-1}. A meandering jet current surrounds each ring. In the Northern Hemisphere, where the jet is turning clockwise, potential vorticity results in there being a local divergence (i.e., upwelling), and where it is turning anticlockwise there is a local convergence (i.e., downwelling). These localized effects influence nutrient supplies, locally enhancing primary production where there is upwelling, and depressing it where there is downwelling. The resultant patchiness in primary production and phytoplankton standing crop influences the zooplankton and its consumers. However, these physical features are ephemeral, and the shears within the water column in the longer term smooth out much of this variability. However, if these features are large enough to persist for several days, vertically migrating species of zooplankton tend to accumulate within the patches of higher productivity. Such accumulation may be a passive result of the range of their migrations being influenced by light intensities. Where the quantities of suspended particles are high, light penetration is reduced which reduces the depth to which migrants move. This reduces the lateral current shears they experience between their upper and lower depth ranges, so that the following evening they tend to return to the surface much closer to where they left it the previous dawn. This creates a "passive" mechanism for migrants that have encountered a productive patch to stay with it, while others from outside it tend to move in (Isaacs et al., 1974). Fish and squids, which have the capability of swimming many kilometres horizontally, also accumulate in localized production hot spots and so may have foraging strategies that enable them to locate the hot spots. Their accumulations in turn attract higher predators, sea birds and cetaceans. Thus biomass distributions are patchy as a result of reproductive responses to the locally enhanced nutrients stimulating growth and reproduction in phytoplankton and microbial grazers, and by behavioural responses of the more mobile taxa.

The fate of species which are entrapped within an eddy as it forms along a front is largely determined by their vertical migratory behaviour. The species that are non-migratory are passively advected within the eddy and so tend to persist within it. Those that are advected into adverse conditions show signs of malnourishment and physiological stress as the ambient conditions deteriorate (Wiebe and Boyd, 1978). Species with diel vertical migration initially entrapped in the newly formed eddy tend to get spun out of it relatively quickly, as they traverse differential shears within the water column during their vertical excursions. Thus, within rings and eddies, the assemblages of species change more rapidly than might otherwise be expected. This generates chaotic heterogeneity in the distributions of pelagic species with fractal characteristics similar to that of the eddy structure of the water. Behavioural, feeding and reproductive strategies in pelagic species can be expected to be adapted to this heterogeneity in the biotic and abiotic environment. The effects of mesoscale features are transmitted to deep-sea environments. Many eddies extend all the way from the surface to the bottom and are one mechanism whereby "benthic storms" are generated in deep water (Weatherly and Kelley, 1985; Kontar and Sokov, 1994). They may also transport the planktonic species and the pelagic larvae of benthic species far beyond the bounds of their normal distributional ranges, as has been observed for planktonic foraminifers (Fairbanks et al., 1980).

Other features that generate heterogeneity within pelagic environments include:

(1) "Streamers", which are tongues of cold water that can be seen in satellite images extending >100 km offshore from upwelling regions (e.g., Mittelstaedt, 1991).

(2) Shelf-break fronts, which develop as a result of internal waves breaking beneath the surface, enabling vertical mixing to take place (e.g., New and Pingree, 1990).

(3) The influence of seamounts often results in local enhancement of primary production downstream, so that secondary and tertiary producers also accumulate in their vicinity (Haury et al., 2000). Currents flowing over seamounts are accelerated and destabilized by the shoaling topography, the so-called "Taylor column" effect, so that eddies and internal waves are developed downstream (Nof, 1985). Taylor column effects can extend 1000 m or so above the top of a seabed feature, so that even quite deep features can induce perturbations of the wind-mixed layer. There is enhancement of both primary and secondary production around seamounts, so that they are frequently utilized as sites for the aggregation and spawning of oceanic species, and also for colonization by suspension-feeding benthos.

UPWELLING

At latitudes >40° the main mechanism re-supplying nutrients to the euphotic zone is the seasonal mixing that occurs when winter cooling breaks down the stratification. But, in the subtropics and tropics where the seasonal thermocline persists throughout the year, the re-supply of nutrients via vertical mixing is limited except where there is upwelling. As discussed above, localized upwelling occurs along divergent fronts around eddies and along some of the major oceanographic features. Much more significant upwelling occurs in eastern boundary coastal regions, where trade winds blow along the coast towards the equator. The effects of Coriolis Force (a turning force generated away from the equator by the rotation of the Earth) result in the winds pushing the surface water offshore; it is then replaced by cool, nutrient-rich water from below the thermocline. There are five main areas where upwelling occurs: off California, off Chile and Peru, off Northwest and South-west Africa, and in the Arabian and Somali Seas. Coastal upwelling tends to be an episodic rather than a continuous process, and is linked to periods of windy weather. Moreover, the winds that favour upwelling tend to blow more strongly and more frequently during specific seasons (Summerhayes et al., 1995a). High productivity is stimulated by the nutrient-rich subthermocline waters being drawn up to the surface. These upwelling regions are important centres for fisheries. Upwelling also occurs in the open ocean, notably along the equator in the Central and Eastern Pacific, and in the Eastern Atlantic. The winds on either side of the equator blow divergently away from it, so that upwelling occurs along a narrow band close to the equator. In the Arabian Sea upwelling also occurs well off-shore – again as a result of wind divergence generated by the Findlater jet (a region where the wind curl reverses).

In upwelling regions, standing crops of zooplankton are very high, but are dominated by a very few species which have life histories specially adapted to take maximum advantage of the upwelling events. One of the dominant species common to many upwelling areas is the copepod *Calanoides carinatus*. Its life history involves extensive ontogenetic migrations into deep water, whereby it pre-seeds with its progeny bodies of water that may ultimately be upwelled. Thus it is able to take the fullest advantage of the ensuing bloom of phytoplankton (Smith, 1984; Verheye, 1991). In the Benguela Current region there are two euphausiid species (*Euphausia hanseni* and *Nyctiphanes capensis*) that also have life cycles that serve to maintain the populations within the circulation cells involved in the upwelling (Barange and Pillar, 1992). The peaks in productivity resulting from the seasonality of the upwelling events have an influence similar to that of the seasonal cycles at temperate and subpolar latitudes. There is a pulsing in the export of organic matter to the neighbouring deep ocean, which, in turn, generates seasonality in the deep communities.

There are marked differences in productivity between the various upwelling regions. These arise because of differences in the nutrient concentrations of the various water masses that are being upwelled. For example, the water that upwells off California comes from much the same subthermocline depths (*c.* 150 m) as the water that upwells off Northwest Africa, but it stimulates much higher productivity. Even within the Northwest African upwelling region there are marked differences in productivity to the north and south of Cap Blanc. To the south the water upwelled is South Atlantic Central Water, which is “older” and richer in nutrients than the North Atlantic Central Water upwelled to the north of the Cape (Gardner, 1977).

Another feature of upwelling regions is that the concentrations of dissolved oxygen in the subthermocline water tend to be lower than normal. This is because microbial degradation of the copious quantities of organic matter sedimenting from the surface uses up much of it. Generally there is an oxygen minimum at the permanent thermocline, at a depth of about 1000 m where the waters are the “oldest”. In the Atlantic, dissolved oxygen concentrations in the oxygen minimum are mostly in excess of $2\,\mathrm{ml}\,\ell^{-1}$, and do not restrict the ranges of pelagic species. Beneath some of the upwelling regions, however, the inputs of organic matter can be large enough for all the dissolved oxygen available in the water to be used up. A severe oxygen minimum occurs seasonally in the Arabian Sea (e.g., Herring et al., 1998) and in the Benguela Current region. Oxygen concentrations fall so low that aerobic respiration is inhibited; to survive there the organisms either have to rely on anaerobic respiration, or to use alternative sources of oxygen. One source is by reducing sulphate ions to sulphide. Sulphides not only smell of bad eggs but are also highly toxic, and if sulphide-rich water is upwelled it can cause mass mortalities of fish and marine invertebrates. In the Arabian Sea a strong oxygen minimum develops seasonally as a response to the upwelling induced by the south-west monsoon at a time when the standing crop of organisms in the water column is correspondingly high. Many of the pelagic species inhabiting the sea area become restricted to the upper 70–100 m. A notable example is the swimming crab *Charybdis smithii*, which swarms at the surface at night. During the day it stays within the well-oxygenated water of the wind-mixed layer, where it is more vulnerable to predation by tuna, although elsewhere and in other seasons it migrates down to daytime depths of 200–300 m (Van Couwelaar et al., 1997). Other diel migrants, including several species of fish, decapods and euphausiids, are able to tolerate the low oxygen conditions and migrate down to spend the day deep within the oxygen minimum, possibly taking refuge from their usual array of predators (Herring et al., 1998).

BIOPHYSICS AND OCEANIC FOOD-WEBS

In shallow seas where the seabed is illuminated and the substratum is stable fixed plants can grow; a substantial proportion of the primary production is then produced by macroalgae and a small range of higher plants such as mangroves and sea-grasses. The relatively large size and/or high concentration of plant biomass enable many of the grazers and browsers similarly to be large in size; even some quite sizeable fish are herbivorous. Additionally, the large plants provide three-dimensional microhabitats, analogous in structure to forest environments on land. Variations in the local geology and differences in exposure to waves and currents, suspended sediments, and differing tidal regimes and run-off from land, create many fine-scaled habitat mosaics in the littoral and sublittoral zones, each of which supports distinctive assemblages of species and subcommunities. Similarly in shallow tropical waters, corals containing symbiotic photosynthetic algae also create highly complex 3-dimensional fine-scaled microhabitats, which support a high diversity of species.

Offshore, where it is too deep for enough sunlight to reach the seabed to fuel photosynthesis, phytoplankton suspended in the near-surface waters is solely responsible for primary production [apart from the estimated 0.03% produced by chemosynthesis at hydrothermal vents (Chapter 4)]. Phytoplankton cells are small and their turnover is rapid, so that the standing crop of plant biomass is small and dilute. Moreover, it has been estimated that the total global flora of oceanic pelagic primary producers consists of only about 5000 species (Tett and Barton, 1995) in the oceans, a very low species richness compared with the estimate of 250 000 species of green plant on land. Bearing in mind that a single tree, the sessile oak *Quercus robur,* has about 600 species of insects associated with it in the United Kingdom, the low diversity of phytoplankton is likely to be reflected in an equally low diversity of herbivores. Moreover, oceanic herbivores are either suspension-feeders or individual particle feeders; hence they too are functionally constrained to being much smaller than most terrestrial herbivores. Most are small zooplankton, the only exceptions being found in those regions (or seasons) where large diatoms, which can be sieved mechanically out of suspension, are the dominant primary producers. Thus, in the upwelling region off Peru/Chile, the dominant fish, the anchovetta (*Engraulis ringens*) is able to sieve large diatoms directly on to its gill rakers. Even so, in the North Pacific the abundant populations of large copepods, formerly thought to be herbivores, have now been shown to be detritivores and do not feed directly on phytoplankton (Dagg, 1993). In oligotrophic regions, 50 to 80% of primary production is produced by picoplankton – cells <2μm in diameter. The majority of the animals that compose the microbial loop and are able to consume these tiny cells (mostly ciliates) need to be just as small – too small to generate particles that will sediment under the influence of gravity. Hence very little of the organic production that flows through the microbial food web is exported to deep water, most being recycled within the euphotic zone.

Another trend is for food webs to be more complex, particularly at low latitudes, and for the component chains to be longer. Thus, a greater proportion of carbon is recycled before it reaches the end-consumers. Also, although the aqueous medium gives much greater physical support, which makes it possible for marine animals to reach much larger body sizes – one may compare the size of the blue whale with that of an elephant – the mean individual biomass of metazoa in the ocean is considerably smaller. Smaller animals have much shorter generation times, so that the ocean ecosystems cycle energy and material at a faster rate than most terrestrial ecosystems.

In addition, most of the organic matter that is synthesized by the autotrophs is removed very rapidly by grazing and microbial degradation. This not only keeps the standing stocks of grazers and detritivores at much lower levels, but it also means that seldom is there any build-up of large accumulations of organic matter, as occurs in freshwater wetlands and forests.

Elton (1935), a terrestrial ecologist, argued that there are global principles governing the functioning of ecosystems. He claimed that body size is a fundamental characteristic – “Animals form food chains in which the species become progressively larger in size or, in the case of parasites, smaller in size. A little consideration will show that size is the main reason underlying the existence of these food chains .... We have very little information as to the exact relative sizes of enemies and prey, but future work will no doubt show that the relation is fairly regular throughout all animal communities”. The size spectra and spatial distribution of primary producers in open-ocean ecosystems are strikingly different from those in terrestrial and even most shallow-water ecosystems. Standing crops of plants are quite often much smaller than the annual primary production. Turnover rates are high and residence times of organic carbon in oceanic biomass are much shorter, being about 0.08 years compared with 11.2 years in terrestrial ecosystems (Harte, 1988) – a 140-fold difference, which is large enough to be real, even if the data are imprecise.

The small size and unpredictable occurrence of phytoplankton in the oceans appears to have inhibited the evolution of the sorts of specific associations between animal and plant species that are such a notable feature of terrestrial ecosystems. Away from shallow coastal waters, plants are seldom large enough to provide a physical substratum for the herbivores, *Sargassum* weed being the obvious exception. In addition, autotrophs are almost entirely restricted to the upper sunlit depths, which constitute a very small fraction (*c.* 2.5%) of the total living space within the oceans. This not only limits the distributional ranges of herbivorous grazers to the upper waters but also, because their food is so tiny, most grazers are constrained physiologically to being quite small in size. Animals of small size have limited ability to regulate their vertical ranges. Even those which are large enough

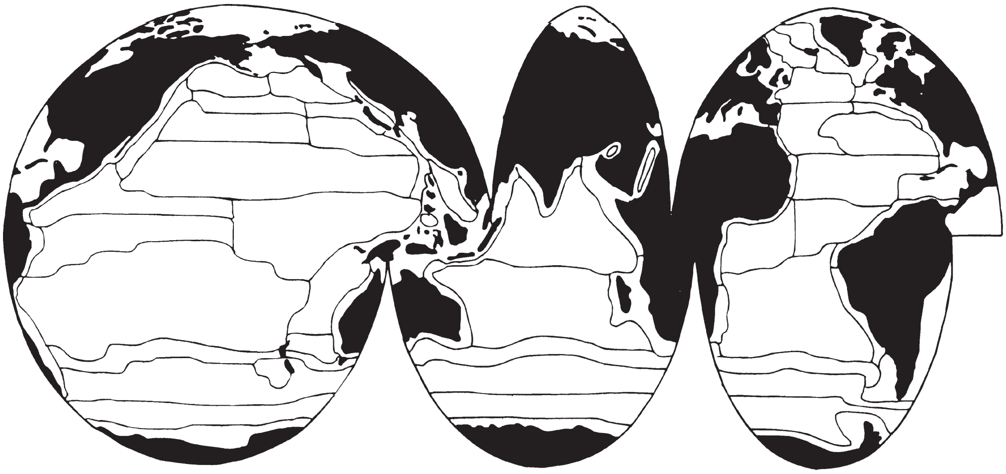

Fig. 3.12. The distribution of the biogeochemical subdomains based on the productivity cycles illustrated in Fig. 3.11 and the approximate climatological positions of major oceanographic discontinuities identified from a combination of remotely-sensed and hydrographic data. These correlate closely with classical biogeographical provinces identified in each ocean, suggesting that these large-scale distribution patterns are determined by bottom-up processes. There are indications that these domains are also mirrored in the deep benthic communities. Redrawn from Longhurst (1995).

to be capable of diel vertical migration are still limited to as little as 10–15% of the total ocean volume. Herbivores are absent from most oceanic volume, and so detritivory is the basis for food chains in most deep-ocean scenarios. Thus, unlike the Eltonian concept, Platt et al. (1981) found that oceanic food webs can be modelled more closely on the basis of size spectra than on functional relationships.

These characteristics of ocean food webs also mean that there are few opportunities for specialization, and this may account for the low global species richness of open ocean fishes; certainly relative to freshwater species. A single river system in Africa, the Zaire, is inhabited by >690 species, 84% of which are endemic. In Lake Malawi there are >600 fish species of which 96% are endemic, and 92.5% belong to a single family, the cichlids (Ribbink, 1994). Together these two freshwater systems host nearly as many fish species as are found throughout the whole of the North Atlantic.

PATTERNS OF PRODUCTIVITY AND BIOGEOGRAPHY

In the open ocean the annual quantity and seasonal cycling of primary production is determined by vertical stratification, the light cycle and the persistence of nutrient supplies. Longhurst (1995) has used remotely sensed climatological data for chlorophyll (derived from the Coastal Zone Color Scanner) and sea surface temperature data (from the satellite Nimbus 7) in combination with climatological data for mixed-layer depths and nutrient concentrations (Levitus et al., 1993) to identify three basic production domains in the open ocean – polar, temperate and tropical. Each of these domains has a fundamentally different seasonal cycle of water column stability, nutrient supply and illumination. Coastal (shelf) waters provide a fourth domain, which is subdivided into a mosaic of very much smaller-scale regions. Longhurst also identified eight basic types of production cycle (Fig. 3.11), which sub-divides the three basic domains into 56 biogeographical provinces. The provinces are bounded by recurrent physical features – fronts bounding ocean currents, topographic features and sea-surface chlorophyll distributions (Fig. 3.12). Many of the boundaries to Longhurst's provinces coincide with the biogeographical patterns described in classical studies of biodiversity and species distributions (e.g., Backus, 1986); the inference is that the zoogeographical patterns are probably determined by the production cycles and hence the prevailing biogeochemical environmental conditions (e.g., Angel, 1993).

Within each province the structure of pelagic food webs and communities appears to be relatively consistent. The quantities and dynamics of export production (i.e., the amounts of organic carbon that are exported from the euphotic zone into the deep ocean) are also likely to be directly influenced by the production cycles and the pelagic community structure. Similarly the differing seasonal patterns of input of organic carbon to the bottom-living communities will influence their structure and dynamics. There is initial evidence of there being some coherence between Longhurst's provinces and the zoogeographical distributions of benthic abyssal species (Sokolova, 1990; Rex et al.,1993).

Merrett (1987) had already suggested that benthic abyssal fishes show a clear faunal boundary in species richness and dominance at around 40ºN in the Northeastern Atlantic – a boundary that is coincident with the change from a domain in which there are markedly-pulsed seasonal inputs to the subtropical/tropical domain in which the sedimentary inputs are far less variable. At temperate latitudes, sediment trap records show that the sedimentary fluxes vary by over two orders of magnitude (Wefer, 1989; Fig. 3.13) and there is heavy seasonal deposition of phytodetritus on the sea-floor (Billett et al., 1983; Rice et al., 1994). Deposition of phytodetritus has also been observed beneath the high-productivity zone along the equator in the Pacific (Smith et al., 1996). At lower latitudes, such as the area off Bermuda (e.g., Deuser, 1987), the sediment trap fluxes vary by about an order of magnitude throughout the year and there have been no reports of deposition of phytodetritus. Lampitt and Antia (1997) have recently analysed all the published data on fluxes normalized to a depth of 2000 m from 67 long-term sediment-trap records. Several of their conclusions are unexpected. Organic carbon fluxes at depths of 2000 m ranged just over an order of magnitude, from 0.38 to 4.2 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ in most oceanic areas, but the range was greater in polar seas (0.01–5.9 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$). Where fluxes were most variable throughout the year, a greater proportion of primary production was being exported. Where primary production less than 200 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ there is a positive correlation between productivity and organic carbon fluxes at 2000 m. But unexpectedly further increases in productivity did not result in any further increases in fluxes. The relationship between production and flux follows a hyperbolic tangential curve, and reaches a maximum flux of *c.* 3.5 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. Once export production attained this maximum, there was no evidence of the deep fluxes being affected by further increases in primary production. Thus, the ratio between export production, as measured by sediment traps, and total productivity declines as primary production increases beyond 200 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. In correlating flux patterns with Longhurst's (1995) eight planktonic climatological categories, Lampitt and Antia (1997) found that each province has a characteristic level of flux variability throughout the year; the greatest range of variation is in the Antarctic and the lowest in the tropics. Only fluxes of inorganic carbon showed any clear latitudinal trend, with the inorganic fluxes reaching 2 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ in equatorial regions, four times the inorganic carbon fluxes at high latitudes. None of the other fluxes they analysed – dry mass, organic carbon and silicate (opal) – showed any latitudinal trends. There was a trend for an increase in depth to smooth the variability of the fluxes.

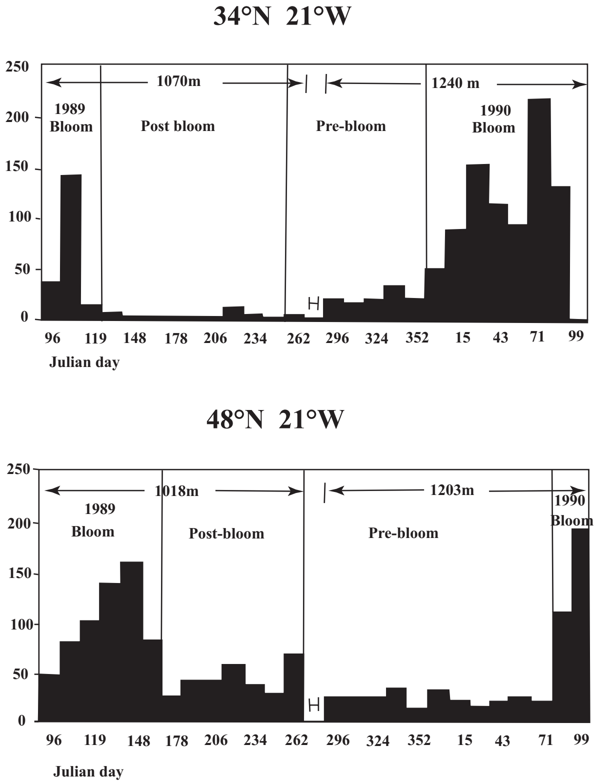

Fig. 3.13. Seasonality of sedimentary fluxes measured in sediment traps at Northeast Atlantic stations at depths of *c.* 1 km at 34ºN 21ºW (upper) and 48ºN 21ºW (lower) in 1989–1990. Modified from Honjo and Manganini (1993).

It seems hard to reconcile some of these observations with other reports. For example the relationship between deep-living pelagic biomass and primary productivity does not show a similar tangential hyperbolic relationship; instead, deep biomass continues to increase with increasing primary productivity. Lampitt and Antia (1997) pointed out that there are clear differences between benthic environments with differing benthic fluxes and with different intra-annual fluctuations. Over the Porcupine Abyssal Plain, in some years the sediments become blanketed seasonally by a cover of phytodetritus within a relatively few days of the onset of the Spring Bloom. In this area the benthic communities are dominated by sediment feeders, which create considerable bioturbation of the sediment interface. In contrast, only 16° further south on the sediments of the Madeiran Abyssal Plain where no seasonal deposition of phytodetritus has been observed, there is little modification of the sediment interface by bioturbation and there is a notable absence of benthic megafauna (Lampitt, 1985; Rice et al., 1994). Thus, there is a very direct link between the processes and community structure of deep-sea benthic environments and the processes occurring in the overlying water column.

Lampitt and Antia (1997) identified three potential reasons why fluxes may not increase in line with high levels of primary production:

(1) Increases in primary production above 200 g C m^{-2} y^{-1} result from an increasing dependence on regenerated nutrients, and hence the f-ratio decreases with increasing production.

(2) The degradation of particles proceeds faster within the upper 2000 m when the levels of flux are higher – that is: the higher productivity promotes larger mesopelagic populations. But why are these populations more efficient in their assimilation?

(3) Horizontal advection prevents the sedimenting material from reaching depths of 2000 m.

Other possible explanations are based on the methodology: for example, sediment traps may not measure all components of the fluxes. Significant fluxes may occur in the form of dissolved organic matter (DOM) carried into deeper water by downwelling and deep-water formation. Extra large particles that are not intercepted by the traps may make proportionately larger contributions to the total flux. There are empirical relationships between primary productivity and the organic content of sediments used as palaeo-indicators (Summerhayes et al., 1995b), and such relationships imply that organic fluxes continue to increase with increasing productivity. Populations of benthopelagic scavengers attracted to baited cameras and traps are known to consume large food packages, and tend to increase below highly productive regions (Thurston, 1990); since the mean size of pelagic populations tends to increase between low, temperate and subpolar latitudes (Angel, 1997), fluxes of large packages may increase with increasing primary production. This may also contribute to the discrepancies between the flux estimates produced by Jahnke (1996) based on sediment oxygen consumption and those of Lampitt and Antia (1997) based on sediment trap fluxes extrapolated to total ocean areas. These two studies were in reasonable agreement for the Atlantic (0.126 and 0.100 Gt C_{org} y^{-1}, respectively), but quite disparate for the Pacific (0.214 and 0.110 Gt C_{org} y^{-1}, respectively) and even more so for the Indian Ocean (0.142 and 0.012 Gt C_{org} y^{-1}, respectively; Gt = Gigatonnes), although riverine inputs may also be contributing to the sediment metabolism.

PHYSIOLOGY AND BEHAVIOUR

All organisms are faced with three basic challenges: 1) how to survive; 2) how to find enough food for growth and reproduction; and 3) how to reproduce successfully. The optimal strategies to meet these challenges individually often conflict. Where food abounds, other animals are attracted in, so that the dangers of predation (e.g., Lampitt et al., 1983) or being injured accidentally in feeding-frenzies increase. Most species occur at very low densities, which means that finding a mate cannot be left to chance encounters; instead, species either form breeding swarms or "advertise" their presence with scent or sound, again increasing their vulnerability to predation. Observed macroplankton abundances are generally less than 1 per 1000 m^3, but observations from submersibles (e.g., Wolff, 1971; Childress et al., 1989) have suggested that random net observations may well miss significant concentrations of pelagic organisms, which often occur in thin layers and may be assembled either passively as a result of currents and eddies, or actively as a result of behavioural responses to environmental cues.

The need to take risks associated with fulfilling these basic activities shifts during the life cycle of a species. Early larval stages are often spent in the upper water column where food abounds. The higher risk of predation is presumably outweighed by the benefit of achieving more rapid growth. Size also plays a role: the smaller an animal is, the shorter the range over which it can be visually detected. Thus, as an animal grows, it either has to adopt an effective camouflage (such as a high degree of transparency) or it may move down into deeper water where the light is dimmer, which diminishes the range at which it can seen. Hence many pelagic species undergo ontogenetic

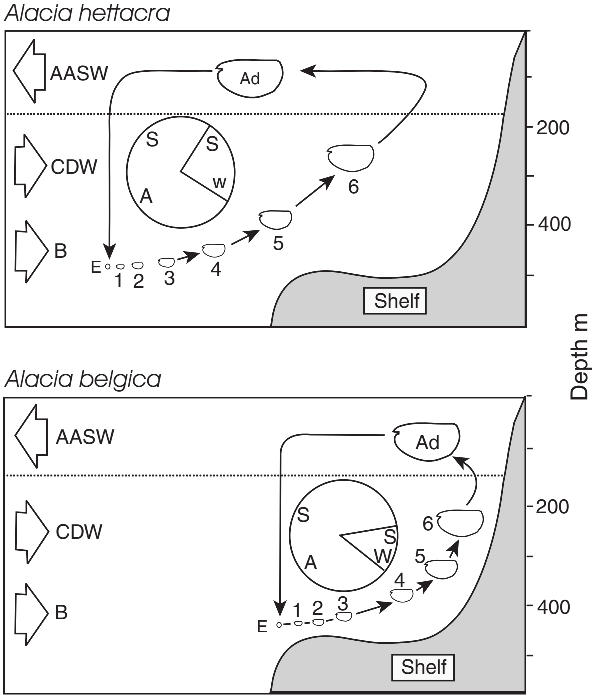

Fig. 3.14. Models of the life cycles of the halocyprid ostracods *Alacia hettacra* and *A. belgicae* in the region of the Antarctic Peninsula. Adults (Ad) while occupying Antarctic Surface Water (AASW) in the upper 100 m of the water column are advected offshore. They migrate down 500 m into Circumpolar Deep Water (CDW) in autumn (a) where they release their eggs. The eggs hatch and develop through six juvenile stages during the winter (w) and early spring (s), while being advected back in over the shelf. The later stages migrate back up towards the surface, where they develop into adults as they move back into the upper layers. Redrawn from Kock (1992).

migrations, changing their depth ranges during their growth and development (Fig. 3.14). Clearly the risks associated with finding a mate can be postponed until the individual has reached sexual maturity.

Seasonality of food supply also has far-reaching effects on development and behaviour. Reproduction tends to be timed so that the young stages encounter optimum feeding conditions. Thus, in temperate waters, breeding often coincides with the springtime maximum in primary production; in tropical seas, on the other hand, this may be during the winter months.

Buoyancy

In pelagic animals it is clearly advantageous to keep the density of the body as close to that of the sea water as is possible. Thus, if an organism stops swimming, it neither sinks nor floats up, and manoeuvrability is improved. Protoplasm is heavier than water, so in many animals some means of gaining buoyancy has been adopted. Some of the larger, very active and powerful pelagic animals, like large squid and tuna, have no major buoyancy mechanisms but just swim continuously. In sharks, the pectoral fins are angled so that they generate lift as the animal swims, and further lift comes from the asymmetrical (heterocercal) tail fin in which the upper fin is the longer. Fishes have blood that is 50% less salty than seawater, and this gives a modicum of buoyancy. Sharks also control their blood ionically, replacing the heavier ions like sodium with urea. Many of the neustonic animals that are specialized to live at the air/water interface have a variety of gas floats: – the Portuguese-man-o'war *Physalia* has a float that also acts as a sail, the nudibranch *Glaucus* gulps air from the surface, so that its gut acts as a swimbladder, the snail *Ianthina* uses its foot to envelop a series of air bubbles encased in mucus which hardens to form a multichambered float.

Many types of subsurface organisms are able to secrete gas into floats (e.g., physonect siphonophores), swimbladders (e.g., many fishes) or chambered shells (e.g., cephalopods, like *Spirula, Nautilus* and cuttlefish). Gas bubbles provide considerable buoyancy, but have the disadvantage that, if the volume of gas is allowed to change, the buoyancy changes with depth, particularly near the surface. Another problem is that the partial pressure of gases dissolved in seawater decreases with increasing depth. Thus the gas becomes more soluble, and the animals have to work harder and harder to secrete gas into the organ, and to keep it there. As the use of gas-filled swim bladders becomes progressively more demanding energetically with depth, other less demanding methods are used. Thus in *Gonostoma* (Fig. 3.7), the bathypelagic species has waterier tissues, the bones are no longer so heavily calcified, many organs are reduced in relative size, and the lipid content of the body is increased. An increase in wateriness is often associated with ionic regulation. Thus, in the large and watery planktonic ostracod *Gigantocypris* and the gelatinous octopod *Japetella*, pumping sulphate ions out of the blood is sufficient to render them neutrally buoyant. Another mode of ionic control occurs in other gelatinous squids such as the cranchids, which replace the sodium in their blood with ammonium ions. At depths >500 m many of these adaptations become progressively more advantageous; the dangers of encountering marauding visually hunting predators dwindles with increasing depth, so that there is no longer a need to have a rapid escape capability. Hence the high energetic costs of having and maintaining heavy muscles and their associated skeletal support no longer have to be met. Thus many of the elaborately developed sensory systems supported by large brains and a well developed central nervous system, typical of many species in the upper mesopelagic and epipelagic zones, become a liability rather than an asset (Marshall, 1971). As a result many bathypelagic species are physiologically more akin to jellyfish than they are to their evolutionary closest relatives (Childress and Thuesen, 1992). In the many bathypelagic fishes that have larval stages that live and feed near the surface, as the maturing larvae migrate down into deep water many of their sensory systems such as eyes regress. There are also reductions in those parts of the central nervous system which become redundant as the sensory systems they previously supported become non-functional. Visual receptors are often replaced by elaborations of the lateral-line mechano-receptors and olfactory organs. Thus, physiological demands on animals living deeper within the water column are reduced as a result of this relaxation of predation and competitive pressures, and this enables the organisms to cope with the smaller and possibly less predictable food supply.

Physiological adaptations

Oxygen consumption rates can be used as an indicator of general activity levels. The rates of consumption of oxygen by pelagic animals decrease rapidly over the first kilometre of the water column (Childress, 1975; Torres et al., 1979; Cowles et al., 1991; Thuesen and Childress, 1993a,b). Initially it was assumed that this decline was a result of the lower temperatures in deep water and changes in chemical composition. However, careful observational and experimental studies have shown that these factors play a relatively small role in the decline in metabolic rates (Childress and Thuesen, 1992). For example, in the Southern Ocean both pelagic crustaceans (Ikeda, 1988) and midwater fishes (Torres and Somero, 1988) show bathymetric declines in their metabolic rates, although there is little difference in temperatures between the near surface and the deep waters.

Two hypotheses have been advanced to explain why the basal metabolic rates of decapods and fish decline with depth. The first is that the diminishing availability of food favours the selection of lower metabolic rates and so increases the efficiency with which the available energy is utilized. The second is that, as the ambient light levels decline, so the range over which organisms can be detected visually increases. The resulting reduction in the intensity of visual predator–prey interactions with depth reduces the selection pressure for strong swimming capabilities to avoid predators. If the first hypothesis is valid, then species inhabiting the low-productivity oligotrophic waters off Hawaii, where food availability is very low, would be expected to have lower metabolic rates than similar species inhabiting the highly productive, food-rich waters of the California Current. However, Cowles et al. (1991) found that oxygen consumption rates are comparable in the two contrasting regions. An important test of the second hypothesis has been the examination of the metabolic rates of species that do not orientate visually such as chaetognaths and medusae. According to the first hypothesis these taxa should show similar declines in metabolic activity with depth as occur in decapods and fish. The second hypothesis implies that their metabolic rates will be independent of their bathymetric distribution. Thuesen and Childress (1993a) found that there are considerable variations in the metabolic rates of different chaetognath species, but these variations have proved to be independent of the depths at which they occur and only partially related to body size, thus vindicating the second hypothesis.

Childress and Thuesen (1992) have estimated the contribution made by pelagic assemblages to carbon fluxes using biomass estimates and the sparse reliable data on respiration rates (Table 3.5). About half of the reduction in metabolic activity is a result of reduced locomotory abilities as exemplified by the mysid, *Gnathophausia ingens* (Cowles and Childress, 1988). Childress and Thuesen argued that, since there

Table 3.5
Metabolic carbon flux resulting from energy metabolism of pelagic and benthic assemblages for the Pacific [1]

Depth (metres)	Biomass (g wet weight m^{-2})	Respiration (mg C m^{-2} d^{-1})
Pycnocline to 500 m	4.04	20.80
500 to 1000 m	3.51	0.69
1000 to 4000 m	1.03	0.13
100 to 0 m above bottom	3.13	0.13
Sea floor	0.05	2.00

[1] From Childress and Thuesen (1992).

is progressive reduction in reliance on vision with increasing depths (Hiller-Adams and Case, 1988), non-visually hunting species might be expected to show only temperature-related reductions in metabolic rates. There are some limited physiological data available for gelatinous plankton which support this hypothesis (Childress and Mickel, 1985; Thuesen and Childress, 1993b, 1994). Childress and Thuesen (1992) drew up a speculative budget for metabolic carbon flux for the oceanic Pacific (Table 3.5). They derived a total global estimate of oceanic biomass to be 8.7 gigatons wet weight of which 3% was benthic and 20% was benthopelagic. The total annual respiratory flux they derived was 5.4 gigatons C (10^{15} g), of which just 0.4% was benthopelagic and 9% benthic.

Thus many of the characteristics of pelagic species and communities that were originally inferred from observations of their bathymetric profiles are being confirmed and improved upon as a result of improved techniques of sampling and measuring living organisms. One important conclusion to be drawn from these new insights is that the tendency for modellers to treat midwater processes as "black boxes" in drawing up chemical budgets is fraught with dangers. If large-scale and long-term changes are indeed being induced by natural and anthropogenic changes in climate, there may be substantial impacts on processes within the water column of the deep ocean that have significant positive or negative feed-back effects on deep-ocean budgets, which may well cause some surprises.

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Chapter 4

REDUCING ENVIRONMENTS OF THE DEEP-SEA FLOOR

Verena TUNNICLIFFE, S. Kim JUNIPER and Myriam SIBUET

INTRODUCTION

The deep ocean harbours several types of habitat in which dissolved oxygen is low or virtually absent. While this condition is problematic for most marine organisms, many have adapted to dysaerobic or reducing conditions. Procaryotic life emerged on Earth under anaerobic circumstances, and many of these archaebacterial lineages remain active. These habitats are characterized by the presence of hydrogen sulphide and, sometimes, methane. Sulphide originates from sulphate reduction either by microbes or inorganic processes beneath the seafloor. Methane is usually derived from reduction of organic matter either by thermogenic processes or by biogenic processes (methanogens) although, at ridge crests, this volatile can also be inorganic in origin. Throughout this chapter, unless otherwise stated, the term “sulphide” refers to the sum of all dissolved chemical species of hydrogen sulphide.

Much attention has focused on these habitats, even though they occupy a very small proportion of the sea floor, because of the unusual nature of many inhabitants. With the discovery of hydrothermal vents in the eastern Pacific in the late 1970s, came the recognition that complex ecosystems can be sponsored on Earth using energy that is not solar. Geothermal processes supply reduced chemical species which, through microbial mediation, provide chemical energy for production of organic carbon. Other features of vent communities captured the attention of biologists: the dense biomass, unusual symbioses, novel systematic relations, among others. The remarkable visual impact of giant tube worms (vestimentiferans) and “black smokers” is truly captivating – and not only to the “general public”. Much justification for work in these habitats lies in elucidation of how biological systems can adapt to extremes. The potential of biotechnological exploitation has figured in some of this work. Investigations into evolutionary relationships of both procaryotes and eucaryotes have given rise to numerous hypotheses, not the least of which is the development of scenarios around the origin of life in such habitats (see *inter alia* Corliss et al., 1981; Holm, 1992; Nisbet and Fowler, 1996).

Researchers realized, with further seafloor exploration, that a community based on chemotrophs is not unique to vents, nor are many of the organisms. Other sulphide- and methane-rich habitats such as seeps on continental margins foster communities that share some characters with hydrothermal vent communities on spreading ridges. While knowledge of the varied seeps and organic-enriched habitats in the deep sea is still limited, cold-seep ecology is expanding, and links between the faunas of seeps and hydrothermal vents continue to be identified (Sibuet and Olu, 1998).

Ecosystem characters in these habitats are understood incompletely – for some properties, very poorly. Often, workers are reduced to documentation of species present and visual description of the habitat. As deep-sea technologies develop to meet requirements to measure physico-chemical properties and to assess spatial and temporal variability, scientific understanding continues to grow.

REDUCING ENVIRONMENTS IN THE DEEP SEA

Hydrothermal vents

The release of heat from the Earth’s interior dictates the nature and behaviour of the overlying crust. Hydrothermal circulation represents an important mechanism for cooling newly generated crust. Vigorous surface

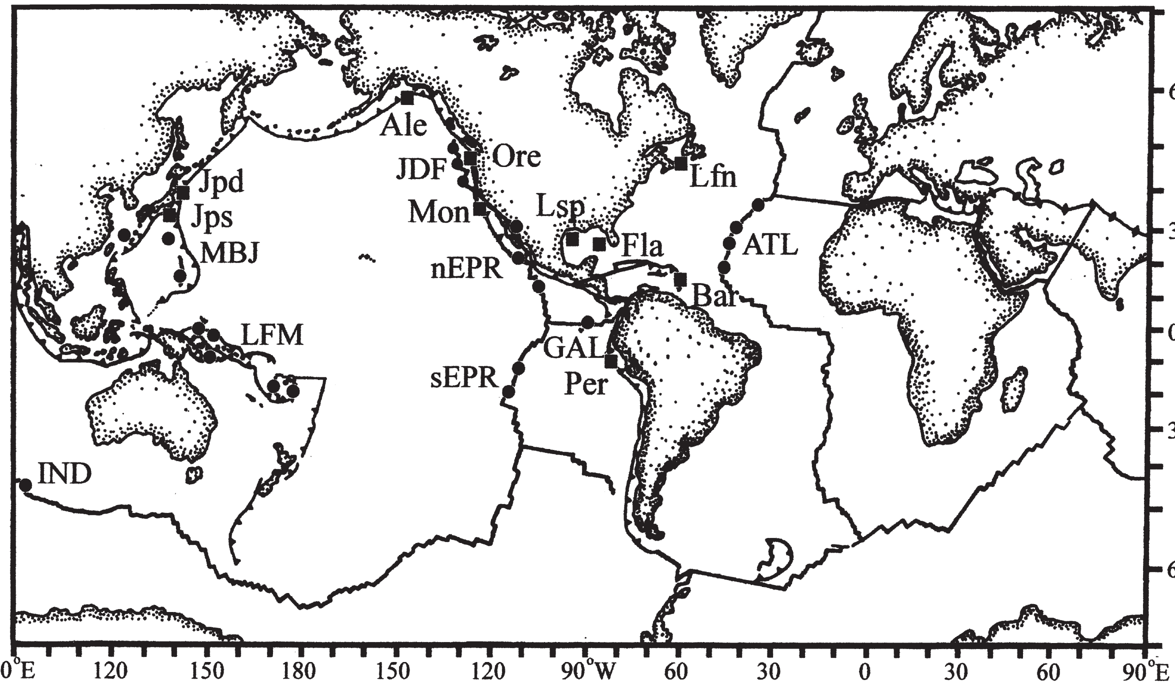

Fig. 4.1. Distribution of vents (dots) and seeps (squares) in the deep sea. Several other sites are known but poorly documented; the majority of the ocean's ridge crests and continental margins remain unexplored. Vents: NEP, numerous sites on Explorer, Juan de Fuca and Gorda Ridges; GMS, Guaymas Basin; nEPR, numerous sites from 21°N to 9°N, East Pacific Rise; GAL, Galapagos Rift; sEPR, numerous sites from 17°S to 21°S, East Pacific Rise; MAR, five sites on Mid-Atlantic Ridge; IND, southeast Indian Ridge; LFM, several sites around Fiji, Lau, and Manus Back-Arc Basins; MBJ, two major sites in Marianus Back-Arc Basin and Okinawa Trough. Seeps: Ore, Oregon Margin; Per, Peru Margin; Bar, Barbados Prism; Lsp, Louisiana and Gulf of Mexico; Fla, Florida Escarpment; Lfn, Laurentian Fan; Jps, shallow Japan margin; Jpd, deep Japan margin.

venting occurs at both divergent plate boundaries (spreading centres) and convergent ocean plates where back-arc spreading occurs; the western Pacific ridges are generated by this process in which melt from the subsumed plate rises behind the island arc to form small spreading ridges.

The immediate subsurface heat source is a magma chamber localized a few kilometres below the ridge crest. The exact nature of these chambers, and how the circulating fluid interacts, are poorly understood. However, it is clear that different ridge systems have different spreading behaviours and venting manifestations (Fornari and Embley, 1995).

Figure 4.1 depicts the distribution of known vent sites along mid-ocean and back-arc spreading ridges. On several well-studied ridges, most of the vent sites are probably known: Galapagos, the northern East Pacific Rise, the Juan de Fuca Ridge. However, much of the remaining ridge crests are poorly explored; thus, many new discoveries are likely. For example, recent work on the southern East Pacific Rise has identified indicators of very extensive venting (Urabe et al., 1995; Auzende et al., 1996). This ridge crest has very fast spreading rates – over 16 cm yr^{-1} – compared to the slow rates (under 3 cm yr^{-1}) at the Mid-Atlantic Ridge. Baker et al. (1995) find a strong linear relation between spreading rate and the incidence of hydrothermal plumes over a ridge; such buoyant plumes are excellent indicators of vent emissions.

Venting at the seafloor can take several forms. The emergence of undiluted high-temperature fluid occurs from depth in direct, sealed conduits resulting in superheated high-velocity water jets. The maximum attainable temperature of the solution that forms subsurface appears to be 400°C; greater heat input results in phase separation. This boiling can also occur when venting occurs at shallow sites such as seamounts on a ridge (Butterfield et al., 1990; Sakai et al., 1990). As the hot fluids emerge into the cold bottom water, their load of dissolved metals and minerals is precipitated, often as complexes with sulphide. Thus form the spectacular "black smokers" atop extensive polymetallic sulphide

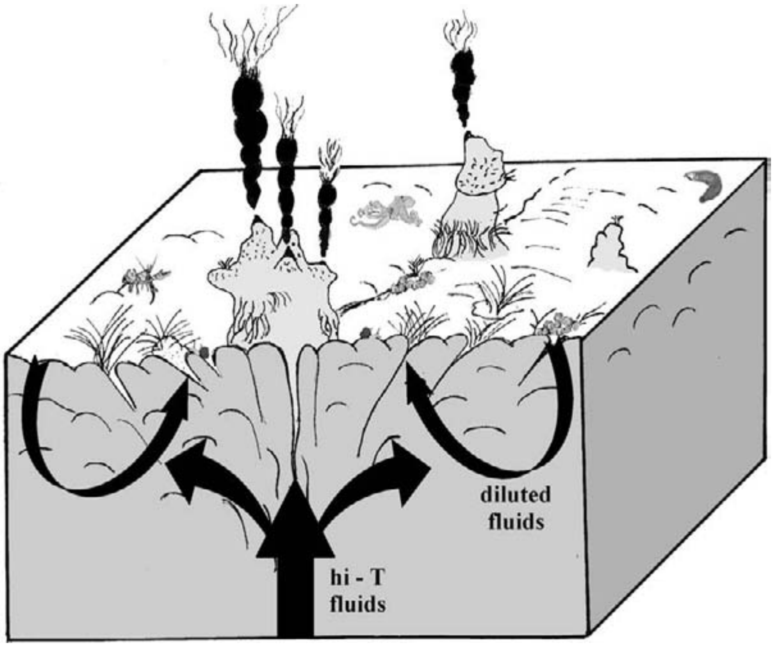

Fig. 4.2. High-temperature water flows from sealed conduits in the crustal basalts that allow fluids to emerge nearly undiluted. Laden with dissolved minerals and sulphide (converted from seawater sulphates), precipitation of mineral sulphide complexes occurs at the seafloor to form chimneys and "black smokers". Diffuse, lower-temperature venting can also occur as sea water percolates through cracked basalts to dilute the "end-member" hydrothermal ("hi-T") fluids. The extent of this venting depends largely on the nature of the basalts and cracks. Low-temperature sites are usually colonized – sometimes only by microbial mats. The scenario represented here might be found on ridges of the eastern Pacific Ocean.

mineral deposits, which may build up over thousands of years in a stable site like TAG on the Mid-Atlantic Ridge (Lalou et al., 1993); some chimneys may last only a few years as the subsurface conduits shift or clog (Hannington et al., 1995).

Mineralized chimneys form at temperatures over 250ºC. Lateral percolation of cooler fluid around and through chimney walls provides extensive habitat for vent animals. A second major habitat forms around cooler, less focused flows where fluid diffuses through cracks in the basalts (Fig. 4.2). Mixing with primary hydrothermal fluid has occurred below the surface, and emerging fluids may range in temperature from 2º to about 100ºC. The composition of vent fluids varies markedly from site to site and can change over time. Dissolved oxygen is rapidly scavenged by reduced chemical compounds, and is present in trace amounts only. Chemical composition changes with dilution and temperature. Johnson et al. (1988) have demonstrated both spatial and temporal variability in micromolar concentrations of oxygen and sulphide which co-vary inversely over scales of centimetres and seconds.

Distribution of hydrothermal vent sites (Fig. 4.1) is sparse and uneven – a pattern that is mirrored on smaller scales. The global ridge is about 50 000 km long but underlying heat sources are not continuous. Regional ridges are divided into separate segments usually 30 to 100 km long. Magmatic activity beneath them can be quite different (Batiza, 1995). Figure 4.3 is an oblique view of the Juan de Fuca Ridge in the northeast Pacific. Seven segments of this ridge sponsor quite different venting characters: small eruptions have occurred on two segments in the last 15 years, while two more are relatively quiescent with little venting. The central volcano lies over an active mantle hot spot that erupted in January, 1998. To the north, deep tectonic faults feed relatively stable vent fields with large polymetallic sulphide accumulations.

A single vent field may contain from a few to hundreds of openings that create a mosaic of colonies. Fields vary in size from metres to hundreds of metres across. Ultimately, field vigour and extent are governed by the nature of the underlying magma chamber and by the porosity and stability of the intervening rocks (Alt, 1995). The overall nature of hydrothermalism in a ridge segment is dictated by the geophysical processes

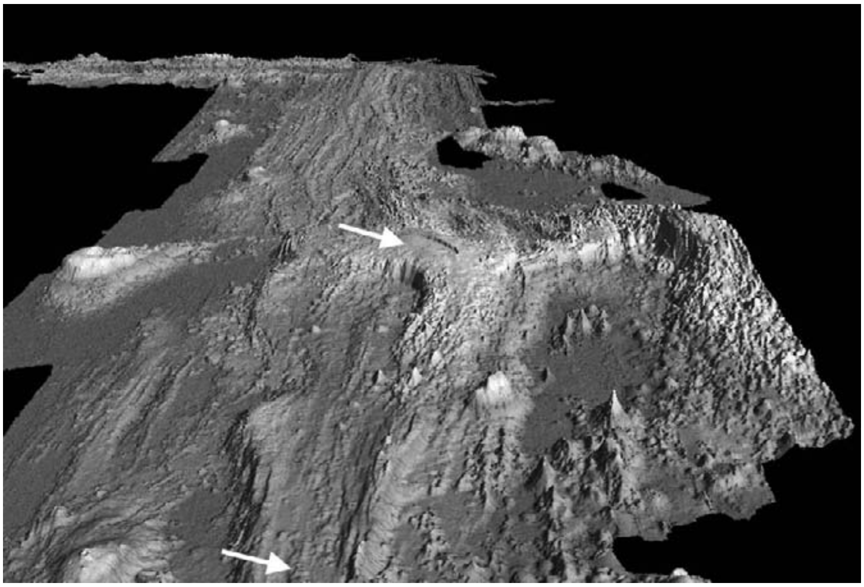

Fig. 4.3. Oblique view of southern Juan de Fuca Ridge looking south from about 47ºN. Lighter areas are higher. This image illustrates the variable morphology of the ridge crest habitat and the division of the spreading axis into segments. The most southerly Cleft Segment gives way to the overlapping Vance Segment which curves into Axial Seamount. The spreading zone emerges on the northern flank of the Axial Seamount and then displaces eastward (to the left) onto the CoAxial Segment. The sites of the 1993 CoAxial and 1998 Axial Volcano eruptions are indicated. Courtesy C. Keeley.

controlling seafloor spreading in that area. The balance between the tectonism that pulls two seafloor plates apart and the volcanism that provides new magmatic material may vary (Fornari and Embley, 1995). Thus, different ridges have different behaviours and spreading rates. For example, the Mid-Atlantic Ridge has a very slow spreading rate with little recent magmatic activity. Deep cracking in a stable tectonic setting has favoured the building of large sulphide mounds with a venting history of many thousands of years (Karson and Brown, 1988; Lalou et al., 1995).

Seeps of continental margins

Reducing environments also form where oxygen-depleted fluids diffuse from sediments along continental margins. As flow rate is usually slow and fluids have only small temperature anomalies, these sites are called “cold seeps”. Seeps can occur on both active subduction margins and on passive continental margins (both the north-west and east sides of North America, for example). The causes and nature of these seeping fluids are quite varied (Table 4.1). To date, 24 deep cold seeps have been discovered, but only about half of them are well-known biologically (Fig. 4.1). Extensive comparisons and generalized models may be premature, but a recent review established patterns of biodiversity, biogeography, trophic behaviour and fluid dependence (Sibuet and Olu, 1998).

Seep processes relate to geological phenomena such as tectonically induced high pore-fluid pressures, petroleum or natural gas escape, artesian flow or catastrophic erosion and submarine slides. Subduction-zone seeps occur both on well-developed accretionary prisms and along erosive margins to a depth of at least 6000 m (the limit of the deepest research submersibles). On active margins, the subducting plate scrapes much of its sediment burden against the overlying continental plate to form a compressed wedge of sediments over the subduction zone known as an accretionary prism. In some settings, mud volcanoes are created by an influx of water from deep over-pressured zones – as in the Barbados prism, located where the Atlantic plate subducts under the Caribbean plate (Olu et al., 1997). Water within the sediment is forced out along weak bedding planes or faults (Fig. 4.4). At some sites, the subduction trench is pulling apart, and the associated seismic activity forces out fluids; in these cases, seeping may be less stable. On some passive margins, such as the Gulf of Mexico, “salt tectonics” creates conduits for seeping fluids. Ancient salt deposits lie below sediments where hydrocarbons and methane

Table 4.1
An illustrative sampling of better-known cold seeps

Site[1]	Depth (m)	Setting	Seepage	Major biota
Gulf of Mexico	400–2200	Faulted slope; salt diapirs [intrusive structures]	CH_4, other hydrocarbons, natural gas, H_2S	Tube worms, clams, mussels, grazers
Florida Escarpment	3270	Faulted carbonate platform	CH_4, NH_4 in brines	Mussels, tube worms
Barbados Prism	1000–5000	Mud volcanoes, faults, ridges on subduction zone	CH_4, H_2S in porewater	Clams, mussels
Laurentian Fan	3800	Seismic disrupted turbidite on passive margin	?H_2S, CH_4 in porewater	Clams
Japan Trench	3800–6000	Eroding prism on subduction margin	CH_4, ?H_2S in porewater	Clams
Oregon Margin	600–2000	Carbonates in accretionary prism on subduction zone	CH_4, H_2S in gas hydrates	Clams, tube worms, grazers
Peruvian Margin	2600–5600	Accreting prism on subduction margin	Reduced fluids – continental origin	Clams

[1] Sites are indicated in Fig. 4.1.

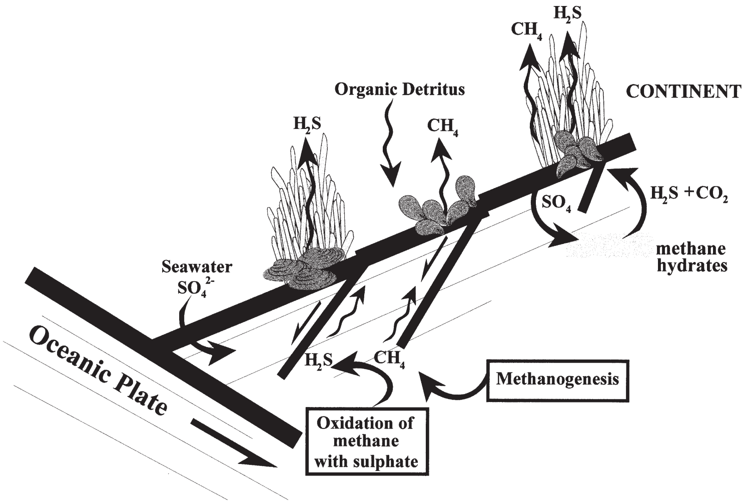

Fig. 4.4. Generalized view of seepage of reduced fluids at an active continental margin. The downslipping oceanic plate piles sediment on the continental margin as an accretionary prism. Faults develop in the compacting sediments, providing conduits for trapped fluid which may be of both continental or ocean origin. Organic carbon in the sediments is oxidized to methane by biogenic or thermogenic processes. Subsurface sulphide is produced mainly through the oxidation of methane with seawater sulphate. The rising methane may be frozen to a solid form called gas hydrates in which methane is trapped in a clathrate structure; this form is also oxidized. Rising dissolved gases sponsor chemoautotrophic production in free-living and symbiotic microbes. This general relationship of faulting, fluid conduits and formation of reduced compounds is found in other settings listed in Table 4.2. Fluids can contain H_2S, CH_4 or both – the type of symbiont-containing invertebrate that dominates may depend on which compound(s) the symbionts can exploit.

have accumulated; however, as salt is less dense than compacting sediments, the salt domes tend to push upward, forming deep cracks in the sediments through which gases and petroleum escapes (Kennicutt et al., 1985; Brooks et al., 1990).

Cold-seep fluid composition is as varied as the settings. Initially, fluids are mainly characterized by high methane concentration and are generally without sulphide. Methane is a common product generated thermogenically in sediments or from methanogenic microbial processes. Migrating fluids can be enriched in hydrogen sulphide in near-surface sediments by microbial sulphate reduction coupled to methane oxidation (Kulm et al., 1986; Masuzawa et al., 1992;

Martin et al., 1996). The carbon sources are organic: methane, petroleum, other hydrocarbon gases, or from solid gas hydrates (Simoneit et al., 1990; Aharon, 1994; MacDonald et al., 1994). These compounds derive from accumulated sedimentary organic carbon and thus are photosynthetic in origin. At several sites, petroleum products are abundant enough to coat collected biota with oil. Ice-bound methane (or methane hydrates) can slowly release enough gas to support a dependent community (Suess et al., 1999). This commentary addresses only the seeps of the deep sea. Numerous shallow-water settings of methane and natural gas release are known where a variety of organisms and microbial activity is reported. Dando et al. (1995) and Jensen et al. (1992) have provided shallow examples.

The extent of seepage communities in the deep ocean is unknown, as margin environments are incompletely explored. Areal extent can be large: Olu et al. (1996a) have described cold-seep communities dispersed along a 40 km transect from a depth of 2600 to 5300 m on the Peruvian margin. The major clam field has a total surface area of 1000 m^2 with clusters of 1000 individuals m^{-2}. Observations of demographic features, trophic complexity and high species richness suggest sustained seepage at several sites (Carney, 1994; Olu et al., 1996b). Carbon-14 ages of mussel shells from the Barbados prism yield dates of 10 000 to 20 000 years ago (Gonthier et al., 1994). Aharon et al. (1997) have proposed that the current seeps of the Gulf of Mexico have been active since the last glaciation period. Indeed, ages of extinct shallow sites indicate that the area has been seeping for at least 200 000 years.

Organic remains

Windfalls of organic origin on the ocean floor can attract a wide array of deep-sea animals to this sudden bounty. However, sometimes the nature of the windfall is such that it generates an anoxic habitat inaccessible to many animals. Very often, the same chemoautotrophic microbial production occurs as is found at vents and seeps, albeit on a smaller and more ephemeral scale. Perhaps the best known is that of large carcasses. The fortuitous discovery of whale skeletons led to descriptions of a community of invertebrates with many features similar to those of vent communities (Smith et al., 1989; Bennett et al., 1994; Naganuma et al., 1996). This community relies on autotrophic microbes using reduced compounds generated from the slow release and decay of organics from the lipid-rich bones. The high (pre-whaling) abundance of marine mammals has formed a reliable enough organic source to develop a distinct 'following' in the deep sea of organisms apparently adapted entirely to subsistence on carcasses. Martill et al. (1995) have speculated that the abundant marine reptiles of the Jurassic and Triassic may have provided an even older source of scattered reducing habitats.

Wood has been around since the upper Paleozoic. While the biomass sequestered in a single tree is insufficient to develop an extensive reducing environment, most animals adapted to submerged wood are allied to those known at other reducing sites. The organisms involved are mostly molluscs (Turner, 1973; Warén and Bouchet, 1993) and polychaetes (Wolff, 1979; Desbruyères and Laubier, 1988). One interesting find is that of a vestimentiferan (Pogonophora, Obturata) tube worm and mussel in the wreck of a cargo ship (Dando et al., 1992). Both genera reported are known from seeps and vents, and contain symbiotic microbes. The animals were found among the cargo of beans, sunflower seeds and sisal – all organic-rich and liable to produce sulphide upon decay.

Dysaerobic basins

There are several places in the ocean in which oxygen concentrations are low and occasionally are zero (see Chapter 2); dysaerobia (or a hypoxic condition) occurs below 2 ml ℓ^{-1} oxygen. Larger basins occur mostly in marginal areas where organic input is relatively high. Microbial oxidation depletes dissolved oxygen, and hydrogen sulphide can build up in bottom waters and sediments. The Peruvian Trench, Californian Basin, Black Sea and numerous deep fjords are well-published examples; Diaz and Rosenberg (1995) have presented a comprehensive list and reviewed the effects of depleted oxygen on benthic communities. Often these basins experience oxygen levels fluctuating on annual to centenary scales. Work on long cores of sediment has identified the nature of such variability in bottom oxygen from basins on the west coast of North America (i.e. Kennett and Ingram, 1995). The lack of macrofauna in the sediments allows annual lamination to develop, reflecting seasonal diatom production. However, periods of delamination and bioturbation indicate development of benthic communities during prolonged periods of oxygenation.

Benthos of hypoxic basins is specialized (Bacesco, 1963; Rhoads and Morse, 1971; Tunnicliffe, 1981). Generally, taxonomic diversity decreases with oxygen level; in sediments, the polychaetes, nematodes and crustaceans appear to be most resistant. Rhoads and Morse (1971) have presented a model for response to different oxygen levels and drew interesting analogies to the evolution of benthos in oxygen-poor waters in the early Phanerozoic. In many basins, mats of filamentous sulphur-oxidizing microbes are seen where oxygen is highly depleted, and macrofaunal abundance decreases in their presence (Rosenberg et al., 1983; Juniper and Brinkhurst, 1986).

Subsurface reducing habitats

The most voluminous reducing habitat in the deep-sea lies below the seafloor in anoxic sediments and crustal rocks. As far as can be determined, this environment is populated only by micro-organisms capable of anaerobic metabolism, although zones of aerobic microbial growth may exist in near-surface rocks. In sediments, anoxia is created during early stages of organic-matter degradation by the consumption of available pore-water oxygen. The depth below the sediment/water interface at which anoxia occurs is determined by the rate of organic-matter sedimentation; this depth varies from a few millimetres in carbon-rich sediments near the continents to tens of centimetres in the oligotrophic environment of the open ocean. Microbial life extends for hundreds of metres below the seafloor in oceanic sediments (Parkes et al., 1994, 2000), approaching the zone where hydrocarbon formation occurs (Wellsbury et al., 1997). At these depths, microbial communities are millions of years old.

For the most part, deep-living sediment micro-organisms are deriving energy and nutrients from fossil organic material, and do not interact with life in the overlying ocean. An exception occurs in the seep environment where metabolic products of deep-living sediment microbes are discharged at the seafloor surface and fuel chemosynthesis. An important local, subsurface microbial process at seeps is the anaerobic oxidation of methane, which is coupled to sulphate reduction. Indications of microbial life have also been found in drill holes below the seafloor which have penetrated through sediments into crustal rock. In this nutrient-poor environment, chemosynthetic microbes can derive energy from oxidation of hydrogen generated by sea-water/rock interactions, as long as there are fractures and pore spaces for sea water. Signs of dissolution of basaltic glass by microbes have also been noted in drill-hole samples (Furnes et al., 1996), although it is not clear how this phenomenon is related to energy metabolism.

The most dynamic subsurface microbial habitat may be within the crustal rocks at mid-ocean ridges. The heat-driven circulation of energy-rich fluids within a large volume of porous and permeable rock should be very favorable to microbial growth. The potential for microbial life in the subsurface hydrothermal environment has been a source for considerable speculation (Gold, 1992; Deming and Baross, 1993), but direct observation is difficult. Present technology for deep-sea drilling does not permit penetration into the basaltic rock at mid-ocean ridges so observation of subsurface microbial growth must depend on analysis of material discharged from the subsurface by hydrothermal systems. The venting of microbial floc from so-called ‘snowblower vents’ that appear in the weeks and months following seafloor eruptions on ridge crests (Haymon et al., 1993; Juniper et al., 1995) indicates that microbial growth is occurring below the seafloor, although much of the solid material may be metabolic waste rather than biomass (Taylor and Wirsen, 1997). The isolation of hyperthermophilic microbes (growing at 90ºC and above) from venting fluids following seafloor eruptions (Tunnicliffe et al., 1997; Holden et al., 1998) provides evidence for a high-temperature subsurface microbial habitat. In addition to the exportation of biomass, subsurface microbial growth at ridge crests may have a significant impact on the chemical composition of hydrothermal fluids (Lilley et al., 1982, 1983). This chemical evolution may, in turn, influence the colonization of vents by free-living micro-organisms and vent animals (Tunnicliffe et al., 1997). Deming and Baross (1993) have pointed out that hydrothermal vents provide “windows” into a subsurface biosphere that cannot be otherwise studied. Occasional glimpses of subsurface life have been provided by eruptive events, but a systematic approach to gather chemical and microbial evidence remains elusive.

HABITAT CONDITIONS

Substrata and supply of reducing substances

For benthic organisms in reducing habitats, substratum and supply of reducing substances are intimately linked. Substrata are colonized because they serve as medium for molecular diffusion or fluid flow (sediments, sulphide deposits, whale bones) or are located in the path of fluid discharge; thus, they provide access to reducing substances or the products of chemosynthesis. Vesicomyid clams are commonest at sedimented sites, where they assume a partially-buried position and take up sulphide through the foot. Certain alvinellid polychaetes are found only on active hydrothermal structures (Juniper and Martineu, 1995). Serpulid polychaetes are limited to rock or shell surfaces, and at vents occur only away from direct hydrothermal flow (Fustec et al., 1987). Bathymodiolid mussels, on the other hand, can form abundant aggregations on sediment, bare rock and polymetallic sulphide surfaces wherever there is an appropriate supply of fluids from vents (Van Dover et al., 1996a) or seeps (Olu et al., 1996b) for their symbionts. One very large species (to 36 cm length), *Bathymodiolus boomerang,* lives partially buried in mud at low seepages (Von Cosel and Olu, 1998). Free-living micro-organisms are similarly flexible with respect to substrata, as is evident in the growth of filamentous tufts and mats on most animal or mineral surfaces that provide access to reducing substances (Jannasch and Wirsen, 1981). Locally, the availability of appropriate substrata may influence faunal community composition. A few recent studies have identified flow rate as a key variable influencing the structure of communities around vents and subduction-zone seeps (Henry et al., 1992; Sarrazin et al., 1997). Fluid flow determines the rate of supply of reducing substances for microbial chemosynthesis. Vigorous diffuse flow may even reduce the availability of dissolved oxygen within faunal aggregations, although appropriate data remain to be acquired.

In the mid-ocean ridge and back-arc ridge settings of hydrothermalism, hard substratum is the most common benthic habitat, occurring as basaltic rock or sulphide mounds and structures. Low-temperature hydrothermal fluids flow through fractures in the substratum or diffuse through porous sulphides, supporting aggregations of vent organisms (Fig. 4.5a). Often vent openings are multiple, particularly on sulphide edifices, resulting in a continuous patchwork of vent communities. Organisms can also exploit high-temperature venting by colonizing adjacent surfaces which have been diluted and cooled by ambient seawater (Sarrazin et al., 1997) (Fig. 4.5b). Geologic settings that favour venting through sediment are uncommon. The predominance of hard substrata at vents may limit the presence of some species. Juniper et al. (1992) suggested that the high species diversity at one sedimented site may derive partly from the mixture of soft and hard substrata. Strong affinities among the faunas of three sedimented hydrothermal sites in the eastern Pacific provide further evidence for a strong substratum effect on faunal composition at vents (Tunnicliffe et al., 1996). The external surfaces of many vent animals, particularly vestimentiferan tubes, can represent an important substratum for microbial growth and colonization by small metazoans (Sarrazin et al., 1999).

Fig. 4.5. Hydrothermal vents of the mid-ocean ridge. A. Diffuse venting through basalts on the northern East Pacific Rise. Vestimentiferans are *Riftia pachyptila*; bathymodiolid mussels and galatheid crabs are also seen. Image is about 2 m across. B. High temperature venting on Juan de Fuca Ridge. Fluid at 370ºC emerges from chimney spouts atop a sulphide mound 8 m high. The vestimentiferan *Ridgeia piscesae* surrounds the high-sulphide fluid.

Subduction-zone and hydrocarbon seeps are predominantly soft-bottom environments, but hard surfaces exist in the form of carbonate concretions formed by methane oxidation (followed by the reaction of bicarbonate with calcium in seawater), rocky outcrops, clam shells and even outcropping methane hydrates (Juniper and Sibuet, 1987; Olu et al., 1997; Suess et al., 1999). While there may be considerable variety

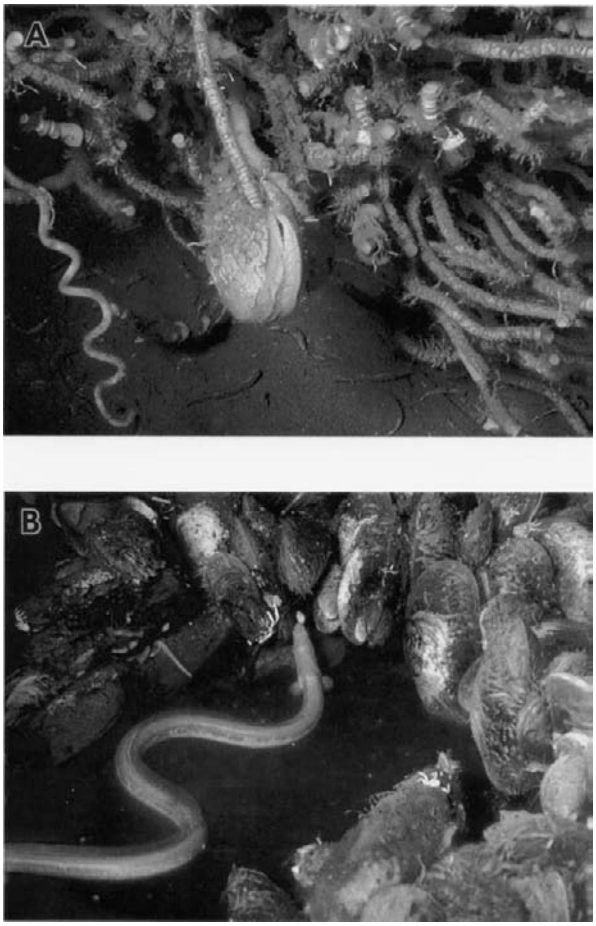

Fig. 4.6. Cold seeps in the Gulf of Mexico (courtesy I. MacDonald and J. Blair). A. Tube-worm clump (*Lamellibrachia* sp.) in sediment. The central bivalve is a scallop (*Acesta* sp.). B. Synaphobranchiid fish investigating a clump of bathymodiolid mussels.

in hard substrata at seeps, understanding of their importance to seep-community composition and diversity is very incomplete. Epilithic and epizoic microbial growth have been little studied at cold seeps. In subduction zones, fluid discharge can occur at discrete points, resulting in the development of small, well-demarcated colonies of bivalves or vestimentiferans and even loosely-dispersed fields of clams. Fluid-flow measurements from subduction-zone seeps cover a tremendous range from a few metres per year to several centimetres per second, the highest rates being associated with fluid expulsion through mud volcanoes where intense localized flow can be observed visually (Henry et al., 1992; Olu et al., 1997). Methane diffusion occurs through large areas of the Barbados prism, sustaining extensive mussel populations covering at least 300 m^2 on outcrops of hard substrata (Olu et al., 1996b). Hydrocarbon seeps along the Louisiana margin can cover vast areas of the seafloor, supporting hectares of tube worm growth (MacDonald et al., 1989) through widespread diffusion of sulphide and methane (Fig. 4.6a). In this same site, discrete, densely-packed mussel communities can be found ringing the edge of methane-rich brine pools (Fig. 4.6b), presumably supported by methane diffusing out of the brine (MacDonald et al., 1990b).

Whale bones and adjacent sediments provide substrata for chemosynthetic communities associated with large carcass falls. Processes of putrefaction and sulphate reduction provide hydrogen sulphide for chemosynthetic symbioses. Species capable of colonizing hard substrata occur directly on bone surfaces, along with microbial mats. In addition to organisms with a direct requirement for hydrogen sulphide, Bennett et al. (1994) reported other species attached to vertebrae recovered from a whale skeleton in the Santa Catalina Basin. Transport of reductants produced by organic remains occurs by molecular diffusion into adjacent waters and sediments rather than by fluid migration. This limits chemosynthetic processes to the immediate vicinity of the decomposing material.

Temperature

Temperature varies considerably within and between hydrothermal-vent habitats, and likely plays an important role in controlling faunal and microbial distribution. The most extreme thermal gradients are found at "black smoker" vents where temperature can range from ambient seawater (~2ºC) to 350–400ºC over a distance of a few centimetres. High temperatures are a barrier to life. Few animals are seen in habitats above 30ºC. Known hyperthermophilic bacteria and archaea can have maximal growth temperatures in the 90º–115ºC range and survive exposure to temperatures around 120ºC (Baross and Deming, 1995; Jannasch, 1997); early reports of growth of vent micro-organisms at temperatures to 250ºC (Baross and Deming, 1983) have not been repeated. Several studies identify distinct macrofaunal assemblages associated with the hotter areas of active sulphide edifices and mounds (Fustec et al., 1987; Sarrazin et al., 1997). Descriptive models of temperature control of species distribution have been proposed (Fustec et al., 1987; Tunnicliffe and Juniper, 1990; Segonzac et al., 1993). However, temperature and chemical properties of hydrothermal fluids are often highly correlated (Johnson et al., 1988), rendering difficult the separate determination of temperature and chemical influences on species distribution (Sarrazin et al., 1999).

High-temperature sulphide chimneys must be one of the most extreme habitats in the ocean. Measurement of actual temperatures experienced by animals is very difficult although values over 80ºC are reported for the polychaete *Alvinella pompejana* (Chevaldonné et al., 1992; Cary et al., 1998). As conduits clog and new orifices form, water pathways can rapidly change. Assemblages on chimneys shift dramatically, die and/or regrow from year to year (Fustec et al., 1987; Copley et al., 1997; Sarrazin et al., 1997). The animals themselves may be responsible for modifying the rock surface and altering flow characteristics.

Faunal communities at seeps and organic remains mostly experience ambient seawater temperatures that range from <2ºC in deep waters to 7–8ºC at seeps on the Louisiana Slope (MacDonald et al., 1994). Temperature anomalies of less than 1ºC are unlikely to influence organism distribution in non-hydrothermal reducing habitats. However, temperatures to 21ºC were measured in a convecting mud "lake" (Henry et al., 1996), where the only macrofauna were symbiont-containing sponges and vesicomyid clams around the edges.

Chemical environment

Redox conditions in deep-sea reducing habitats range from that of a completely anoxic milieu in which reducing substances accumulate, and which are suitable only for prokaryote life, to the highly reactive interface of oxic and anoxic environments where aerobic chemosynthesis and dependent animal life flourish. Total anoxia dominates in subsurface sediments, in hydrothermal aquifers and within organic remains. Oxic–anoxic interfaces are usually located on the seafloor at vent and seep discharge points and on or near organic remains. Subsurface mixing of oxic and anoxic fluids can occur in hydrothermal systems, permitting chemical oxidations and aerobic microbial growth below the seafloor (Karl, 1995).

Common to most seafloor reducing habitats colonized by animals and/or micro-organisms is the presence of micromolar to millimolar concentrations of hydrogen sulphide in escaping hydrothermal fluids, sediment pore waters or diffusing from organic remains (Johnson et al., 1988; Naganuma et al., 1996; Barry et al., 1997). At hydrothermal vents, organisms in direct contact with venting fluids are usually exposed to hydrogen sulphide. *In situ* chemical analysers can describe the chemical habitat of different vent species (Johnson et al., 1988; Sarrazin et al., 1999). Limited data from seeps suggest that dissolved sulphide does not escape from near-surface sediments, restricting the utilization of sulphide to animals that extend part of their body into the sediment to access the sulphide (clams, lamellibrachiid vestimentiferans) or to sediment micro-organisms. Sulphide concentrations may influence colonization patterns of vesicomyid clams (Barry et al., 1997). Naganuma et al. (1996) found, in sediment pore water, that sulphide concentrations and counts of autotrophic bacteria dropped sharply within a few decimetres of the vertebral axis of a whale skeleton. Vesicomyid clams appear to be restricted to sediments within 20 cm of whale bones (Bennett et al., 1994). Sulphide is probably present in the surface boundary layer on some areas of decaying whale bones, as indicated by the presence of small, symbiont-bearing bivalves, which take up sulphide through their gills.

Dissolved methane at above-background levels is usually detectable in hydrothermal fluids, subduction zone seeps and, of course, at hydrocarbon seeps. Hydrothermal fluids are the most chemically complex of the reducing solutions occurring in the marine environment. In addition to an abundance of trace, minor and major elements (e.g., Von Damm, 1995), hydrothermal fluids contain most substances known to support microbial chemosynthesis (Table 4.2), including H_2S, CH_4, H_2, Fe^{2+} and Mn^{2+}.

ORGANIC MATTER PRODUCTION IN REDUCING ENVIRONMENTS

Energy metabolism and carbon sources

Plant life is impossible in the total darkness of the deep sea, thus, food resources are at a premium. The discovery in 1977 of luxuriant oases of giant worms, clams and mussels clustering around hydrothermal vents over 2000 m deep (Corliss et al., 1979) came as a complete surprise to biologists, who scrambled to identify the food source for this unusual ecosystem. The presence of hydrogen sulphide in hydrothermal fluids, and an abundance of sulphide-oxidizing bacteria, were the first clues leading to the hypothesis that faunal communities at hydrothermal vents are

Table 4.2
Potential microbial metabolic processes in deep-sea reducing habitats [1]

Electron (energy) donor	Electron acceptor	Carbon source	Metabolic process
Aerobic conditions			
H_2	O_2	CO_2	*H oxidation*
HS^-, S^o, $S_2O_3^{2-}$	O_2	CO_2	*S oxidation*
Fe^{2+}	O_2	CO_2	*Fe oxidation*
Mn^{2+}	O_2	?	Fe oxidation
CH_4 (and other C-1 compounds)	O_2	CH_4, CO_2, CO	Methane (C-1) oxidation
Organic compounds	O_2	Organic compounds	Heterotrophic metabolism
Anaerobic conditions			
H_2	CO_2	CO_2	*Methanogenesis*
H_2	S^o, SO_4^{2-}	CO_2	*S and sulphate reduction*
H_2	NO_3^-	CO_2	*H oxidation*
Organic compounds	NO_3	Organic compounds	Denitrification
CH_4	SO_4^{2-}	?	Methane oxidation
Organic compounds	S^o, SO_4^{2-}	Organic compounds	S and sulphate reduction
Organic compounds	Organic compounds	Organic compounds	Fermentation

[1] Processes known to involve the chemosynthetic production of new organic matter are given in italics. Heterotrophic metabolism also occurs in these systems and involves the decomposition of organic matter produced at vents or imported from the surrounding ocean. Organisms representative of most of these forms of metabolism have been isolated and cultured from hydrothermal vent samples but the quantitative importance of the various electron donor and acceptor pathways in overall ecosystem metabolism is poorly understood. Adapted from Karl (1995).

sustained by micro-organisms that chemosynthesize organic matter from carbon dioxide and mineral nutrients; photosynthetically-produced organic matter contributes little. The microbes catalyze oxidation of hydrogen sulphide and other reducing substances present in vent fluids, and use the chemical energy released to produce adenosine triphosphate (ATP) required for chemosynthesis. Since hydrothermal fluids are formed by reaction of sea water with hot rock, researchers then understood that vent ecosystems were ultimately powered by heat from the mantle.

Chemosynthesis is also the primary energy source for faunal communities in continental-margin seep environments although, in this case, the reducing substances are derived, not from the high-temperature reaction of rock with crustal seawater, but from the degradation of sedimentary organic matter. In subduction-zone settings, large-scale tectonic compression of sediments expels interstitial fluids containing methane. These fluids migrate along faults and fractures and, as they approach the seafloor, they can mix with near-surface pore waters which are slightly more oxidizing and contain dissolved sulphate (Martin et al., 1996). In these mixing zones, microbially catalyzed oxidation of methane using sulphate as an oxidant can then add hydrogen sulphide to seep fluids. At the seafloor, both hydrogen sulphide and methane provide energy for microbial chemosynthesis.

Common microbial processes

Chemosynthetic microbial growth in reducing habitats is coupled to the oxidation of H_2S, CH_4, H_2, Fe^{2+}, Mn^{2+} and other substances. Karl (1995) has provided an extensive discussion of common carbon fixation pathways, the major physiological groups of bacteria listed in Table 4.2, and considered the role of bacteria in the hydrothermal environment. A thermodynamic modelling study by McCollom and Shock (1997) identified aerobic sulphide oxidation as the most important potential energy source for chemolithoautotrophic growth in seafloor hydrothermal systems (Fig. 4.7). Chemolithoautotrophy is the generation of organic carbon compounds using chemical energy derived from reduction or oxidation of non-organic compounds. Both aerobic and anaerobic methane oxidation are probably more important chemosynthetic processes at continental-margin seeps where methane is initially the most abundant reducing substance in migrating fluids. Technically speaking, organic-matter production based on methane oxidation cannot always be considered as primary production. When the carbon fixed comes from organically-derived methane rather than from carbon dioxide, it may simply represent the re-incorporation of organic carbon fixed by photosynthesis; this process is not very different from the derivation of energy and carbon from dissolved sugars by heterotrophic bacteria. On the other hand, most if not all methane at hydrothermal vents comes from a mineral source, and methanogenic bacteria at vents can generally be considered as primary producers.

At seeps, and in association with organic remains,

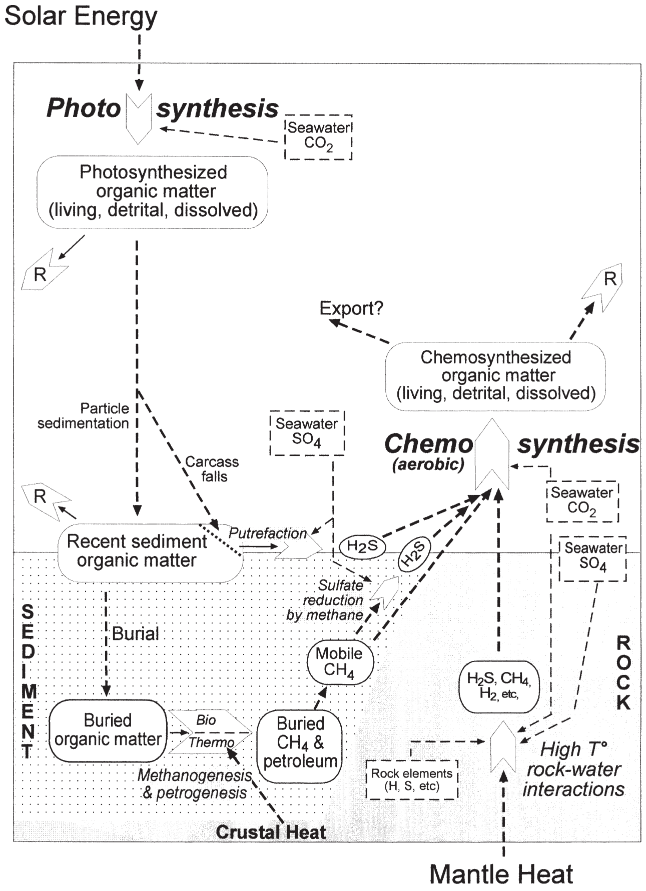

Fig. 4.7. Simplified energy-flow diagram illustrating the relationship of chemosynthetic organic-matter synthesis in deep-sea reducing habitats to mantle (heat) and solar (light) energy sources. Boxes represent principal reservoirs of energy, and arrow-head symbols indicate energy transformation from one form to another. Physical displacement of potential energy is indicated by dotted lines. Solar energy enters the flow by incorporation into organic matter during photosynthesis in the surface ocean. Energy embodied in photosynthetic organic matter is primarily respired (lost as heat); some is buried in sediments or, in the case of large carcass falls, directly incorporated into reduced inorganic compounds during putrefaction on the seafloor. Some of the carbon in buried organic material is converted to methane and other hydrocarbons through biogenic or petrogenic processes, and can later be released at seafloor seeps. Petrogenic (thermogenic) production of methane requires crustal heat available in deeply buried sediments; that heat derives from radioelements in the Earth's crust. In accretion settings, crustal rock is heated at depth and reacts with infiltrating seawater to form hydrothermal fluids (containing H_2S, CH_4, H_2, etc.). Mantle and crustal heat must first be converted to chemical energy before it can power chemosynthesis of organic matter. Chemosynthesis in reducing habitats can thus be driven by mantle heat only (hydrothermal vents), solar energy only (organic remains), or by a combination of crustal heat and solar energy (seeps).

two anaerobic processes are important to chemosynthesis based on sulphide oxidation. Sulphide (H_2S) at subduction-zone seeps is produced in near-surface sediments by anaerobic oxidation of methane in migrating fluids, using sulphate as the oxidant (Fig. 4.7). This process may also add extra hydrogen sulphide to low-temperature hydrothermal fluids, which mix with crustal sea water prior to venting. Reduction of sulphate in sea water also occurs as a terminal metabolic process in the anaerobic degradation of organic remains, providing sulphide for development of microbial mats and invertebrate symbioses.

Whereas chemosynthesis is identified as a key, albeit unquantified, form of energy metabolism in reducing habitats, the significance of heterotrophic microbial processes in these environments is virtually unknown (Karl, 1995). Elsewhere in the ocean, organic-matter degradation and nutrient recycling by micro-organisms are important to ecosystem function. On organic remains, heterotrophy necessarily dominates

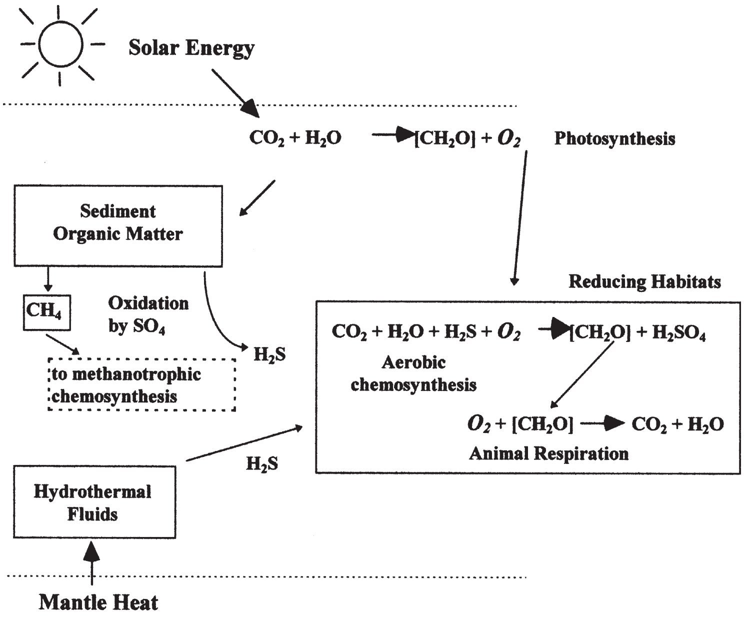

Fig. 4.8. Representative energy-consuming (chemosynthesis) and energy-producing (respiration) reactions in reducing habitat metabolism and their relationship to solar and geothermal energy sources. For simplicity, only chemosynthesis based on sulphide oxidation is illustrated. A requirement for dissolved O_2 links aerobic chemosynthesis and animal respiration to photosynthesis in the sunlit surface ocean. Geothermal energy is incorporated into potential chemical energy in hydrothermal fluids through high-temperature rock–water interactions enriching fluids in H_2S, which is subsequently oxidized by chemosynthetic micro-organisms. Hydrogen sulphide in organic remains and seep habitats is derived directly or indirectly (CH_4 oxidation by SO_4) from degradation of photosynthetically produced organic material.

over chemosynthesis in terms of energy flow. Whether vents and seeps are primarily flow-through systems which export organic matter to the surrounding deep sea remains to be seen.

Links to photosynthesis

Reducing ecosystems, as we know them, are not completely independent of sunlight. All animals and many micro-organisms at vents require dissolved oxygen for their metabolism (Fig. 4.8). Since dissolved oxygen in the world's oceans is a by-product of photosynthesis, there is a critical link between ecosystems such as those of the vents and the photosynthetic ecosystems in the upper layers of the sea. Had photosynthesis not evolved on Earth, hydrothermal vents would only be populated by micro-organisms independent of dissolved oxygen, such as methanogens deriving energy for growth by converting hydrogen into methane using carbon dioxide as an oxidant. Seep ecosystems are even more closely linked to photosynthesis. As at vents, molecular oxygen is required for animal and some microbial respiration. In addition, the methane that powers seep chemosynthesis is derived from photosynthetically-produced organic matter, which may be very old (seeps associated with subduction and salt tectonics) or of more recent origin (organic debris).

Free-living bacterial growth

The synthesis of organic-matter by free-living micro-organisms appears important in reducing habitats but remains unquantified. Chemosynthesis in biofilms and filamentous mats on mineral and animal surfaces provides food for grazing and deposit-feeding animals. Microbial chemosynthesis also occurs in subsurface hydrothermal conduits and in water-column plumes that overlie vent fields, but faunal exploitation of microbial biomass produced in these two environments is not well known.

During eruptions, a bolus of hot water is pushed through the seafloor and emerges as a "megaplume" with distinct chemical features. Formation of such a plume event in the deep sea occasions relatively rapid changes in bacterial and viral abundances over periods ranging from days to weeks (Juniper et al., 1998; Cowen et al., 1999). The sources of such populations include the normal deep sea, the seafloor, and sediments underlying it.

Symbioses

A great deal of organic-matter synthesis occurs in symbiotic associations between bacteria and invertebrate hosts, in which the chemosynthetic symbionts convert carbon dioxide into organic matter which nourishes themselves and their hosts. Vestimentiferan and bivalve symbioses in seep environments are dependent on aerobic oxidation of sulphide or methane. There are three general models for the functioning of the commonest forms of host–symbiont associations in reducing environments: vestimentiferan tube worms, vesicomyid clams, and bathymodiolid mussels (Fisher, 1990). The most integrated symbiosis occurs in the tube worms, which have no mouth or digestive system and are entirely reliant on their symbiotic bacteria for nutrition. Pogonophora are all dependent on symbiotic chemoautotrophic bacteria. Evidence for sulphide-fuelled chemoautotrophy first came from studies of the vent tube worm *Riftia* (Cavanaugh et al., 1981; Felbeck, 1981). Similar dependence on sulphur oxidation is known in the cold-seep genera *Escarpia* and *Lamellibrachia* (see Southward et al. (1995) for review). While no one has examined deep cold-seep perviate Pogonophora for chemoautotrophy, it is worth noting that methanotrophic bacteria are found in one pogonophore species living at a shallow-water methane seep (Schmaljohann and Flügel, 1987), while all other perviates investigated use sulphur-oxidizing (thiotrophic) bacteria. In vestimentiferans, symbionts are housed in a specialized organ known as the trophosome. Substrates for microbial metabolism (HS^-, CO_2, O_2, etc.) are taken up at the branchial plume and transported to the trophosome in the worm's blood by a multiglobin system (Zal et al., 1998). Some vestimentiferans absorb sulphide through the tube (Scott and Fisher, 1995).

The vesicomyid clams are filter-feeding animals, but their digestive tract is highly reduced and they are unable to survive without a supply of sulphide for their symbionts. They host their symbionts in the tissue of their large modified gills. Carbon dioxide and oxygen diffuse directly into the gills from the external environment, while the clams take up sulphide into their blood through the foot, which they extend into fractures or sediments where dissolved hydrogen sulphide is available. The mussels also house their symbionts in gill tissue, but have a functional digestive system. The best-studied mytilid symbiosis is that in *Bathymodiolus thermophilus* from the East Pacific Rise, which hosts sulphide-oxidizing bacteria. It may represent a more primitive symbiosis, compared to the vestifmentiferans or the vesicomyid clams. For example, it lacks the specific blood proteins for the binding and transport of sulphide and oxygen that are found in the vestimentiferans and clams. Unlike the vesicomyid clams, filtration of particles of organic matter from the surrounding water appears to provide a supplement to the mussel's nutrition (Page et al., 1990), although the digestive tract is reduced in some species (Von Cosel and Olu, 1998).

Methanotrophic symbioses are known in mussels from seeps on the Louisiana Slope (Childress et al., 1986) and the much deeper Florida Escarpment seeps, as well as seep sites on the southern part of the Barbados accretionary prism (Olu et al., 1996b). Some mussels are known to house sulphide-oxidizing and methanotrophic symbionts within a single bacteriocyte, suggesting an ability to exploit both hydrogen sulphide and methane as energy sources (Fisher, 1997). Nix et al. (1995) have demonstrated growth rates, when methane is abundant, to be comparable to those of shallow-water mussels.

Three other families of bivalves bearing symbionts are known from reducing habitats in both shallow and deep water: Families Lucinidae, Solemyidae and Thyasiridae. They are generally deep burrowers, requiring significant sediment accumulations. More than 20 symbioses, all thiotrophic, have been identified among the lucinacean bivalves (Families Lucinidae and Thyasiridae) (Anderson, 1995), and several more have been described among the solemyids (Fisher, 1990). Lucinids, present in sediments from the intertidal zone to the deep-sea, host symbiotic bacteria in their fleshy gills. Thyasirids are related bivalves which may represent a more ancestral stage in the association with symbionts, as the microbes are extracellular and sometimes quite scarce. Dependence on chemoautrophic symbiosis has not been demonstrated for cold-seep species belonging to any of these three families (Sibuet and Olu, 1998).

An unusual methanotrophic symbiosis in a new species of cladorhizid sponge has been described from mud-volcano seeps on the Barbados accretionary prism (Vacelet et al., 1995). While symbiotic bacteria are common in sponges, this is the first case of an association with autotrophic bacteria. Symbionts are extracellular, but appear to be digested intracellularly.

Several very specific extracellular symbioses have been described from polychaetes, shrimps and gastropods endemic to hydrothermal vents. Polychaetes of the genus *Alvinella* which colonize hydrothermal chimneys on the East Pacific Rise have a characteristic bacterial flora associated with their integument, on which there are well-developed attachment structures for bacteria (Gaill et al., 1986; Juniper and Martineu, 1995). Bresiliid shrimps on the Mid-Atlantic Ridge have specific attachment structures for bacteria within an enlarged branchial chamber. In the shrimp the ecto-symbionts likely have a nutritional function, while oxidation of reduced sulphur on the polychaete may protect the host's respiratory process. Less specific microbial growth on other animal surfaces at hydrothermal vents are probably best described as fouling. The question of extracellular growth of micro-organisms on the tissues, tubes and exoskeletal surfaces of hydrothermal-vent animals is in need of systematic comparative study to clarify the specificity of observed associations and their possible nutritional and detoxifying roles.

THE FAUNA

Reducing environments span a range of conditions from uninhabitable to mildly challenging. Despite a great dependence by some microbial autotrophs on hydrogen sulphide, it is a metabolic poison for aerobic metazoans, and is incompatible with an abundant oxygen supply. Such conditions select for a small pool of inhabitants compared to the huge diversity available in the deep sea. The adaptations required to partake of the enhanced productivity of such environments have greatly limited the dominant inhabitants to a relatively few groups. While the oasis analogy is used to describe these islands of plenty (i.e. Carney, 1994), few taxa have found it to their liking. Much attention has been paid to animals from hydrothermal vents because of their unusual adaptations or systematic positions. While information from seeps is more limited, data from recent collections lengthen the list of seep species and reveal more about their relations with other faunas. Many discoveries are still so new that systematists remain busy. A major problem for all work in the deep sea is the poor support for systematics, which means that experts in many faunal groups are few.

Common taxonomic characteristics

There are common links across reducing habitats. In some cases, relationships can be traced among habitats, although phylogenetic work is limited to a few taxa. One can imagine that adaptations to sulphide-rich habitats provide entry to similar habitats throughout the ocean. However, extreme conditions have invoked extreme adaptations which often separate taxa at fairly high levels from their nearest relatives in the deep sea. Thus, most animals found at hydrothermal vents are newly-described species, as are about half the genera (Tunnicliffe et al., 1996); the few species that are also found in the "normal" deep sea tend to live on the periphery of the vents or occur as occasional visitors. Many endemic taxa occur at vents – these animals are presently not known elsewhere. With the discovery of seep and whale-bone faunas, the similarity to vent animals was immediately recognized and the concept that these habitats might serve as dispersal stepping stones for vents was broached (Hecker, 1985; Smith et al., 1989). In fact, while few species are held in common (Smith and Baco, 1998), many genera and families are shared.

Tunnicliffe et al. (1996) and Sibuet and Olu (1998) have discussed the common elements of the faunas of vents, seeps and deep-sea organic remains. Relationships among these faunas appear very restricted at the level of species; however, at the level of genera and families the similarity reflects some evolutionary connection through common ancestors. Certain taxa re-occur: vesicomyid clams, bathymodiolid mussels and vestimentiferans – all of which contain symbionts – are the most famous examples. To date, the species found in common among vents, seeps and carcasses number less than five. The polychaete *Nereis* and the squat lobster *Munidopsis* are also present in low-oxygen basins. The former is well-known for its ability to tolerate low oxygen concentrations in intertidal sediments, and the latter is wide-ranging throughout the deep sea.

Vestimentiferans and pogonophorans

Vestimentiferans (= obturate pogonophorans) range in length from millimetres to metres. They have been considered to be annelids, pogonophorans or a separate phylum, depending upon authority. Southward (1988) has provided extensive descriptions of the anatomy and functions of these animals. Usually, a

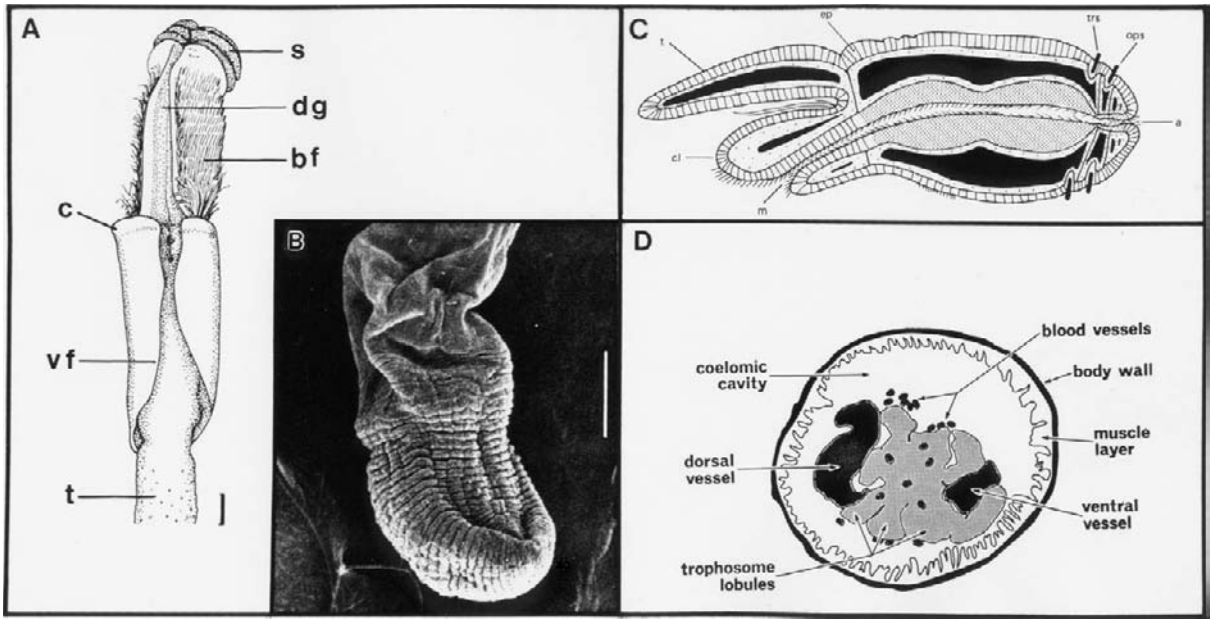

Fig. 4.9. The vestimentiferan *Ridgeia piscesae* from Juan de Fuca Ridge. A. The anterior end of the worm showing obturaculum with branchial filaments and the muscular vestimentum that wedges the worm in its tube; s, protective ‘saucers’; dg, dorsal groove; bf, branchial filaments; c, collar; vf, vestimental fold; t, trunk. Scale bar: 2 mm. B. Scanning electron-microscope image of the opisthosome at posterior end to illustrate the segmentation reminiscent of annelids. Scale bar: 250 µm. C. Sketch of the two-tentacle stage of a *Ridgeia* juvenile which has settled but appears to be mobile and capable of ingesting microbes; coelomic spaces are black, gut endoderm is heavily stippled and trophosome has not yet developed: a, anus; cl, cephalic lobe; ep, epithelium; m, mouth; ops, opithosome seta; t, tentacle; trs, trunk seta. Size about 300µm. D. Cross-section of an older specimen with developed trophosome to house symbionts; there is no sign of gut here and gonads will develop later. Size about 2 mm across. A and C adapted from Southward (1988).

red branchial crown extends from the tube, while the body is wedged in by a muscular collar and lower opisthosome (Fig. 4.9a,b). Early in life, these animals have a functional gut allowing ingestion of microbes in benthic habitats (Fig. 4.9c). The gut soon closes, and all vestimentiferans acquire chemosynthetic symbiotic bacteria (Cavanaugh et al., 1981; Felbeck, 1981) in the trophosome (Fig. 4.9d). These tubicolous animals reside in waters, hot and cold, where both oxygen and sulphide are available (Childress and Fisher, 1992). The separate sexes produce gametes which fertilize on the animal or in the water, but the resultant larvae have not been captured; initial stages of embryogenesis and development are known from culture (Young et al., 1996). The largest vestimentiferan, *Riftia pachyptila,* inhabits vents of the East Pacific Rise. The ability of this animal to deal with large concentrations of sulphide without poisoning itself is impressive. A special molecular transport system in its blood immobilizes sulphide and oxygen (Somero et al., 1989; Zal et al., 1998). Moreover, *Riftia* is able to take advantage of temporal changes in the concentrations of these compounds and store excess gases.

At vents, different obturate genera appear in different biogeographic regions. While in the northeastern Pacific only one species is found, several are known on the East Pacific Rise. The genus *Lamellibrachia* is notable for its wide distribution from vents in the western Pacific to seeps in the eastern Pacific and western Atlantic; there are also records on the Uruguay margin and on coffee beans sunk near Portugal (Southward et al., 1996). Cold-seep vestimentiferans live in a different flow regime. Sulphide is very low around their gills, but high in the sediments in which the worm bases are buried. Here, sulphide may be taken up through the thin tube at the posterior end of the worm, not at the branchiae (Scott and Fisher, 1995).

Perviate pogonophorans are rare at vents, not uncommon at deep seeps, but most abundant and diverse in low-oxygen basins where sulphide builds in the sediments. The symbionts of these animals are in the lower trunk, where sulphide diffuses across a permeable tube. Perviates range in depth from 30 m in

Norwegian fjords to 10 000 m in trenches. Monoliferan pogonophorans are found in sunken organic debris – even clothing. Monoliferans and perviates are recorded from much deeper water than the vestimentiferans of vents and seeps. Whether this distribution relates to depth limitations or the location of the habitats is unknown.

Bivalves

A large amount of biomass is held in bivalves of the families Lucinidae, Thyasiridae, Solemyidae, Mytilidae and Vesicomyidae. Despite their long geological history and likely association with sulphide-rich habitats (Reid and Brand, 1986), the first three families are not common at vents. Their contribution to total biomass and productivity at vents and seeps is probably minor, but their deep-burrowing habit makes them difficult to observe quantitatively or to sample from submersibles. Lucinids, present in sediments from the intertidal zone to the deep sea, host symbiotic bacteria in their fleshy gills (Fisher, 1990). Their ability to establish at very low sulphide levels suggests that these animals may access the local concentration of sulphide through extensive tubes which enhance interaction with iron sulphides in the sediments (Dando et al., 1985). Thyasirids live in burrows where sulphide levels are usually low (Dando et al., 1986). Solemyids may lose the gut altogether, and are most commonly known from areas of sewage outfall or pulp log accumulation where sulphide levels may reach $12\,\mathrm{mM}\,\ell^{-1}$ (Childress and Lowell, 1982).

About seventeen mussel species are known from vents and seeps – most are in the new subfamily Bathymodiolinae (Gustafson et al., 1998). The geographic extent of *Bathymodiolus* is relatively large at both vents and seeps, although there are notable absences at the deep seeps off Japan, seeps of the eastern Pacific, and vents of the northeast Pacific. Distel et al. (2000) have proposed that sunken wood and whale carcasses may be important phylogenetic vectors in the dispersion of seep and vent species. Mussels are recorded from a wide range of environmental conditions, where they may occur in groups of hundreds to thousands. Fisher et al. (1988b) have described a broad variability in physiological characteristics for one vent species (*Bathymodiolus thermophilus*), which appears to be related to highly variable water flow. Mussels are common at seeps in both the Atlantic and the west Pacific. These animals can use the abundant methane in the seep habitat; two species are known to have methylotrophic microbes as symbionts (Childress et al., 1986; Cavanaugh et al., 1987).

The "giant vent clam" *Calyptogena magnifica* is restricted to low-flow areas where variability in dissolved gases is reflected in several physiological indices (Fisher et al., 1988a). Both vent and seep vesicomyids can concentrate dissolved sulphide in their blood at levels higher than those in the immediate environment (Scott and Fisher, 1995). Vesicomyids are known from nearly all seep sites described to date (Sibuet and Olu, 1998). In Sagami Bay ("Jps" site in Fig. 4.1), *Calyptogena soyae* populations reach densities of about 1000 individuals m^{-2} (Hashimoto et al., 1989). Sulphide concentrations peak around $0.6\,\mathrm{mmol\,g}^{-1}$ about 20 cm into the sediment (Hashimoto et al., 1995). Deeper populations in the Peru Trench yield even higher peak abundances (Olu et al., 1996a). Studies (i.e. Juniper and Sibuet, 1987; Rosman et al., 1987) yield glimpses of the great extent of such communities in the deep sea and leave open the possibility that many more such areas remain to be discovered.

Shrimps

Caridean shrimps are known from most vent regions, and from seeps in the Gulf of Mexico, Florida and Barbados areas. They are presently placed in the Family Bresilidae. Phylogenetic work on one mitochondrial locus has identified three clades within the vent/seep shrimps, one of which is exclusive to the Mid-Atlantic Ridge (Shank et al., 1999). Interest focused on this group with the discovery of vents on the Mid-Atlantic Ridge where they constitute a large part of the biomass. Several species are known from venting chimneys where densities reach $3000\,\mathrm{m}^{-2}$ (Gebruk et al., 2000). These shrimps swarm around hot fluids, and many specimens are scarred from hot-water contact (Gebruk et al., 1997). One species, *Rimicaris exoculata,* was named for its absence of normal eyes; but a large white organ on the dorsal carapace is capable of gathering very dim light in the infrared wavelengths (O'Neill et al., 1995; Van Dover et al., 1996b). High-temperature vents emit black-body radiation which may be visible to these animals, thus allowing them to relocate the "smokers" if dislodged by turbulence or their neighbours; presumably, the high sulphide levels are needed to encourage growth of their exosymbionts (Pelli and Chamberlain, 1989). Other vent shrimps have similar dorsal organs, though of lesser size.

Chorocaris chacei and *Rimicaris exoculata* encourage growth of filamentous sulphur bacteria on specialized mouthparts, which they then crop (Gebruk et al., 1993, 2000; Segonzac et al., 1993). Other species of shrimp either prey on *Rimicaris,* or are opportunists that can utilize organic matter from other shrimps, mussels and encrusting bacteria (Gebruk et al., 2000).

All the shrimps on the Mid-Atlantic Ridge have an extended larval life in the water column (Herring and Dixon, 1998), where they build up reserves of photosynthetic origin, including essential fatty acids. These reserves are used up during metamorphosis to the adult stage, while the bacteriophores develop (Gebruk et al., 2000). The shrimps are thus not wholly driven by chemosynthesis.

Faunal relations between seeps and vents

Vent and seep animals occupy geographically separate habitats, but many similarities in the assemblages exist. Although few species are shared, the many similarities among taxonomic groups indicate a strong historical linkage even if there is not extensive gene flow today. At most vents and seeps, biomass is dominated by bathymodiolid mussels, vesicomyid clams and vestimentiferan worms. Little is known about their symbiont origins beyond their placement in the gamma subdivision of the Proteobacteria and their independent origins among the host groups (Distel et al., 1988). While symbiont transmission between generations in the clams likely occurs through the eggs (Cary and Giovannoni, 1993), the vestimentiferan juvenile appears to acquire symbionts during a feeding benthic stage (Southward, 1988). The symbionts of vent vestimentiferans are very similar – if not the same – but are distinct from those at seeps (Feldman et al., 1997).

Genetic studies reveal that four invertebrate groups show close links between vent and seep species. Vent mussels are more derived than those at seeps, suggesting a later invasion of vents perhaps from seeps (Craddock et al., 1995). Peek et al. (1997) have described a more complicated situation for clam species complexes from vents and seeps. While each clade is limited to a single habitat, there is no clear overall ancestral habitat. Baco et al. (1999) have extended the vesicomyid work, to show that specimens from whale skeletons off California relate to three different clades found at both vents and seeps. The vestimentiferan lineage, however, could be a recent diversification. *Lamellibrachia* appears to be the basal taxon, suggesting that the tube worms at vents derive from seep ancestors (Black et al., 1997). McHugh (1997) has postulated that both vestimentiferans and pogonophorans belong within the Annelida; Rouse and Fauchald (1997) have suggested the family name Siboglinidae within the Polychaeta.

Among the gastropods, there are many families that are found at vents and seeps. Shared groups such as the Neolepetopsidae, Provannidae and Pyropeltidae are currently found nowhere else, and surely have close evolutionary ties (Tunnicliffe et al., 1998). However, some gastropod groups may have been sustained at vents long after their extinction elsewhere. The Neomphalina, for instance, are endemic at vents and show a deep phylogenetic split from their closest relatives when examined with molecular techniques; they may represent a relic group which has found a refuge at vents (McArthur and Koop, 1999).

COMMUNITY CHARACTERISTICS

Biomass and growth

There are few comprehensive estimates of production and biomass in reducing environments. Quantitative sampling in the deep sea – particularly on hard substrata – remains difficult. Karl (1995) has provided an integrated review of microbial studies at vents. In diffuse waters, counts of microbes from 10^5 to $10^6\,\mathrm{ml}^{-1}$ are one to two orders of magnitude above normal deep-sea water; both water and surface abundances are patchy and variable. Difficulties with measurement of microbial production include providing the right conditions for microbial growth, and interpreting the results. There are many species of heterotrophic bacteria; hence, many measurements can often yield only overall figures for the growth of a mixotrophic community.

The highly patchy and irregular distributions of vent assemblages result in a wide range of biomass estimates: 2 to $15\,\mathrm{kg\,m^{-2}}$ (wet weight) for primary consumers and 0.03 to $0.5\,\mathrm{kg\,m^{-2}}$ for detritivores and carnivores (summarized in Chevaldonné and Jollivet, 1993) for vents on the northern East Pacific Rise. Local *Riftia* populations exceed $50\,\mathrm{kg\,m^{-2}}$ (Fustec et al., 1988). At seeps, most of the biomass is present as bivalves; upper estimates range between

2 and 20 kg m^{-2}. The values exceed average deep-sea estimates by four orders of magnitude (Hashimoto et al., 1989; Olu et al., 1996a).

A few time-series studies have noted growth characteristics of some species. Large individuals of *Calyptogena magnifica* on the East Pacific Rise are estimated to reach ages between 20 and 40 years, and testify to a relative longevity of some vent sites (Lutz et al., 1988). Rates are highly site-dependent, the highest values occurring in areas of high fluid flux and sulphide delivery. Mussels can grow in length by a centimetre a year (Roux et al., 1989). Tube worms from vents are most impressive: species colonizing new vents with optimal conditions grow almost a metre per year (Lutz et al., 1994; Tunnicliffe et al., 1997). On the other hand, the longevity of seep vestimentiferans is equally impressive: Bergquist et al. (2000) have estimated ages over 200 years for seep *Lamellibrachia,* although variability in growth rate is very high.

Benthic fauna of low-oxygen basins has been effectively sampled in many areas using box corers. While the literature generally reports diminishing biomass as oxygen content decreases, several studies report enhanced biological activity in the region of the oxygen minimum zone on the continental shelf in the eastern Pacific (Diaz and Rosenberg, 1995). Organisms here benefit from high flux of relatively undegraded organic matter, so that abundance and biomass peak on the edges of the zone of oxygen depletion.

Diversity and succession

Diversity of these communities is extremely low compared to that in deep-sea sediments (Grassle et al., 1985); overall, there are only several hundred species recorded at all vents and seeps (Sibuet and Olu, 1998; Tunnicliffe et al., 1998), compared to the millions suspected in the deep sea (Grassle and Maciolek, 1992). Diversity in mussel clumps from the Mid-Atlantic Ridge is lower than in intertidal mussel assemblages from Alaska (Van Dover, 2000). Species abundances at vents and seeps vary around the world. Diversification of several vent groups (such as copepods) has occurred in the equatorial eastern Pacific region. Many possible factors influencing the accumulation of species need examination. Seafloor spreading rate may exert a fundamental control on abundance of vents on a ridge, the stability of those vents and their variety – all of which likely are reflected in diversity (Juniper and Tunnicliffe, 1997). Factors that influence speciation at hot vents are now under study. Within regions there is surprisingly good gene flow for most vent species studied (Jollivet, 1996; Vrijenhoek, 1997), although range disjunctions clearly indicate major barriers between regions.

Hydrothermal vent communities live in an unstable habitat, because of their close links to a fluctuating fluid supply and their location atop the most tectonically and volcanically active feature on the Earth. Volcanic eruptions have been recorded by seafloor acoustic hydrophones (Fox et al., 1995) three times on Juan de Fuca Ridge from 1993 to 1998. At one site, microbial colonization was immediate, and invertebrate larvae were recruited from a distance of many tens of kilometres within a year; in two years, tube worms one metre long dominated a diverse community in high-sulphide conditions (Tunnicliffe et al., 1997). In three years, the system was dead. Shank et al. (1998) described a sequential pattern of colonization on the northern East Pacific Rise, after pre-existing communities were overrun with lava. The tube worm *Tevnia* was first to appear, then *Riftia,* and the mussel *Bathymodiolus thermophilus* arrived three years later. This mussel competes for space and vent water with *Riftia,* and can displace the vestimentiferan, likely by its ability to alter local water chemistry and redirect water flow (Hessler et al., 1985; Johnson et al., 1994; Desbruyères, 1998). On the southern East Pacific Rise where the ultrafast spreading is fed by high magma supply, vast areas of apparently new venting were in early stages of succession when observed; indeed, different ages of flows could be distinguished by the associated fauna (Geistdoerfer et al., 1995).

Trophic relations

Tracking trophic connections in these remote communities is not easy. Interpretations from feeding structures, gut contents, behavioural observations and comparisons to nearest relatives can slowly describe the food web. Chemolithoautotrophs supply the basic organic carbon in the form of symbionts, microbial mats and suspended cells. The relative importance of photosynthetic carbon in different sites is not yet known. For most vents and seeps, the major consumer biomass lies in the symbiont hosts. On the Mid-Atlantic Ridge shrimps predominate, thus shifting the trophic pyramid to the grazers, although a symbiotic relationship is proposed through epibionts on some species (Polz et al., 1998). Biofilms and filamentous mats on mineral and animal surfaces provide food for grazing and deposit-feeding animals, while suspension feeders use the suspended material. Predators and scavengers, some local specialists and others attracted from the surrounding deep sea, augment the food web (Fig. 4.10). The vents have fostered development of endemic predators such as certain zoarcid fishes and bythograeid crabs, although deep-sea octopus and crabs are abundant in the vicinity.

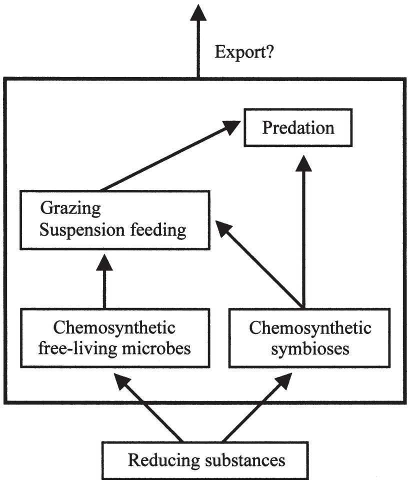

Fig. 4.10. Simplified food web of deep-sea reducing habitats. Pathways and boxes remain to be quantified. The role of heterotrophic bacteria in this system may not be trivial.

The principle of “you are what you eat” is adopted in studies of isotopes in reducing habitat animals. Microbes that fix carbon dioxide discriminate markedly against the heavier carbon isotope if carbon is not limiting, and the depleted $^{13}C/^{12}C$ signature is evident in symbiont hosts (Southward et al., 1981). By combining results from both carbon and nitrogen isotopes, some interpretation of trophic relations among animals is possible (Van Dover and Fry, 1989). There is clear evidence from stable isotopes for the utilization of chemosynthetic food sources by vent organisms, and isotopic shifts with trophic level are recognizable. However, causes of variation in values among animals and sites appear complex, and may not be resolved by use of stable isotopes alone (Southward et al., 1994; Fisher, 1995, Pond et al., 1998). A complementary approach examines fatty acid signatures: the characteristic patterns of long-chain structure in marine invertebrates make these molecules useful as biomarkers. Vent vestimentiferan and bivalve tissues showed strong signatures indicating procaryotic contributions to fatty acids, whereas bivalves from shallow reducing habitats showed input from eucaryote sources; some non-symbiont input is required for certain essential fatty acids not available from bacteria (Ben-Mlih et al., 1992; Fullarton et al., 1995). Further to this last point, Pond et al. (1997a,b) have recently provided lipid evidence from biomarkers for significant consumption of phytoplankton material by early life stages of vent shrimps on the Mid-Atlantic Ridge. This discovery will likely lead to other research into the use of photosynthetic food sources by larval, juvenile and even adult vent organisms. Chemosynthesis remains an unquantified food source in all reducing habitats in the ocean. The possibility of supplementary or even major dependence on photosynthetic sources should not be ignored.

Relations with the deep sea

The productivity of vents, seeps and carcasses is anomalous in the deep sea. One would expect that the surrounding deep-sea community would be augmented, at least in biomass, by the presence of these systems. Greater abundances are not often striking, but increased abundances in crabs, suspension feeders and fish near vents (Tunnicliffe and Jensen, 1987; Arquit, 1990; Gebruk et al., 1997) and infauna near skeletons (Smith et al., 1997) have been documented. Carney (1994) has suggested several studies to examine why seeps and vents have not attracted a greater peripheral assemblage of predator and foraging specialists. Chemical toxicity may be a primary factor; with the cessation of venting, the senescent hydrothermal community is invaded by scavengers such as gastropods, decapods and copepods. Whether seep production is important to surrounding ecosystems is ambiguous. While mobile predators are more abundant at seeps, a clear shift in the carbon-isotope ratio in their tissues away from a photosynthetic signature remains to be demonstrated (MacDonald, 1998).

Another link to the surrounding deep sea lies in the hydrothermal plume that disperses about 100 to 500 m above the bottom. The elevated bacterial biomass in these plumes is probably a result of microbial oxidation of vent-derived manganese and methane (Cowen et al., 1990). High concentrations of zooplankton at the upper boundary of hydrothermal plumes indicate a mechanism for upward flux of plume productivity into the water column, although this pathway remains to be quantified. Shallow-water plankton migrates to depths below 1500 m to graze in the plume (Burd and Thomson, 1995). Vereshchaka and Vinogradov (1999) found a similar aggregation of zooplankton biomass on upper and lower layers of the plume over vents on the Mid-Atlantic Ridge. Sedimentation rates for chemosynthetically-derived organic carbon beneath hydrothermal plumes can equal the flux of organic carbon from the photic zone (Roth and Dymond, 1989).

ISSUES PECULIAR TO VENTS

The hydrothermal-vent ecosystem offers many unusual features in the context of its location, dependencies, featured adaptations and constituency. The reader is directed elsewhere for commentary on diversity (Jollivet, 1996), population genetics (Vrijenhoek, 1997), antiquity (McArthur and Tunnicliffe, 1998), biogeography (Tunnicliffe et al., 1998), reproductive biology (Tyler and Young, 1999) and ecology (Van Dover, 2000). Juniper and Tunnicliffe (1997) have discussed the limitations of current knowledge of this ecosystem. In addition, recent summaries of vent-biology studies are in the conference proceedings edited by Biscoito et al. (1998). Here, we comment on two interesting features of this habitat: stability and dispersion. The location atop a changeable feature – the mid-ocean ridge-crest – means that these communities are directly affected by the volcanic and tectonic processes driving plate tectonics. This irregular habitat is dispersed linearly.

Stability and predictability

Faunal communities of reducing habitats have evolved to exploit an energy source that is discontinuous in both space and time. High-frequency variation in conditions for life is common in the hydrothermal-vent environment. Habitat can alter drastically over periods ranging from days to months, as mineral accretion and tectonic events modify hydrothermal flow through subsurface conduits (Fustec et al., 1987; Tunnicliffe and Juniper, 1990; Sarrazin et al., 1997). Hydrothermal vents tend to occur in clusters on the scale of 10–100 m, or in fields with a common subsurface heat source. Whereas individual orifices may be unstable, vent fields are active for relatively long periods of time. Sites in the eastern Pacific discovered 15 to 20 years ago have since evolved noticeably, but are all still actively venting and supporting life (Hessler et al., 1988; Desbruyères, 1998). Some vent sites may be very long-lived – to tens of thousands of years – as evidenced by the accumulation of some large mineral deposits (Hannington et al., 1995; Lalou et al., 1995). While the literature tends to emphasize the ephemeral nature of vents, it is important to stress that some sites appear quite stable, and others have likely maintained continual venting in the general vicinity even if individual vents are short-lived.

Volcanic eruptions can cause major perturbations of hydrothermal systems and associated communities. A submersible cruise to 9ºN on the East Pacific Rise in 1991 discovered evidence of a very recent (days to weeks) seafloor eruption, and the partial destruction of vent communities. Subsequent recolonization was very rapid, beginning with a burst of subsurface and seafloor microbial growth (Haymon et al., 1993; Shank et al., 1998). The sequence of microbial bloom and faunal colonization of new vent fields was observed again following a remotely-detected eruption at the CoAxial Segment on the Juan de Fuca Ridge in 1993 (Juniper et al., 1995; Tunnicliffe et al., 1997) and the Axial Volcano which extruded lavas over tube-worm fields in 1998 (Embley et al., 1999) (Fig. 4.3). While seafloor eruptions may be locally destructive, they represent a renewal of the subsurface heat source driving the hydrothermal system. At fast and superfast spreading centres, where volcanic activity is most intense, a high frequency of eruption in time and space also has the effect of creating abundant habitat. Juniper and Tunnicliffe (1997) have suggested that habitat abundance may counter instability on these ridges in supporting regional diversity. The same forces that disturb venting at a particular location on the East Pacific Rise (i.e. robust magma supply) will also assure that venting is continuously present within a short distance of the disturbed site.

Dispersal

Spatial distribution of the vent habitat can be likened to that in island chains or the alpine of mountain ranges. One may suppose that dispersal from one site to another poses a particular adaptive challenge. The dispersal stage of most vent inhabitants is a pelagic larva, as is found in most marine invertebrates. Some marine larvae can live for months in the water, and thus have the potential for broad distributions. It is interesting to note that few vent species transgress the different regions shown in Fig. 4.1 (Tunnicliffe et al., 1998). While little is known of the basic biology of most vent species, examination of reproductive features to date reveals no unusual or universal dispersal mode adopted by vent invertebrates (Tyler and Young, 1999). Direct-development, short-dispersing (lecithotrophic) larvae and long-dispersing (planktotrophic) larvae are all known among vent animals – and different modes may occur in closely related species (Mullineaux and France, 1995). It is unlikely that species range is related to the mode of larval development (Jollivet et al., 1998). The image of vents as highly unstable habitats has led to the expectation of a 'weed' strategy among these animals. The lack of support for this concept points to other directions for research. One is that adaptation to instability may not lie only in dispersability – other ecologic adaptations are also important (McHugh and Tunnicliffe, 1994). Another is that the basic hypothesis may be flawed: many vent species may have evolved in relatively stable vent conditions.

Short-range dispersal certainly must affect within-region distributions and gene flow. Tiny larvae must rely on transport by ocean currents which often run parallel to the ridge crest. Peak velocities of tidal flows could move larvae over a kilometre in a few hours (Mullineaux and France, 1995). Another important mechanism may be the hydrothermal plumes that rise some 300 m above the seafloor (Kim et al., 1994). 'Megaplumes' associated with eruption push hydrothermal fluids up over 1000 m and may provide a rare but effective mechanism of long-distance transport. Gene flow along hundreds of kilometres of ridge crest tends to be relatively high, and only large offsetting transform faults induce lower population communication (Vrijenhoek, 1997). The species noted above as initial colonizers in succession may be particularly suited to local dispersal and establishment. Future studies will hopefully show if later species are less efficient in dispersal or whether habitat conditioning is more important.

ISSUES PECULIAR TO SEEPS

Research to understand cold-seep ecosystem processes is still in early stages but observational data indicate that seepage of pore fluids can occur under a very broad range of environmental conditions in the context of flow rates, temporal stability and geological settings. Such variability promotes the question: does species composition, density and biomass (and production) of the associated fauna reflect the different habitat conditions?

Environmental conditions and habitat longevity

Depth of known seep communities ranges from 300 to 6000 m (Sibuet and Olu, 1998). Bathymetric effects may influence species composition, as noted on the Peruvian margin (Olu et al., 1996a); the geographic distribution of species may be secondarily affected. Geological features such as manganese encrustation and depth of sediment cover also control species composition and density (Juniper and Sibuet, 1987; Sibuet et al., 1988). To date, fluid discharge rate is the best-understood local environmental variable. The relationship between discharge rates and species composition, density and general shape of clam colonies is direct enough to be quantitatively modelled (Henry et al., 1992). The effects of flow rate may determine forms of symbiosis (MacDonald et al., 1990a; Olu et al., 1997) and trophic pathways. Just as weak flow rates do not support colonization by some seep species, extremely rapid expulsions with fluid mud can exclude all fauna, probably because of substratum instability; the latter condition can occur on active mud volcanoes and diatremes[1] (Sassen et al., 1994; Olu et al., 1997). Faunal exclusion by extreme chemical conditions may occur, as at sites of intense discharge of hydrocarbons (Roberts and Carney, 1997), including perhaps methane.

In the absence of long-term studies, comparative data provide a first indication of the scales and characteristics of temporal evolution at seeps. Locally, the frequent juxtaposition of living and dead bivalves at several geographic locations (Juniper and Sibuet, 1987; Rosman et al., 1987; Olu et al., 1996b) indicates a relatively rapid dynamic and spatial shifting of fluid flow. At a larger scale, surface renewal events (rapid mud extrusion) for Barbados mud volcanoes are estimated to occur at intervals of 100 to 1000 years. Between events, substrata and fluid discharge properties evolve, and these processes appear to be reflected in the composition of seep communities, with subsurface sulphide oxidation and dependent symbioses appearing in later stages (Olu et al., 1997). Similarly, at hydrocarbon seeps in the Gulf of Mexico, the evolution from rapid

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[1] A *diatreme* is a volcanic intrusion emitting much carbon dioxide into the sediment. See Glossary, p. 477.

flux of fluid mud to seepage of mineral-rich fluids may occur over periods of time that represent hundreds to thousands of years (Roberts and Carney, 1997). At the scale of millennia, the lifetime of gas hydrate accumulations on continental margins follows a cycle at the frequency of sea-level change (Roberts and Carney, 1997).

Colonization and niche specialization

Comparison of the species composition of benthic communities invokes questions about niche specialization and controls on colonization. At seeps, where symbioses are usually a major biomass component, it is important to understand how environmental factors influence the establishment of symbiont-bearing invertebrates. Cold seeps are initially mud bottoms within which hard substratum is mostly secondarily formed as carbonate concretions. Sulphide is the secondary product of anaerobic bacterial oxidation of methane or higher hydrocarbons using seawater sulphate as the oxidizing agent. Thus species requiring hydrogen sulphide and/or hard substrata would likely appear later in the evolution of a seep site. Faunistic differences within sites may be explained in this manner (MacDonald et al., 1990a; Olu et al., 1997).

Colonization of seeps by species not containing symbionts, endemic or otherwise, contributes to the development of a complex ecosystem. Seeps represent localized perturbations of the vast and well-established soft-bottom benthic environment of the deep sea. The participation of non-symbiont deep-sea species in seep food webs is an important feature at several sites (Carney, 1994; Olu et al., 1996a; Barry et al., 1996), where extremely high densities of meiofauna, suspension feeders, deposit feeders and, usually, carnivores occur. Development of this trophic continuity of seeps with the surrounding environment appears to depend on the duration of seepage. At early stages only symbiont-containing species would be present. Later colonization of seeps by the background fauna, influenced by the type of substrata, should vary over the very broad geographic and bathymetric range in which seeps occur (Sibuet and Olu, 1998). Links with the surrounding ecosystem are thus more apparent here than at hydrothermal vents on new oceanic crust.

The relatively high diversity of species at seep sites can be explained by local variation in the intensity of fluid flow, long-term stability, presumed continuous availability of nutrients and the variety of substrata present (Sibuet and Olu, 1998). Currently, there are many more symbiont-containing species known from seeps than from vents; up to 15 such species are known from a single region (Sibuet and Olu, 1998). Has the broader range and longer duration of seep habitat permitted greater specialization? More studies on systematic and molecular phylogeny will be necessary to analyse the evolution of seep fauna some of which (as demonstrated for mussels and vestimentiferans) may be ancestral to those of hydrothermal vents.

CONCLUDING COMMENTS

Reducing habitats present physiological and ecological challenges to organisms. In the deep sea, such ecosystems are uncommon, but foster high biomass and many unusual animals. It is the supply of reduced compounds that allows chemoautotrophic production by microbes using either reduction or oxidation reactions. The extent of production by heterotrophs is unknown, but likely contributes to the mobilization of organic compounds in these systems. While the food source is abundant, the ability to use it or to tolerate the physico-chemical conditions is limited to a relatively small group of organisms. High dissolved sulphide levels, variable and extreme temperatures, unpredictable fluid flows, and the patchy, dispersed nature of the habitat all contribute to the challenges that both macro- and microfauna face in the vent habitats. Cold seeps and organic food falls present less extreme physico-chemical conditions, but chemical toxicity and high habitat dispersion are important factors.

Compared to many other areas in the deep sea, vents and seeps have received much attention from researchers. Description of some fundamental phenomena such as the major role of Archaea in production, the highly integrated animal–microbe symbioses, and discovery of the presence of many novel systematic groups represent major achievements. Nonetheless, there remain many gaps in the knowledge of these ecosystems and their role in deep-sea production, diversity and functioning. Study of evolutionary relationships among the reducing habitats and many others of the deep sea may prove particularly exciting. These systems do not stand alone; a better appreciation of adjacent deep-sea systems could be of great value to reassessment of information from vents, seeps, organic remains and low-oxygen basins.

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Chapter 5

THE DEEP ATLANTIC OCEAN

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INTRODUCTION

The Atlantic Ocean is a long sinuous ocean which originated during the Mesozoic following the break-up of the supercontinent of Pangea. For most of its length, the eastern and western boundaries are clearly defined by land masses, except where it is separated from the Caribbean Sea and Gulf of Mexico by troughs and trenches. The northern and southern limits are more difficult to define. To the north we consider the Atlantic to include the subpolar Greenland and Norwegian Basins. These are linked hydrographically to the rest of the Atlantic, although they are isolated topographically by the ridge system extending between Greenland and Scotland. To the south, the boundary between the South Atlantic and Southern Ocean is generally defined hydrologically by the Subtropical Convergence around 40ºS (e.g., Webb, 1996).

In this chapter we review current knowledge about the distribution and ecology of organisms on the floor of the Atlantic Ocean from the continental slope to the abyss, and describe the environmental setting that they experience. We focus particularly on the North Atlantic, since the literature for this hemisphere is far more voluminous than for the South Atlantic. As with any large review, we have been selective in our coverage of the regional literature, concentrating on aspects with which we are most familiar, or which have received greatest attention from investigators. Our treatment of the Atlantic intentionally omits hydrothermal vent and seep settings, which are covered in Chapter 4 of this volume. Following a description of the environment of the deep Atlantic, and of the biological communities region by region, we have attempted to synthesize general patterns of faunal density and biomass, community respiration, bioturbation and succession.

Distinctive features of the Atlantic Ocean

The two margins of the Atlantic separated between about 175 and 90 million years ago, making it the youngest of the major world oceans. Because of its relative youth, the Atlantic is a narrow ocean, with a relatively high ratio of margin to open water. The configuration of the eastern and western sides strongly influences the movement of surface currents (Longhurst, 1998) and, ultimately, the nature of the deep-sea biota. Because of the high ratio of margin to open water in the Atlantic, mass wasting events on the margins (involving the collapse and slumping of sediments) affect a considerable fraction of the deep ocean. Earthquake-induced turbidity flows may sequester carbon originally deposited on the shallow margins in deep-sea sediments (Thunell et al., 1999). Regions such as the Madeira Abyssal Plain (Weaver et al., 1992), the Grand Banks abyss (Huggett, 1987), or the Cariaco Basin (Thunell et al., 1999) apparently contain turbidite[1] sediments originating on the margin. Despite the frequency of mass wasting along the margin, the Atlantic is generally less tectonically active than the Pacific. There are fewer subduction zones and trenches, and thus less hadal habitat. Hydrocarbon seeps, which are common along much of the active Pacific margin, are apparently relatively rare in the Atlantic, particularly on the eastern margins (Sibuet and Olu, 1998). Sediment deposition is a dominant process on the broad slope and rise. Strong bottom

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[1] Turbidite sediments are produced by deposition from gravity-driven flows of sediment ‘rivers’. They may be homogeneous, or characterized by fining upward. See Glossary, p. 477.

flows, sometimes reaching storm proportions, are more prevalent in the Atlantic than in other oceans. These play an important role in redistributing sediments and organic matter in deep water, leading to the formation of vast sediment drifts (Hollister et al., 1984).

Atlantic water masses exhibit distinctive properties. There is a strong flow of cold abyssal water from both polar regions, whereas very little deep arctic water directly enters the Pacific Ocean. The North Atlantic is the source of much of the World Ocean's deep water. These young, near-bottom water masses are better oxygenated, and the calcium compensation depth[2] is much deeper, than in the Pacific and Indian Oceans. This affects the distribution of sediment types. Carbonate oozes are the dominant sediments in the Atlantic, and carbonate-free red clays, which cover vast tracts of the deep Pacific, are confined to relatively small areas. Sedimentation rates are higher in the central parts of the Atlantic, and manganese nodule fields are less extensive than in the other oceans. Massive upwelling, characteristic of eastern boundaries in the Pacific and Indian Oceans, is less extensive in the Atlantic, and the intense oxygen-minimum zones that develop in these other oceans are limited to a small area off West Africa.

The processes in the upper water column that drive the timing and magnitude of primary production in the Atlantic are different from those operating in the Pacific (Longhurst, 1995, 1998). The spring bloom is more intense and widespread in the North Atlantic than anywhere else in the oceans, leading to a greater degree of seasonality in surface production and to relatively predictable seasonal inputs of phytodetritus to the deep seabed. Particularly in marginal environments, much of the marine primary production is deposited on the seafloor, making the Atlantic margins highly dynamic settings, with important roles in organic-matter cycling. There is evidence that these inputs are more likely to meet the respiratory demands of the benthos than in the Pacific Ocean.

The youth of the Atlantic may also influence zoogeographic patterns. About a third of the benthic species present in deep water appear to be endemic, and the degree of endemism increases with depth (Vinogradova, 1997). Some major groups are apparently absent or poorly represented in the Atlantic. Different families dominate the demersal fish fauna in the Atlantic (in ranked order, the Macrouridae, Alepocephalidae, Ophidiidae, Gadidae and Ragidae), and the NE Pacific (in ranked order, the Scorpaenidae, Liparidae, Zoarcidae, Ragidae, Pleuronectidae and Macrouridae) (Merrett and Haedrich, 1997). Among the protists, the xenophyophore order Stannomida, which is common and diverse in the Pacific, is represented in the Atlantic by a single species. Atlantic vent faunas have distinctive features as well. Vestimentiferans, common in the Pacific, are absent from the Atlantic, whereas bresiliid shrimps are a dominant element in the Atlantic but not the Pacific (Gebruk et al., 1997). Because many researchers and nations have concentrated their efforts in one ocean or another, there are relatively few investigations that compare deep-sea processes in a global context. Future efforts to compare and contrast the Atlantic with other world oceans and seas will undoubtedly reveal additional unique features, as well as unexpected commonalities.

HISTORY OF RESEARCH

The North Atlantic was a cradle for the development of deep-sea biology both during the latter part of the 19th century and in recent decades. To some extent, this reflects proximity to population centers and academic institutions in western Europe and North America.

By the 1860s, a considerable number of observations, many of them made serendipitously during sounding operations in the North Atlantic, strongly suggested that animals could live on the ocean floor (Rice, 1975; Rice et al., 1976; Mills, 1983). However, the first concerted attempts to sample deep-sea animals by means of dredges were made in the late 1860s in the waters to the north and west of the British Isles, initially from H.M.S. *Lightning* (1868) but principally from H.M.S. *Porcupine* (1869, 1870). The deepest sample taken during these early cruises demonstrated that animal life could flourish at a depth of 4289 m. It was these dredging activities which finally and belatedly disproved the azoic theory of Forbes (1844). They also paved the way for the great world-wide *Challenger* Expedition of 1872–1876, which in turn stimulated other European deep-sea campaigns such as the French *Travailleur* and *Talisman* expeditions in the Northeast Atlantic and Mediterranean, and the work of Albert I of Monaco who introduced many innovative methods into deep-sea biology (Mills, 1983). The

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[2] The calcium carbonate (calcite) compensation depth (CCD) is the depth at which <20% of skeletal carbonate is preserved in the sediment.

Danish Ingolf expeditions of 1895 and 1896 around Greenland, Iceland, and the Færøerne were notable for the use of fine-meshed screens (silk gauze) to sift mud recovered by the trawl and dredge. These residues yielded a diversity of small animals, for example, 70 tanaid species (49 of them new) and 121 isopod species (61 of them new) (Hansen, 1913, 1916).

There were parallel developments on the North American margin. An early pioneer was Pourtáles who dredged to a maximum depth of 494 m in the Florida Straits using the U.S. Coast Guard steamer *Corwin* in the summer of 1867. During the following two years Pourtáles and Louis Agassiz obtained abundant animals down to a maximum depth of 1555 m on the U.S. continental margin between Florida and the Grand Bahama Bank from the steamer *Bibb* (Mills, 1983). A decade later (1877–1880), under the direction of Alexander Agassiz, another U.S. Coast Guard steamer, the *Blake*, undertook a series of biological cruises on the continental margin of the eastern United States, during which animals were dredged from depths down to almost 3000 m (Agassiz, 1888). These studies raised issues that continue to concern deep-sea biologists – not least, the question of food supply to the deep-sea benthos.

After fifty years or so of relative quiescence, deep-sea biology has undergone a renaissance since the 1960s, a period during which national and, more recently, international programs have become more focused on specific areas and issues (Table 5.1; Fig. 5.1). Work conducted in the North Atlantic by American and European scientists has contributed substantially to the tremendous development of deep-sea ecology during this period. Perhaps the most significant advance resulted from the recognition by H.L. Sanders, R.R. Hessler and their colleagues, that smaller animals (macroinfauna – animals residing within the sediment column which are retained on a 0.3 or 0.5 mm mesh) are abundant and highly diverse in the deep sea, a discovery made during the mid-1960s on the continental margin of the northeastern United States using novel sampling techniques (Sanders et al., 1965; Hessler and Sanders, 1967). Although to some extent foreshadowed by earlier observations (for instance, those of Hansen referred to above), this discovery overturned the paradigm of low deep-sea species diversity which had been derived from studying large epibenthic megafaunal animals caught in coarse-meshed bottom nets. Many of the ideas which have developed subsequently regarding the magnitude and geographic patterns of deep-sea species diversity have resulted from research carried out on this intensively studied margin (e.g., Rex, 1983; Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992) and elsewhere in the Atlantic Ocean (Rex et al., 1993, 1997; Allen and Sanders, 1996). Two other major developments in deep-sea biology during the last 20 years have been the discovery that the deep-sea floor is subject to seasonal or unpredictable episodic inputs of organic matter which play an important role in structuring benthic communities, and the discovery that certain areas are physically disturbed by periodic strong currents (benthic storms: see Chapter 2). Again, these developments arose largely from work carried out in the North Atlantic Ocean.

The important contribution made by Russian scientists to knowledge of the biology of both the South and North Atlantic Ocean should not be overlooked. Much of the extensive Russian literature on the faunas of the Atlantic slopes and abyssal plains, large-scale faunal distribution patterns, and primary phytoplankton production, is summarized in the English-language volume edited by Gebruk et al. (1997).

GENERAL PHYSICAL AND CHEMICAL CHARACTERISTICS

Seafloor topography and physiography

An excellent and detailed account of the physiography and geology of the Atlantic Ocean has been given by Emery and Uchupi (1984). According to the hypsometric curve of Emery and Uchupi (1984, fig. 9 therein), the mean depth of the Atlantic between 60ºN and 60ºS is 3730 m, very close to the average for the entire World Ocean, with the modal depth lying between 4000 m and 5000 m. The most important first-order feature is the Mid-Atlantic Ridge which divides the ocean longitudinally into two halves, each with a series of major basins delimited by secondary, more or less transverse ridges (Fig. 5.2). The Ridge extends above the 2000 m contour along most of its length and has a major influence on the circulation of near-bottom water masses (Tomczak and Godfrey, 1994). It is interrupted by a series of transform faults including the Romanche Fracture Zone near the equator and the Gibbs Fracture Zone at 53ºN. Both these features provide routes for bottom water to pass from one side of the ocean to the other. Second-order physiographic features include the

Table 5.1
Major national and international research projects and programs in the Atlantic Ocean

	Project	Dates	Study area	Purpose
EUROPE				
Denmark	BIOFAR	1990	Slope SW of Faroes	Faunal survey
France	BIOGAS	1972–1974 1978–1981	Bay of Biscay	Comprehensive environmental and faunal survey, recolonisation experiments, etc.
France	EUMELI	1989–1992	NW African margin	Comparison of faunas under different organic matter input regimes
Germany	BIOTRANS BIO-C-FLUX BIGSET	1984–1989 1989–1994 1996–1999	48º00–48º30ºN 19ºW	Benthic reaction to organic matter flux
Germany	Sondersforschungsbereich 313	1985–1998	Greenland–Norwegian Sea	Particle flux to seafloor and its transformation into paleoceanographic record
The Netherlands	DORA	1984–1986	Porcupine Abyssal Plain	Effect of radioactive waste dumping
UK		1972–present	Rockall Trough	Time series study of macrofauna
UK	IOSDL Porcupine Seabight programme	1977–1986	Porcupine Seabight	Survey of mega-, macro-, meiofauna
European Union (MAST I Framework)	‘Natural variability and the prediction of change in marine benthic ecosystems’	1990–1993	NE Atlantic slope and abyssal plains	Describing environmental and biological variability at different temporal and spatial time scales; investigating effects of disturbance on benthos
European Union (MAST II Framework)	‘Community structure and processes in the deep-sea benthos’	1993–1996	Porcupine, Madeira, Cape Verde Abyssal Plains	Comparison of benthic communities disturbed by phytodetritus with undisturbed communities
European Union (MAST III Framework)	BENGAL: ‘High resolution temporal and spatial study of the benthic biology and geochemistry of a north-eastern Atlantic abyssal locality’	1996–1998	PAP	Flux through water column and modification of flux prior to incorporation in permanent record
European Union (MAST II Framework)	OMEX 1	1992–1996	Transects of continental margin in Goban Spur area	Physical, chemical and biological processes at ocean margins controlling transport of material from shelf into deep sea
U.S.A.				
	Gay Head to Bermuda Transect	1960s	Massachusetts to Bermuda	Quantitative evaluation of deep-sea macrofauna (diversity/abundance)

continued on next page

Table 5.1, *continued*

Project	Dates	Study area	Purpose
Atlantic Continental Slope and Rise Study (ASCAR) North Atlantic Bight, Mid Atlantic Bight, South Atlantic Bight	1983–1986	NW Atlantic slope and rise: 28ºN to 42ºN	US Minerals Management Service, sediment and faunal surveys, canyon study
Shelf Edge Exchange Processes (SEEP I)	1983–1984	U.S. Mid Atlantic Bight, south of Long Island and New Jersey	Carbon export and transformation within shelf and slope sediments
Shelf Edge Exchange Processes (SEEP II)	1988–1989	U.S., Southern Mid Atlantic Bight	Carbon export and transformation within shelf and slope sediments
High Energy Benthic Boundary Layer Experiment (HEBBLE)	1980–1986	Nova Scotia Rise	Physical, geological, and faunal studies of environment subject to benthic storms

wide continental shelves developed off Newfoundland, southern South America and northwestern Europe, and the continental rises and abyssal aprons which are particularly expansive in the South Atlantic and the northern part of the North Atlantic (Emery and Uchupi, 1984: figs. 10–12 therein). Extensive carbonate platforms are developed in the western Atlantic, notably the Blake Plateau and Bermuda Rise. Unlike those in the Pacific, the continental margins on both sides of the Atlantic are largely passive. However, active margins with deep trenches (maximum depths 8414 m and 8264 m, respectively) are present in the western Atlantic (Puerto Rico Trench) and southern Atlantic (South Sandwich Trench). Smaller-scale (third-order) physiographic features include submarine canyons, which are particularly numerous on the continental margin off the northeastern United States, western Europe and parts of northwestern Africa (Emery and Uchupi, 1984: fig. 37 therein). Some extend into deep-sea channels, probably created by turbidity currents originating from the canyons. These features meander across the continental rises and abyssal plains. Canyons may have an important effect on the composition of associated biological communities.

Deep-water hydrography

The large-scale hydrography of the Atlantic Ocean is dominated by the overall northward movement of warm surface and intermediate water, derived ultimately from the Pacific and Indian Oceans, through the South Atlantic and into the North Atlantic, where it becomes more saline through evaporation (Broecker, 1991; Schmitz, 1995). On reaching the Greenland–Norwegian Sea, this water is subject to intense winter cooling and sinks by vertical convection. The resulting Norwegian Sea deep water spills over the Faroe Bank Channel and the Faroe–Iceland Ridge and entrains resident Atlantic water to form Northeast Atlantic Deep Water (NEADW). This water mass finds its way into the Northwest Atlantic basin where it mixes with bottom water flowing through the Denmark Strait and low–salinity water from the Labrador Sea to form a composite water mass termed North Atlantic Deep Water (NADW). North Atlantic Deep Water flows southwards into the South Atlantic and eventually back into the Indian and Pacific Oceans via the Circumpolar Current (Worthington, 1976; Gage and Tyler, 1991). This ‘thermohaline conveyer belt’ (Broecker, 1991; Rahmsdorf, 1997) leads to a net transfer of heat from the south to the north (‘North Atlantic heat piracy’: Berger and Wefer, 1996).

Other water masses are also present in the North Atlantic. The deep (>4500 m) basins off Northwest Africa are occupied by Antarctic Bottom Water (AABW), which enters the North Atlantic via the Vema Gap. At depths greater than 2000 m, the dominant Northeast Atlantic water mass is Mediterranean Water, which flows through the Straits of Gibraltar, around the Northwest European continental margin, and through

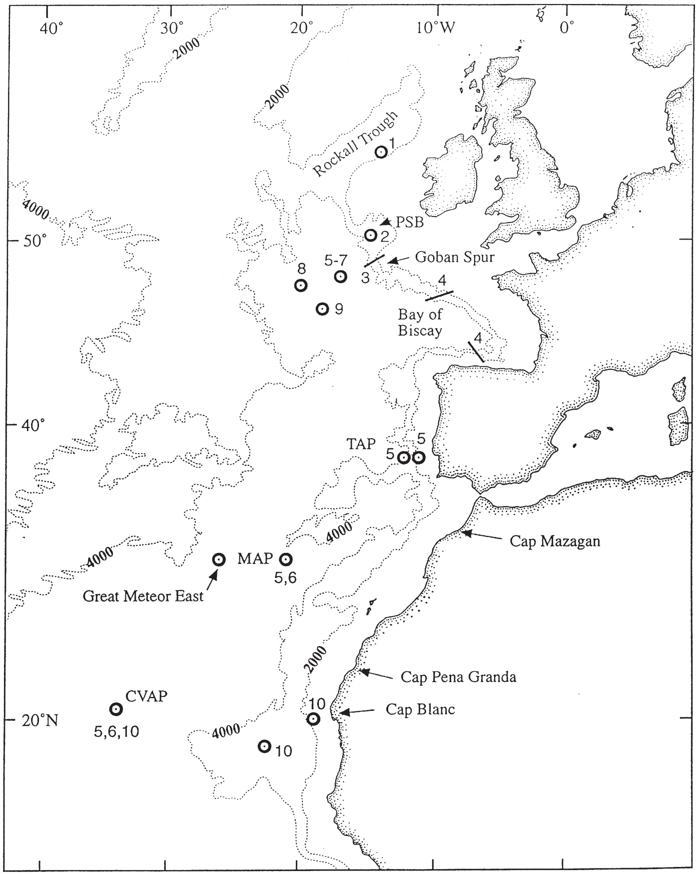

Fig. 5.1. Locations of major sampling programs within the deep Atlantic. CVAP, Cape Verde Abyssal Plain; MAP, Madeira Abyssal Plain; PSB, Porcupine Seabight; TAP, Tagus Abyssal Plain. The numbers identify national and international research projects listed in Table 5.1. (1, Rockall Trough time series; 2, IOSDL Porcupine Seabight Programme; 3, OMEX; 4, BIOGAS; 5, EU MAST I; 6, EU MAST II; 7, EU MAST III; 8, BIOTRANS and its successors; 9, DORA; 10, EUMELI).

the Rockall Trough, becoming progressively diluted as it proceeds northwards. Mediterranean Water is characterized by high density and salinity and by its variable physical properties (Weston, 1985).

The deep bottom water in the South Atlantic lies below the "conveyer belt" and is derived mainly from the Weddell Sea (Mantyla and Reid, 1983; Mackensen et al., 1995). The deep Weddell Sea Bottom Water is too cold and dense to escape from the Antarctic. The AABW which penetrates northwards into the South Atlantic is lighter, and consists of a mixture of three separate water masses, dominated (>50%) by Circumpolar Water (CPW). The AABW flows from the Weddell Sea into the Argentine and Brazil Basins via the Scotia Sea and Georgia Basin, and is characterized by low temperature and salinity and relatively high concentrations of oxygen and nutrients. From the Brazil Basin, it either escapes northwards into the Guiana Basin, or circles eastwards and southwards, via the Romanche Fracture Zone, into the southeastern Atlantic basins.

Bottom-water oxygen concentrations in the Atlantic are generally higher ($>5\,\text{ml}\,\ell^{-1}$) than in the Pacific and Indian Oceans, particularly in water of North Atlantic origin (Mantyla and Reid, 1983; Reid, 1996, fig. 2 therein), and severe oxygen depletion ($<0.2\,\text{ml}\,\ell^{-1}$) is not as extensive as in marginal regions of these other oceans (Diaz and Rosenberg, 1995, fig. 1 therein). Areas of intermediate depth with bottom-water oxygen depletion are associated with upwelling on the eastern side of the Atlantic. The two main areas in the Atlantic are off Northwest Africa, where upwelling is associated with the Canary Current, and off Southwest Africa where it is associated with the Benguela Current

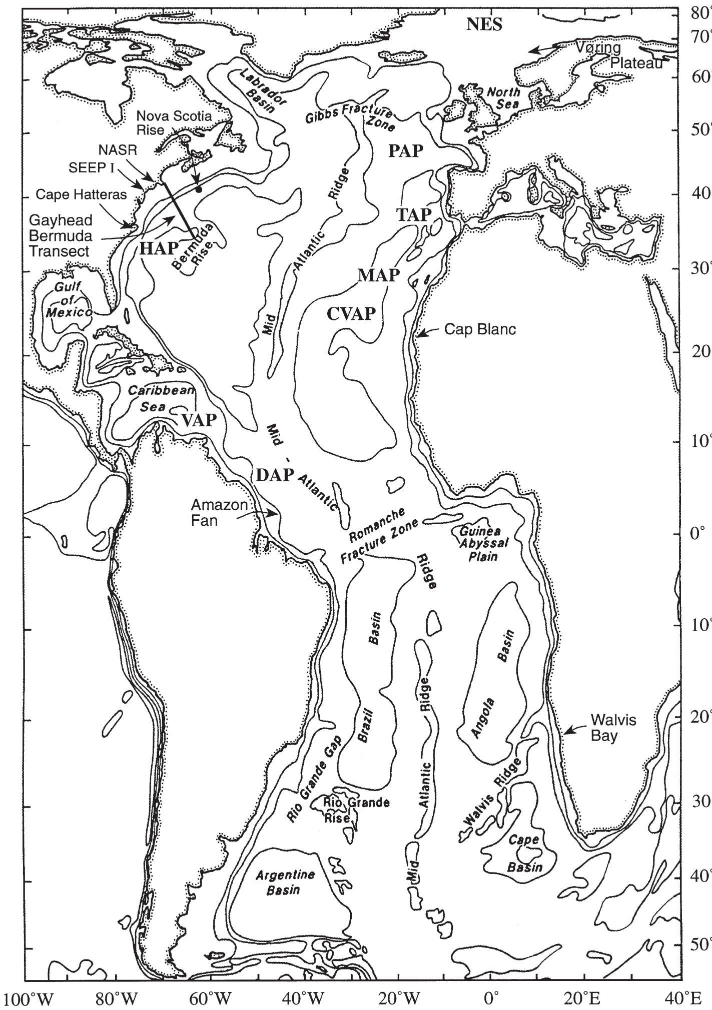

Fig. 5.2. Map of the Atlantic Ocean showing major features and locations discussed in the chapter. CVAP, Cape Verde Abyssal Plain; DAP, Demerara Abyssal Plain; HAP, Hatteras Abyssal Plain; MAP, Madeira Abyssal Plain; NGS, Norwegian–Greenland Sea; PAP, Porcupine Abyssal Plain; VAP, Venezuela Abyssal Plain. Adapted from Tomczak and Godfrey (1994).

(Shannon and Nelson, 1996; Summerhayes et al., 1995; Tomczak and Godfrey, 1994). In both areas, the large organic-matter flux to the seafloor has a profound impact on the structure and function of the underlying benthic communities.

A turbid nepheloid[3] layer often occurs in water several hundred meters above the seabed. In the Atlantic, this layer is best developed where the bottom currents are strongest – that is, beneath strong western boundary currents associated with subtropical gyres (the Gulf Stream and the Brazil Current). Similar features have been described in the Northeast Atlantic, for instance, on the continental slope west of the Porcupine Bank (Dickson and McCave, 1986), on the Feni Drift (van Weering and de Rijk, 1991) and in the foothills of the Mid-Atlantic Ridge next to the Porcupine Abyssal Plain (Nyffeler and Godet, 1986). Where kinetic energy is greatest, mesoscale eddies develop and sediment resuspension occurs. These episodic events, termed 'abyssal storms', can erode and redeposit several centimeters of sediment within a short period. Such events have been studied in detail on the Nova Scotia Rise in the Northwest Atlantic (Hollister and McCave, 1984; Brown et al., 1989).

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[3] A *nepheloid* layer is one containing a high concentration of suspended particles. It is often defined optically by turbidity measurements (with a nephelometer).

Sediments and mass movement

The deep Atlantic Ocean floor is covered by sediments deposited by near-shore and volcanic processes, by turbidity currents and related gravity-driven processes, by bottom currents and by pelagic sedimentation (Emery and Uchupi, 1984). Sokolova (1997) considered the extensive Russian literature on sedimentation processes in the North and South Atlantic. Sands and gravels of terrestrial or biogenic origin are generally restricted to the shelf and upper slope. Sediments become progressively finer with increasing depth and distance from land (Emery and Uchupi, 1984; Lampitt et al., 1986), although in some areas submarine canyons channel coarser sediments onto the continental slope and rise (Mart et al., 1979; Auffret, 1985; Weston, 1985). Over much (67%) of the Atlantic Ocean, however, the surface sediments are carbonate oozes ($CaCO_3$ content 30–50%) with a mean particle size of <100 μm (Apostolescu et al., 1978; Emery and Uchupi, 1984; Auffret, 1985; Lampitt et al., 1986; Udintsev, 1990), a sand-sized fraction consisting predominantly of planktonic foraminiferal tests, and an organic-carbon content generally <0.5% (Emery and Uchupi, 1984, fig. 345B therein). In the central South Atlantic, the calcareous oozes are dominated by pteropod shells. Siliceous (diatomaceous) oozes cover about 7% of the Atlantic floor, mainly in the region to the north of the Antarctic continent (Sverdrup et al., 1970), where their accumulation reflects levels of benthic and benthopelagic dissolution rather than an increased flux of opal (biogenic silicate) to the sea floor (Lampitt and Antia, 1997). The principal clay minerals in deep Atlantic sediments are kaolinite and chlorite, with greater proportions of kaolinite beneath the tropics. Off the Amazon and western Sahara Desert, the kaolinite/chlorite ratio is >10, indicating large kaolinite inputs from these sources (Pinet, 1998).

In general, Atlantic sediments have a much higher calcium carbonate content than Pacific sediments. Differences in ocean chemistry result in a calcium carbonate (calcite) compensation depth (CCD) which is much deeper (>5000 m) in the Atlantic, particularly in eastern basins which are less influenced by corrosive AABW, than in the Pacific (Sverdrup et al., 1970; Berger, 1975; Biscaye et al., 1976). As a result, areas where red clay (from which the carbonate has been removed by dissolution) accumulates are restricted to deep, relatively small basins, for example west and northwest of the Cape Verde Islands, under the Sargasso Sea in the central subtropical Atlantic and in the western South Atlantic (Emery and Uchupi, 1984, fig. 341C therein). The aragonite (essentially pteropod-derived) compensation depth is also relatively deep in the Atlantic, normally being located between 2000 and 3000 m (Berger, 1978) but rising to 400 m under the Northwest African upwelling area (Ganssen and Lutze, 1982).

Sedimentation rates for Central Atlantic foraminiferal oozes are generally in the range 1–5 cm ky^{-1} compared with >5 cm ky^{-1} for the largely terrigenous sediments which accumulate around the margins of the North Atlantic (Brown et al., 1989; Pinet, 1998). The sediment drifts (e.g., the Feni Drift) which are developed in parts of the northeastern Atlantic (Johnson and Schneider, 1969) are also characterized by sedimentation rates of >5 cm ky^{-1} (Thomson et al., 1993). These enhanced rates reflect the advection of fine material by bottom currents.

During the recent geological past, large areas around the Atlantic margin have been disturbed by gravity-driven mass movements, including slumps, slides, debris flows and turbidity currents, which have modified the seafloor to a significant extent (Stoker et al., 1998). These categories may be related; for example, some debris flows seem to be associated with turbidity currents (Masson et al., 1996). Mass movements are well documented off Northwest Europe, Northwest Africa, Southern Africa, the United States between New York and Cape Hatteras, and Brazil (Emery and Uchupi, 1984, fig. 43 therein). Massive sediment transport has been intensively studied on the continental rise and abyssal plain off Northwest Africa, an important area for the development of modern ideas about continental-margin sedimentation (Jacobi and Hayes, 1982; Simms et al., 1991; Masson et al., 1996). Here, debris flows, notably the unusually large Canary and Saharan flows (Embley, 1976; Masson et al., 1994, 1996), have occurred on the upper continental rise, transporting 600 km^3 of sediment from the shelf over a very short period, perhaps days or even hours – as much as the southern California basins have received from turbidity currents in a million years. Elsewhere in the Northeast Atlantic, the mid-Norwegian margin (the 'Storegga' area, 62ºN) is notable for a series of enormous slides, the most recent of which occurred about 7000 years ago (Bugge et al., 1988). These slides and associated debris flows and turbidity currents have transported 6000 km^3 of sediment from the shelf to depths of 3500 m over horizontal distances of 800 km.

Not surprisingly, turbidite deposition is a very important feature of Atlantic sedimentation and turbidite-formed abyssal plains are present off most of the continents, except the southern part of South America (Brown et al., 1989). The best-documented example is the Madeira Abyssal Plain, which is composed of a sequence of large turbidite deposits separated by thin pelagic layers. The turbidites were derived from several sources on the Northwest African margin, and their emplacement appears to be related to changes in climate and sea-level over the past 700 000 years (Weaver et al., 1992). Despite the prevalence of turbidite deposits, the actual currents have rarely been observed. The best-known turbidity flow occurred in 1929, when an earthquake on Grand Banks, Newfoundland, triggered a sediment slump which developed into a turbidity current extending 800 km from its source across the abyssal plain (Heezen and Ewing, 1952). Thunell et al. (1999) observed a striking increase in near-bottom concentrations of suspended sediment and mass flux through the water column in the Venezuela Basin following a 1997 earthquake. These mass-movement events must have had a devastating impact on the benthic fauna at the time of their emplacement, and may have a continuing effect through their influence on the granulometry (Huggett, 1987) and organic-matter content (Thunell et al., 1999) of the sediment.

While most of the material on the Atlantic seabed is pelagic or terrigenous in origin, authigenic[4] deposits occur in certain areas. Manganese nodules (composed of a mixture of iron and manganese oxides) were first recovered from the Atlantic near the Canary Islands during the *Challenger* Expedition. They are most extensively developed in the Argentine, Brazil and Cape Basins in the South Atlantic and in the Sargasso Sea in the North Atlantic. These Atlantic nodules have a somewhat lower manganese content (16%) and higher iron content (21%) than those in the Pacific and Indian Oceans (Brown et al., 1989). Phosphorites (authigenic calcium phosphate) occur on the shelf off south-west Africa (Price and Calvert, 1978), and unconsolidated phosphatic deposits are found in various areas around the Atlantic margin, including the shelf and upper slope off North Carolina and Northwest Africa (e.g., Riggs et al., 1985; Summerhayes et al., 1972).

ORGANIC-MATTER FLUX AND BENTHOPELAGIC COUPLING

General patterns of primary production

Apart from spatially limited areas of hydrothermal vents and seeps (see Chapter 4), almost all food available to the deep-sea benthos is derived from primary production in the euphotic zone. The 'Dahlem map' (Berger, 1989, fig. 11) provides an overview of estimated primary production for the Atlantic Ocean based on previous maps and remote-sensed satellite data. For the North Atlantic, more precise data on new primary production (i.e., production depending on nutrients imported into the euphotic zone) can be derived from surface chlorophyll concentrations determined from satellite imagery (Campbell and Aarup, 1992). Campbell and Aarup identified three areas characterized by different patterns of seasonal production and increasing levels of overall production: (i) a subtropical zone in which production reaches a maximum in the winter and minimum in the late summer (new production = 18 g C m^{-2} y^{-1}), (ii) a mid-latitude zone characterized by a spring bloom followed by oligotrophic conditions throughout the summer (new production = 24 g C m^{-2} y^{-1}), and (iii) a subpolar zone with minimum production in the winter and maximum in the late summer (new production = 43 g C m^{-2} y^{-1}). These three zones represent 20% of the area of the Atlantic and 43% of the North Atlantic, and exclude the entire tropical region where primary production is strongly influenced by upwelling and river inputs.

Longhurst (1995, 1998) and Longhurst et al. (1995) have presented a comprehensive scheme to classify seasonal cycles of primary production and consumption in the World Ocean. Sathyendranath et al. (1995) focused in detail on the Atlantic Ocean. Longhurst and his colleagues recognized four primary ecological domains (three oceanic and one coastal) which have characteristic seasonal cycles of water-column stability, nutrient supply and solar illumination. These are divided into 57 biogeochemical provinces defined on the basis of local features such as currents, fronts and topography. The important Atlantic provinces include, from north to south: North Atlantic Drift (NADR), Subtropical Gyre [STGW (West) and STGE (East)], North Atlantic Tropical Gyre (NATR), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), and South Atlantic Tropical Gyre (SATG) (Sathyendranath

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[4] *Authigenic*: generated locally (*in situ*), usually by a geochemical reaction (e.g., precipitation of Mn or Fe oxides to form nodules).

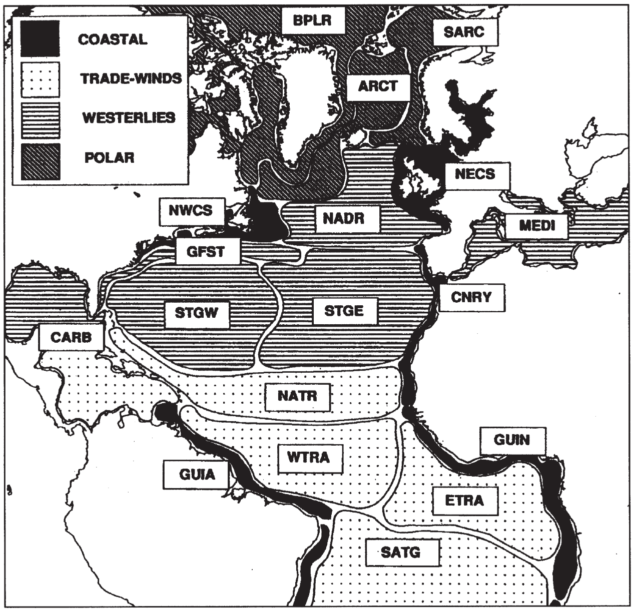

Fig. 5.3. Approximate areas occupied by primary ecological domains and secondary provinces in the Atlantic Ocean. The provinces are as follows. *Coastal Domains*: NW Atlantic (NWCS), NE Atlantic (NECS), E. Atlantic (CNRY), Guinea (GUIN), Guiana (GUIA); *Trade-Wind Domain*: North Atlantic Tropical Gyre (NATR), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), South Atlantic Tropical Gyre (SATG), Caribbean and Gulf (CARB); *West-Wind Domain*: Gulf Stream (GFST), North Atlantic Drift (NADR), Subtropical Gyre (East and West) (STGE & STGW), Mediterranean (MEDI); *Polar Domain*: Boreal Polar (BPLR), Arctic (ARCT), Subarctic (SARC). Reprinted from S. Sathyendranath, A. Longhurst, C.M. Caverhill and T. Platt (1995). Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Res. I,* 42: 1773–1802. With permission from Elsevier Science.

et al., 1995) (Fig. 5.3). The Atlantic pelagic provinces are important because they appear to influence the nature of food flux to the ocean floor, and in particular the variability of the flux over an annual cycle (Lampitt and Antia, 1997). Some correspond, in broad terms, to areas where the food supply to the benthos is seasonally pulsed, others to areas where the benthic food supply is more continuous. The temperate North Atlantic area is unusual among the pelagic provinces of the world in being subject to a distinct spring bloom which is not adequately grazed by zooplankton. This leads to the accumulation of a substantial phytoplankton biomass, and its subsequent aggregation, export from the mixed layer and sedimentation to the ocean floor (Longhurst and Harrison, 1988; Longhurst et al., 1995; Lampitt and Antia, 1997), a process of considerable significance for the underlying benthic communities, as discussed below.

Seasonally pulsed fluxes

The North Atlantic has been an important area for the development of ideas about the delivery of food to the ocean floor (Gooday and Turley, 1990; Rice and Lambshead, 1994). The long-held notion of a uniform (non-seasonal) rain of fine particles was swept aside in the late 1970s and early 1980s by two discoveries. First, it was found that the flux of settling particles may have a distinct seasonal component. Second, in areas of the North Atlantic which experience a strong spring bloom (the Atlantic Westerly Winds biome of Longhurst, 1998), this seasonal flux is dominated by sinking aggregates of phytoplankton detritus (phytodetritus). These escape recycling in the mixed layer of the ocean and settle to the abyssal ocean floor over a period of several weeks (Turley et al., 1995; Lampitt and Antia, 1997). Like many advances in oceanography, these discoveries depended on technological developments, notably of deep-moored sediment traps, long-term photography of the seafloor, and coring devices capable of collecting virtually undisturbed samples. They also reflect the fact that the North Atlantic experiences the strongest and most extensive spring bloom of any oceanic area (Longhurst, 1998).

Some of the earliest sediment-trap studies revealing flux seasonality were made in the North Atlantic.

Deuser et al. (1981) and Deuser (1986) studied samples collected between 1978 and 1984 by a trap moored at 3200 m water depth (1000 m above the seafloor) in the Sargasso Sea. The flux of particles of different sizes and compositions fluctuated seasonally and there was also considerable interannual variation in the magnitude and timing of the flux. More recent studies have been carried out in the Northeast Atlantic, a more productive region than the Sargasso Sea, as part of the Biochemical Ocean Flux Study (BOFS). Traps were deployed by Honjo and Manganini (1993) approximately 4000 m, 3200 m and 700 m above the bottom at 48ºN, 21ºW (water depth 5261 m) and 34ºN, 21ºW (water depth 5083 m), and by Newton et al. (1994) 1455 m and 90 m above the bottom at 47ºN, 20ºW (4555 m water depth). In all cases the particulate flux through the water column was distinctly seasonal.

The mass seasonal deposition of aggregated phytodetritus to the ocean floor was first revealed in studies by the Institute of Oceanographic Sciences Deacon Laboratory (IOSDL; now part of the Southampton Oceanography Centre), conducted during the 1980s in the Porcupine Seabight, an embayment of the continental margin southwest of Ireland (50ºN, 13ºW) (Rice et al., 1991). Phytodetritus was photographed on the seabed down to 4000 m during phototransects using the IOSDL epibenthic sledge and collected using the Barnett-Watson multiple corer (Billett et al., 1983; Rice et al., 1986). Subsequently, its arrival on the seafloor during the late spring and early summer, and its subsequent dispersal and disappearance from the seafloor by late summer, were documented by means of the BATHYSNAP time-lapse camera system (Lampitt and Burnham, 1983; Lampitt, 1985). For example, the BATHYSNAP record for 1984 shows a distinct peak in late May (Lampitt et al., 1995), although the timing of the peak and its intensity often varies between years (Newton et al., 1994). Phytodetritus has been observed at a variety of other continental margin sites in the Northeast Atlantic including the Bay of Biscay (Sibuet, 1985), the Norwegian continental margin (Graf, 1989), and at 20ºN off the Northwest African margin. Its deposition is also well documented in more central oceanic regions of the NE Atlantic, in particular the BIOTRANS[5] area, which is centered around 19º40′W, 47º20′N in the foothills of the Mid-Atlantic Ridge (Thiel et al., 1988/89; Pfannkuche, 1993), and on the adjacent Porcupine Abyssal Plain (Rice et al., 1994). On the western side of the North Atlantic, Hecker (1990b) described the occurrence of phytodetritus between 450 m and 2400 m on the continental slope south of New England. Deposits were heaviest between 1000 m and 1500 m, and were observed to move downslope over a five-day period. Phytodetritus was also observed in the Lydonia canyon (2000 m) during April 1996. The delivery of phytodetritus to the seafloor appears to occur in areas of the North Atlantic where the winter thermocline is relatively deep (>500 m on the Porcupine Abyssal Plain), leading to a strong spring bloom and an accumulation of phytoplankton biomass (Rice et al., 1994). This corresponds broadly to the North Atlantic Drift province of Longhurst (1995) and Sathyendranath et al. (1995), and the mid-latitude zone of Campbell and Aarup (1992). There is no evidence for inputs of phytodetritus in more oligotrophic regions such as the Sargasso Sea. Phytodetritus was not observed in core samples or in long-term BATHYSNAP sequences obtained at the Madeira Abyssal Plain (4940 m; 31ºN, 21ºW) and Cape Verde Abyssal Plain (4535 m; 21ºN, 31ºW) sites of the Southampton Oceanography Centre (Rice et al., 1994). Bottom photographs taken by Christiansen and Thiel (1992) at 31º and 34ºN on the Madeira Plain, however, suggest that some deposition may occur in this region.

North Atlantic phytodetritus has the following general characteristics. It is composed of the remains of various organisms derived from the euphotic zone (including Cyanobacteria, small chlorophyte algae, diatoms, coccolithophorids, silicoflagellates, dinoflagellates, tintinnids, radiolarians and Foraminifera), crustacean moults, small fecal pellets (‘minipellets’), bound together in a gelatinous matrix to form aggregates up to about 1 cm in diameter (Billett et al., 1983; Thiel et al., 1988/89). Phytodetritus contains rich populations of bacteria, some of them barophilic[6], as well as active cyanobacteria which originate from surface waters (Lochte and Turley, 1988) and may make good markers for freshly deposited phytodetritus (Pfannkuche and Lochte, 1993). The aggregates form an often extremely patchy layer (from a few mm to several cm in thickness) on the seafloor, and are typically concentrated in

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[5] *BIOTRANS*: BIOlogical vertical TRANSport and energetics in the benthic boundary layer of the deep sea. The BIOTRANS study area is bounded by the following coordinates: 47º00′–47º30′N, 19º–20ºW.

[6] Requiring high pressure for growth.

depressions or behind mounds and other obstacles (Thiel et al., 1988/89; Rice et al., 1994) (Fig. 5.4). They are light and easily resuspended and redistributed by currents (Lampitt, 1985; Hecker, 1990b). As a result of degradation during its passage through the water column, the organic-carbon content of phytodetritus is surprisingly low: 0.56–1.28% dry weight in the Porcupine Seabight (1000–4500 m) (Rice et al., 1986) and 0.9–7.8% dry weight in the BIOTRANS area (Thiel et al., 1988/89).

Fig. 5.4. Photograph of phytodetritus in depressions from the Porcupine Abyssal Plain (48.50ºN, 16.30ºW, 4850 m).

Phytodetrital deposits have also been observed later in the summer. Duineveld et al. (1997) and De Wilde et al. (1998) describe a ‘mucus layer’ which was present on the surfaces of cores recovered from the lower Celtic margin slope (>3500 m) during late August, 1995. This material was not present at upper-slope sites on the Goban Spur. Unlike ‘normal’ spring phytodetritus, it could not be resuspended easily. The mucus layer contained large numbers of coccoliths and high concentrations of fresh chloroplastic and other pigments (e.g., peridinin), suggesting recent derivation from an offshore bloom dominated by coccolithophorids but also including dinoflagellates and green algae. Additional and less predictable pulses of particulate organic matter may also be important for Atlantic benthic communities. These include the rapid sedimentation of fecal pellets originating from copepods (Graf, 1989) or salp swarms (Pfannkuche and Lochte, 1993), and the deposition of salp bodies and *Sargassum* (Grassle and Morse-Porteous, 1987).

Benthic responses

Pulses of phytodetritus and other forms of organic matter typically evoke a rapid response by the benthic community and serve to couple processes on the deep-sea floor and in the upper water column (Gooday and Turley, 1990). Pfannkuche (1993) estimated that 1.1% of spring bloom primary production and 9.6% of organic matter exported out of the surface 150 m at the BIOTRANS site was respired during the summer, and that 60–80% of the increased benthic activity (as estimated from concentrations of adenosine triphosphate (ATP), electron-transport activity and sediment community oxygen consumption [SCOC]) during this period was attributable to micro-organisms inhabiting the phytodetrital layer. Pfannkuche et al. (1999) investigated in detail the benthic response, indicated by total adenylates, total phospholipids (reflecting biomass of small organisms including bacteria and meiobenthos), and hydrolytic enzyme activity (reflecting metabolic activity) at this site during the period March to August 1992. They reported a precise and rapid coupling between sedimentation events and metabolic activity in early spring and summer, but very little corresponding biomass increase. Results from a shallower (1430 m) site on the Vøring Plateau (Norwegian continental margin) also imply a very rapid benthic metabolic response to food fluxes. Here, Graf (1989) detected an increase in chlorophyll a, and a corresponding increase in metabolic activity (ATP concentration), within days of the arrival of a pulse of copepod fecal pellets from the euphotic zone. Moreover, the response occurred at depth within the core, not just at the surface; chlorophyll was present down to 9 cm, and ATP peaks were apparent at 6 cm and 8 cm depth in two cores. A deposit of mucus-like phytodetritus sampled in August 1995 on the Celtic margin yielded high RNA and DNA concentrations, indicative of enhanced microbial activity (De Wilde et al., 1998).

A seasonal community response is not always apparent, however. Lampitt et al. (1995) could detect no seasonal variation in SCOC (measured using the hanging-core technique) at a site 2000-m deep in the Porcupine Seabight. Moreover, the oxygen demand of cores without a layer of phytodetritus was not obviously different from that of cores with phytodetritus. Likewise, there was no SCOC response to the spring deposition of phytodetritus on the nearby Goban Spur (Celtic margin) (Duineveld et al., 1997). In this case, the deposit had probably been laterally advected, and was therefore more degraded than material derived from the overlying water column. Similarly, Sayles et al. (1994) reported that sediment oxygen consumption at an oligotrophic site near Bermuda (4400 m water depth) was nearly constant between March 1989 and October 1992, despite strong seasonal variations in the organic-matter flux to the seafloor.

There is evidence for changes in the abundance and biomass of particular size classes and taxa following organic-matter inputs. In a detailed study of the BIOTRANS area (4550 m depth) of the Northeast Atlantic, Pfannkuche (1992, 1993) and Lochte (1992) found: (a) a doubling of bacterial biomass between March and July, and (b) a switch from dominance of the meiofaunal fraction by metazoans in March and May to dominance by Foraminifera in July and September. Small barophilic flagellates also thrive within organic aggregates (Lochte and Turley, 1988). Thus, the response to phytodetritus at the BIOTRANS site is accounted for mainly by Bacteria and protozoans (see also Pfannkuche and Soltwedel, 1998). Among benthic Foraminifera, the immediate response seems to be largely confined to certain opportunistic species which live mainly in the phytodetrital layer (Gooday, 1988, 1993, 1996b) and undergo rapid population increases during the summer (Gooday and Lambshead, 1989; Gooday and Turley, 1990). The opportunists include *Alabaminella weddellensis* and *Epistominella exigua*, both calcareous forms, and the allogromiid *Tinogullmia riemanni.*

A link between food pulses and metazoan population dynamics has proved more difficult to establish. Unlike Foraminifera and Bacteria, the metazoan meiofauna and macrofauna exhibited no significant increase in either numbers or biomass following phytodetrital deposition at the abyssal BIOTRANS site (Pfannkuche, 1992, 1993) and in the bathyal Porcupine Seabight (Gooday et al., 1996). There is some evidence from the Hebridean margin, however, that meiofaunal densities increase during the summer (Mitchell et al., 1996). Similar results have been obtained in the bathyal Mediterranean (de Bovée et al., 1990). However, direct evidence that phytodetritus may influence growth rates is provided by BATHYSNAP photographs showing a specimen of the barnacle *Poecilasma kaempferi* growing more quickly during and following the deposition of phytodetritus on the Goban Spur (1520 m depth) than prior to the flux event (Lampitt, 1990). Some echinoderms certainly feed on phytodetritus. Pigment analysis of the gut contents of certain holothurian species suggests that they consume phytodetritus almost exclusively when it is present on the seafloor (Billett et al., 1988; Lauerman et al., 1997). There is good evidence from gut contents and sea-floor photographs that the echinoid *Echinus affinis* feeds on fresh phytodetrital deposits (Campos-Creasey et al., 1994), and that this triggers the seasonal growth and reproduction reported in this species (Tyler and Gage, 1984; Gage and Tyler, 1985). Seasonal growth and reproduction reported in a range of other North Atlantic deep-sea invertebrates (sponges, actiniarians, brachiopods, protobranch bivalves, echinoids, asteroids, ophiuroids, spider crabs and hermit crabs) may also be linked to seasonality in food supply, although the evidence is largely circumstantial (Tyler, 1986, 1988, 1995; Gooday and Turley, 1990; Gage and Tyler, 1991; Van-Praët, 1990; Witte, 1996).

REGIONAL DESCRIPTIONS

The Northwest Atlantic continental margin

The Atlantic continental slope and rise (ASCAR region; 28–42ºN, 200–4000 m water depth) off the eastern United States has been studied extensively (Milliman and Wright, 1987). Several large programs (Table 5.1) have focused on aspects of carbon cycling and benthic biological patterns on the slope, though much additional work has taken place on the continental shelf. A dominant physical feature is the warm Gulf Stream, which flows north from the Florida Strait along the slope and then diverges eastwards off Cape Hatteras. The western Boundary undercurrent, associated with North Atlantic deep water, flows southwest along the entire rise below about 2000 m. Colder coastal and slope water, derived from various sources, occurs generally inshore of the Gulf Stream (Schmitz et al., 1987). The direct influence of the Gulf Stream on the bottom can be detected to a depth of over 600 m in some places. Both cold-core (cyclonic) and warm-core (anticyclonic) rings, associated with the Gulf Stream, introduce water with different properties into the major ASCAR water masses. However, ring effects are concentrated in the upper 1000 m (Schmitz et al., 1987).

General discussions of the biological communities of the ASCAR region can be found in Hessler and Sanders (1967), Hecker et al. (1983), Blake et al. (1985, 1987), Maciolek et al. (1987a,b), Wiebe et al. (1987), and articles within Diaz et al. (1994). Many of these reports are the result of extensive surveys made under the auspices of the United States Minerals Management Service, which is charged with evaluating natural resources (e.g., hydrocarbons) and the impact of exploiting these. These reports divide the ASCAR region into the North, Mid and South Atlantic Bights (NAB, MAB and SAB, respectively), covering the United States margin from Georgia to Canada.

Gay Head–Bermuda transect

Historically, perhaps the most important study of Atlantic deep-sea infaunal communities was carried out by Sanders, Hessler and coworkers (Sanders et al., 1965). They sampled sediments along a transect from the Massachusetts shelf (20 m) to Bermuda (1000 m), encompassing the intervening slope, rise and abyssal environments; this is now referred to as the Gay Head–Bermuda transect. Quantitative samples were taken with an anchor dredge and washed through a 0.42 mm mesh. They revealed much higher faunal densities and diversity than expected (Hessler and Sanders, 1967), and initiated a persistent fascination with the quantification and explanation of high diversity in the deep sea (Rex, 1983; Grassle, 1989; Rex et al., 1997). Macrofaunal densities decreased with both depth and distance from land (Sanders et al., 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969), and each region along the transect was found to support characteristic faunal densities (individuals m^{-2}): the outer continental shelf 6000–13 000; the upper slope 6000–23 000; the lower slope 1500–3000, the continental rise 500–1200; the abyss beneath the Gulf Stream 150–270; the abyss in the Sargasso Sea 30–130; the lower Bermuda Slope 120–300 and the upper Bermuda slope 500–750 (Sanders et al., 1965). Polychaetes formed 34–84%, crustaceans 3.5–50% and bivalves 1–24% of these faunal assemblages. The best-represented polychaete families were the Ampharetidae, Maldanidae, Paraonidae, Phyllodocidae, Spionidae and Syllidae, which together accounted for 88 of the 266 polychaete species present (Sanders et al., 1965). Bivalves were mainly Eulamellibranchiata and Protobranchiata (93% of total). No consistent relationship was observed between animal densities and the organic-carbon or nitrogen content of the sediments, and it was noted that some of the highest densities occurred on the upper slope where organic-carbon values were low (Sanders et al., 1965). Sanders et al. (1965) proposed that the absence of correlation was related to the refractory nature of sedimentary organic matter, an idea substantiated by later studies on the northwest margin (references in Diaz et al., 1994).

Epibenthic sled samples taken along the Gay Head–Bermuda transect yielded a spectrum of species different from that given by the anchor dredge, but substantiated the finding of high faunal diversity in individual samples (Hessler and Sanders, 1967; Sanders and Hessler, 1969). Along the transect, sharp faunal breaks were observed for polychaetes, bivalves and crustaceans at the shelf–slope boundary (100 to 300 m), a region taken as the upper limit of the deep-sea benthos in this part of the Atlantic. Despite an absence of abrupt boundaries at bathyal or abyssal depths, Sanders and Hessler (1969) considered depth to be a primary determinant of species composition. They pointed out that, while 48% of bivalve species were shared between a 1400-m station on the Gay Head–Bermuda transect and a 1700-m station off West Africa, an 800-m change in depth on the Northwest Atlantic margin (along the Gay Head–Bermuda transect) produced much greater differences in species composition. Sanders and Hessler (1969) also argued that depth change has a greater impact on densities than distance from land. For example, densities at their 4500 m and 5000 m stations were less than at 200 m by a factor of 50–390, despite surface productivity being half as great at the deeper stations.

Studies of the respiration of the benthic community, conducted along the Gay Head–Bermuda transect with grab respirometers (Smith, 1978), indicated decreasing oxygen consumption by the sediment community with increasing water depth and distance from shore (Smith and Hinga, 1983). Respiration varied by a factor of 25 from the shallowest station (1850 m) to the deepest (5200 m). Smith (1978) formulated a predictive equation for sediment-community oxygen consumption (SCOC) which explained 92.4% of the variation in measurements. Depth alone accounted for 83.1% of this, with sediment nitrogen content, C:N ratio, faunal biomass and water temperature also contributing.

Nova Scotia rise

The Nova Scotia rise is the best-studied high-energy habitat in the deep Atlantic Ocean. An area centered around 40º27′N, 62º20′W (4600 to 4800 m) experiences episodic, intense sediment-transport events. This was the site of the High Energy Benthic Boundary Layer Experiment (HEBBLE), which focused on the physical aspects, sediment transport and biological dynamics of this energetic benthic environment. Currents within 59 m of the seabed, measured over a 4.5 year period, exhibited increased speeds (15–23 cm sec^{-1}) during periods termed benthic storms. These occurred approximately every 21 days, and lasted on average for 7 days. Every 10 months there was a storm with average velocity >23 cm sec^{-1} (Aller, 1989). The storms caused the following sequence of events: (a) erosion, in which surface sediment, surficial organic matter, bacteria, larvae and juveniles were swept away; (b) intermediate current velocity, during which there was deposition of fresh organic matter, removal of metabolites, and mechanical stimulation of microbes; and (c) decelerating currents, involving deposition of several centimeters of sediment, burial of organisms and infilling of burrows. Maximal foraminiferal and metazoan abundances were observed during this period (Aller, 1989).

At the HEBBLE site the sediments support unusually high densities of bacteria, polychaetes, bivalves, isopods and tanaids relative to other locations at comparable depths (Thistle et al., 1985, 1991). Thistle et al. (1991) suggested that this indicated a fairly high flux of food to the seafloor. Community structure is distinct, in that macrofaunal assemblages are dominated by 2 species of ampharetid polychaetes, which comprise over 60% of the individuals collected. A predominance in the macrofauna of juveniles, rather than adults (as is more typical of abyssal sites), suggests that the fauna is continually responding to disturbance (Thistle et al., 1985). Comparable ‘opportunistic’ characteristics were observed in deep-sea recolonization experiments carried out at a depth of around 2000 m by Grassle (1977) and Desbruyères et al. (1980). The macrofaunal taxa at the HEBBLE site are mainly deposit feeders which can take advantage of organic matter deposited on the sediment surface (Thistle et al., 1985). They appear to mix sediments actively (DeMaster et al., 1991).

Densities of nematodes and harpacticoid copepods at the HEBBLE site, and diversity of copepods, did not differ from those reported in other abyssal areas (Thistle et al., 1985, 1991). Thistle and Sherman (1985) suggested that some nematodes use long retractable tails to avoid resuspension, but in general the nematode fauna exhibited few of the adaptations normally found in nematodes from high-energy, coarse-grained environments.

Taxa residing in surficial sediment (isopods, nematodes and harpacticoid copepods) exhibited variation in abundance over time that was attributed to erosion by storms (Thistle, 1988; Thistle et al., 1991). Standing stocks of polychaetes, bivalves, and tanaids, many of which burrow, remained relatively constant during the study (Thistle et al., 1991). Thistle and Wilson (1987, 1996) observed that surface-dwelling isopods, presumably exposed to erosion, were much less common at the HEBBLE site than in other, more quiescent, deep-sea regions.

North-Atlantic (NAB) and Mid-Atlantic Bights (MAB)

Continental slope and rise: Hecker (1990a) examined variation in the megafauna with depth and geographic location on the continental margin south of New England, on the eastern and western edges of Georges Bank, and along the SEEP I transect (34 m to 2394 m) (Fig. 5.2). In this region, 80% of the continental slope consists of gully and ridge morphology (Scanlon, 1984). Hecker (1990a) described four megafaunal zones with fairly abrupt boundaries. The upper slope was dominated by solitary scleractinians and quill worms (*Hyalinoecia artifex*), and the lower slope by the brittlestar *Ophiomusium lymani*, cerianthid anemones, sea pens and the urchin *Echinus affinis*. These two regions exhibited highest densities. The upper mid-slope was occupied by lower numbers of red crabs and fishes, and the transition zone by cerianthids, sea pens and ophiuroids. Animal distributions were controlled by effects of local topography on currents, and accompanying effects on food availability. The mid-slope, where densities were lowest, is a broad depositional band; higher currents are present on the upper and lower slopes where megafaunal densities were greatest.

Comparable studies of megafaunal zonation in the Mid-Atlantic Bight were carried out by Hecker et al. (1983) on the continental margin (100 m to 2300 m) east of New Jersey. Five major zones were observed, with faunal breaks at 400 m, 750 m, 1450 m and 1600 m. The megafauna between 200 and 400 m comprised mainly crabs (*Cancer* spp., *Munida iris*), sea pens (*Stylatula elegans*), and anemones (*Cerianthus borealis*). Between 400 m and 750 m dominants were the red crab (*Geryon quinquedens*), the anemone *Bolocera tuediae*, quill worms (*Hyalinoecia artifex*), rattails (*Nezumia* spp.) and hake (*Urophycis chesteri*). Between 700 m and 1400 m the eel *Synaphobranchus* spp. became dominant. From 1400 m to 2300 m *Ophiomusium lymani* and *Echinus affinis,* cerianthid anemones and the sea pen *Distichoptilum gracile* were dominant. As in the North Atlantic Bight, megafaunal abundances were highest in the shallower (<600 m) and deeper (>1400 m) parts of the margin. Species richness was higher in areas with boulders, outcrops and cliffs than in primarily muddy areas (Hecker et al., 1983).

Surveys of the macrofauna on the North Atlantic and Mid-Atlantic Bight margins have been carried out by Wigley and Theroux (1981), Rowe et al. (1974, 1982), and Maciolek et al. (1987a,b). Wigley and Theroux (1981) reported on a study carried out in the 1960s of macrobenthic invertebrates (>1 mm) in the Mid-Atlantic Bight between Boston and Cape Hatteras at 563 locations, at depths from 4 m to 3080 m. Macrofaunal densities averaged 293 individuals m^{-2} at 400–999 m, 72 individuals m^{-2} from 1000–1999 m, and 46 individuals m^{-2} from 2000–3080 m. These low densities were probably a result of the large mesh size and sampling bias of the grab samplers used. Corresponding biomass values were 12, 7 and 8 g m^{-2}, respectively. Densities were generally higher off southern New England than in the New York or Chesapeake Bight areas. A number of groups, including pogonophorans, thyasirid bivalves, hyalinoecid polychaetes, selected ophiuroids, and scaphopods, were most abundant at slope and rise depths.

Rowe et al. (1974) reported average densities and biomass on the continental slope south of New England (550–2080 m) to be 3325 individuals m^{-2} and 5.93 g m^{-2}, respectively. Values for the continental rise (2425–3923 m) were 789 individuals m^{-2} and 0.69 g m^{-2}; values for the abyssal plain (4901–4950 m) were 175 individuals m^{-2} and 0.22 g m^{-2}. These slope values were 3 times the densities and 10 times the biomass observed at comparable depths by Rowe et al. (1974) in the Gulf of Mexico.

Rowe et al. (1982) observed that, on the margin off New England, densities and biomass of macrofauna (>420 μm) showed significant declines with increasing water depth ($r^2 = 0.59$, $P < 0.01$, and $r^2 = 0.56$, $P < 0.01$, respectively). Considerable overlap was observed between upper-slope assemblages and those characteristic of shallower waters in the Gulf of Maine. The sharpest faunal boundaries were observed at depths of 1400–1700 m. Dominant taxa were oligochaetes (30%) from 203 to 570 m; polychaetes (*Cossura longocirrata* and *Heteromastus filiformis* – 27%) from 1141 to 1437 m; bivalves and polychaetes (*Deminucula cancellata* and *Poecilochaetus fulgoris* – 19%) from 1707 to 1815 m (DOS I), polychaetes, oligochaetes and aplacophorans (*Glycera capitata*, oligochaete spp. and *Prochaetoderma* sp. – 17%) from 2341 to 2673 m (DWD 106), sipunculans and spionid and oweniid polychaetes (20%) from 2749 to 3264 m (Hudson Rise) and scaphopods and the polychaete *Ophelina abranchiata* (15%) at 3659 m (DOS II). Diversity was greatest at mid-slope depths.

Detailed surveys of the macrofauna (>0.3 mm) in the North, Mid- and South Atlantic Bights were carried out by the United States Minerals Management Service as part of an oil exploration effort (Maciolek et al., 1987a,b; Blake et al., 1985). The North Atlantic Bight study examined stations between 255 and 2180 m from the United States/Canada border to the region south of Georges Bank off New England (Maciolek et al., 1987a). The Mid-Atlantic Bight study examined stations from 1500 to 2505 m off New Jersey, near Dump Site 106, and in a test drilling area (Maciolek et al., 1987b). The South Atlantic Bight results are discussed below. Faunas of the North Atlantic Bight and Mid-Atlantic Bight were remarkably similar. Polychaetes comprised 44–47% of the total macrofauna, arthropods 22% and molluscs 14%. Sipunculans and pogonophorans were common as well, particularly at the 1220–1350 m station in the North Atlantic Bight and the 2100 m station in the Mid-Atlantic Bight. Cirratulid, dorvilleid, paraonid and spionid polychaetes were among the most abundant taxa. Diversities were maximal at 1220–1350 m in the North Atlantic Bight and 1500–1600 m in the Mid-Atlantic Bight.

Densities in the North Atlantic Bight ranged from a high of 18 778 individuals m^{-2} at 255 m to a low of 3078 individuals m^{-2} at 2100 m. Dominant taxa included the bivalve *Thyasira ferruginea* at 255 m (overall the most abundant in the North Atlantic Bight study), the polychaetes *Prionospio aluta* and *Tharyx* spp. at 550 m, the sipunculans *Aspidosiphon zinni* and *Golfingia (Nephasoma) daphanes* at 1220–1350 m, and the polychaete *Aurospio dibranchiata* at 2100 m (Maciolek et al., 1987a). In the Mid-Atlantic Bight (1500–2505 m) dominant taxa were polychaetes (*Aurospio dibranchiata* [6.6%], *Pholoe anoculata* [4.4%], *Tharyx* sp. 1 [4.1%], and *Prionospio* sp. [3%]) and 2 prochaetadermatid aplacophorans [together 7%] (Maciolek et al., 1987b).

Canyons: The continental margin of the Northwest Atlantic is heavily carved by submarine canyons and gullies. Submarine canyons offer a highly heterogeneous substratum relative to similar depths on slopes. Several investigations have focused on the benthic faunas of these canyons and the adjacent slope areas, often with differing results. Rowe (1971b) reported that Hatteras

Canyon, studied with camera and trawl samples, exhibited reduced abundances of some megafaunal species relative to slope habitats, but that other taxa were unique to the canyon. Haedrich et al. (1975, 1980) and Valentine et al. (1980), on the other hand, found that megafaunal assemblages in Alvin, Hudson and Oceanographer Canyons were similar to those on nearby slopes. Houston and Haedrich (1984) studied the macrofauna (>0.52 mm) within and outside Carson submarine canyon (76–1129 m) on the Grand Banks. They found no difference in abundance, biomass or average body size (weight) inside or outside the canyon, or with water depth. They noted unexpectedly low abundance and biomass values, which they attributed to low organic-carbon content of the sediment (0.3%). Rowe et al. (1982), in studies of the Hudson Canyon off New York, found that macrofaunal composition did not differ inside the canyon from the adjacent slope. Macrofaunal densities were higher within the canyon head only at upper continental slope depths, most likely a result of trapping of labile organic matter. Canyon densities in deeper regions were comparable to those on the outer slope.

Maciolek et al. (1987a) examined macrofauna within and outside Lydonia Canyon (40º20′N, 67º40′W) at 550 and 2100 m during three cruises. At the shallower station, macrofauna were more abundant within the canyon, owing in part to high densities of the polychaetes *Tharyx annulosus* (32% of total fauna) and *Prionospio aluta* (8.3% of total fauna). Over half of the dominant species exhibited significant density differences at the canyon stations. No macrofaunal differences between the canyon and slope were observed at the deeper station, however.

A series of seven cruises examined the megafauna of the canyons and slopes of the North Atlantic and Mid-Atlantic Bights, using bathymetric profiling, a towed camera sled, and submersible observations (Hecker et al., 1983). Lydonia Canyon in the North Atlantic Bight was studied in detail. At most depths (300–2100 m), densities of megafauna in the canyon were greater than on the slope. Between 300 and 400 m this difference resulted from dense assemblages of the sea pen *Pennatula aculeata* and the brittle star *Ophiura* sp. in the sediment-covered axis, to the coral *Eunephthya florida* on cliffs and to the quill worm *Hyalinoecia artifex* on the lower flanks. Between 500 and 1500 m the canyon contained 38–614 individuals m^{-2}, consisting largely of localized, dense populations of corals, sponges and shrimps. The sponge *Asbestopluma* sp. was especially abundant between 800 and 950 m. Below 1500 m the brittle star *Ophiomusium lymani* became very abundant in Lydonia Canyon and on the slope. In the canyon, maximum *O. lymani* densities occurred between 1750 and 1800 m, and the species remained dominant to at least 2350 m. Other common taxa within Lydonia Canyon and on the nearby slope were the decapod crustaceans *Cancer borealis*, *C. irroratus* and *Geryon quinquedens,* and a several species of hake (*Urophycis* spp.) and grenadier (*Coryphaenoides carpinus*, *C. rupestris* and *Nezumia aequalis/bairdii*). At least two species, the longfin hake (*U. chesteri*) and the red crab (*G. quinquedens*), occurred at higher abundances on the slope outside the canyon. Filter feeders and scavengers dominated the canyon fauna at depths less than 1000 m, while deposit feeders (mainly *Ophiomusium lymani*) were dominant below 1500 m. In general, Hecker et al. (1983) found faunal patterns to be more complex and megafaunal assemblages less cohesive within Lydonia Canyon than on the slope.

Baltimore Canyon (38º5′N, 73º40′W) in the Mid-Atlantic Bight was compared to two slope areas located on the continental margin east of New Jersey (Hecker et al., 1983). Consistent elevation of megafaunal densities was not observed within Baltimore Canyon relative to the comparison slope sites, as was the case in Lydonia Canyon. However, densities from Hendrickson Canyon were consistently higher than at comparable depths on the slope (Hecker et al., 1983). At depths greater than 500 m, dense aggregations of anemones (*Halcurias pilatus* and *Hormathia nodosa*) occurred on the canyon walls. Several dominants on the slope, including a burrowing brittle star (*Amphilimna* spp.), a sea pen (*Stylatula elegans*) and a scleractinian (*Desmosmilia lymani*), were less abundant in the canyon. In the Mid-Atlantic Bight, as in the North Atlantic Bight, crabs and hake were dominant within canyons and on the surrounding slope, but they did not differentiate between these habitats. The rattail *Coryphaenoides rupestris* was the dominant grenadier within Baltimore and Hendrickson Canyons, and appears to be a canyon 'indicator' species. The holothurian *Peniagone* sp. and the sea pen *Distichoptilum gracile* were especially abundant within Hendrickson Canyon. In Baltimore Canyon, scavengers and carnivores dominated the megafauna above a depth of 1400 m, filter feeders dominated between 1400 and 1600 m and deposit feeders dominated below 1600 m (Hecker et al., 1983).

The extent to which canyon faunas appear distinct

Table 5.2
Sedimentary and biological characteristics of 3 sites located at 850 m on the North Carolina continental slope[1] (mean ± 1 SD)

	SITE I (32°52′N, 76°27′W)	SITE II (34°15′N, 75°44′W)	SITE III (35°24′N, 74°48′W)
% Organic carbon	1.2	2.1	1.7
Sediment accumulation rate (cm ky^{-1})	6.7	160	<1100
Organic C deposition (g m^{-2} y^{-1})	10	37	<170
Organic C accumulation (g m^{-2} y–^{1})	0.65	20	<150
D_b (Th-234) (cm^{2} y^{-1})	6.0±6.2	4.6±5.2	109±11
Σ CO$_2$ flux (μmol m^{-2} d^{-1})	2.2±0.2	3.8±0.4	4.7±0.4
Methane	Absent	Absent	Present
Macrofaunal abundance (ind m^{-2}; 300 μm)	9400±3100	21 400±5000	55 400±15 000
% of most abundant macrofaunal species	15.8	14.3	26.3
Macrofaunal biomass (g wet wt m^{-2})	7.19±5.51	8.16±3.99	54.52±14.44
Polychaete diversity (H') (base e)	4.66±0.81	4.57±0.75	2.76±0.54
Megafaunal density (ind m^{-2}) 700–1599 m	0.49±0.08	2.65±0.95	0.88±0.15
Dominant surface features	Sand ripples, arborescent foraminifera	Pits and mounds	*Bathysiphon filiformis* tubes

[1] Data are from Schaff et al. (1992), DeMaster et al. (1994), Blair et al. (1994), and Hecker (1994).

from those on the surrounding slope is a function of sampling technique and canyon attributes (Hecker et al., 1983). Canyons with low topographic relief and little exposed hard substratum are most likely to resemble open-slope environments. Similarly, trawl sampling is less effective in regions with high topographic relief, but obtains more sediment-dwelling fauna, again causing samples to resemble muddy-slope faunas.

South Atlantic Bight (SAB)

The North American continental shelf and slope between West Palm Beach, Florida, and Cape Hatteras, North Carolina, constitute the South Atlantic Bight (Atkinson and Menzel, 1985). Early studies of the deep benthic faunas of this area were carried out by Frankenberg (1971), Rowe and Menzies (1969), Rowe (1971a,b) and Grassle et al. (1975). The continental-slope environment off North and South Carolina has been particularly well studied, partly because of interest in the potential effects of mining the oil and gas reserves in the region (Diaz et al., 1994). The Carolina slope and rise exhibit remarkable variability in sedimentary and biological features because of the interaction of topography, ocean currents and major estuarine inputs. The Charleston Bump deflects the Gulf Stream producing a gyre, behind which are some of the most species-rich benthic assemblages known in the marine environment (Blake and Grassle, 1994; Blake and Hilbig, 1994). The slope of the South Atlantic Bight is deeply cut by canyons and gullies. Some of these, such as the Wilmington Canyon, are the result of fluvial drainage across the shelf and slope during times of lower sea level. But many of the steep canyons off Cape Hatteras are thought to result from mass wasting and slumping, and to be maintained presently by headwall and sidewall submarine erosion, with significant sediment drape deposited on crests during the Quaternary (Mellor and Paull, 1994).

Studies of three intensely investigated North Carolina mid-slope sites (each at a depth of 850 m) spaced 150 to 180 km apart, demonstrate the extent of geochemical and biological heterogeneity that can occur in margin settings (Table 5.2). Organic-carbon content of the sediments, consisting of fairly refractory material, varies little at the three sites, but measures of organic-matter flux into the seabed and rates of accumulation of organic carbon differ among stations by factors of from 4 to 200 (Blair et al., 1994; DeMaster et al., 1994). These differences are associated with strong gradients in rates of carbon remineralization (CO$_2$ flux), macrobenthic and megafaunal densities, species diversity patterns and bioturbation rates (Table 5.2). Cross-margin transects into greater depths off Capes Hatteras, Lookout, Fear and Charleston also indicate considerable regional heterogeneity off the Carolinas (Blake and Grassle, 1994).

Comparisons of macrofauna from four transects in the South Atlantic Bight with comparable data from the North and Mid-Atlantic Bights, indicate that both the highest and lowest macrofaunal diversities can be found in the South Atlantic Bight. Generally it is mid-slope depths (1220 to 1500 m) that exhibit highest species richness and evenness, but in the South Atlantic Bight some stations at 800 m and 3000 m were diverse. The low-diversity assemblages found off Cape Hatteras (Blake and Grassle, 1994) are discussed below.

Analyses of macrofaunal species composition for 146 quantitative boxcore samples collected from depths of 600–3500 m between Cape Hatteras and Charleston Bump yielded 1300 species, of which over 30% were new to science (Hilbig, 1994). Half of these were polychaetes, 22% were crustaceans and 16% were molluscs. This study found that the zoogeographic barrier reported to occur between Capes Lookout and Hatteras (Cutler, 1975) was non-existent for bivalves, but was confirmed for most cumaceans, some aplacophorans and many polychaetes (Hilbig, 1994).

Cape Hatteras: The slope off Cape Hatteras appears to be atypical with respect to the rest of the Western Atlantic slope in terms of sedimentation and benthic standing stocks (Table 5.2). It has been suggested that the sedimentary/nutrient regime is more typical of estuarine or shelf environments (Rhoads and Hecker, 1994). The Cape Hatteras region receives high input of organic matter comparable to that occurring in coastal estuaries (DeMaster et al., 1994). The high inputs are associated with high sedimentation rates resulting from outwelling from nearshore embayments and topographic funneling of nutrients from the shelf out to the slope (Blake and Diaz, 1994). The Gulf Stream and Virginia currents converge in this region. This convergence, combined with the topographic position of the Cape on the outer edge of the shelf, leads to a funneling of water masses and their constituents offshore (Rhoads and Hecker, 1994). Thus, much of the organic input in this region is terrigenous, coming from Chesapeake and Delaware Bays to the north, North Carolina sounds, and the shelf. Evidence for terrigenous inputs comes from lighter $\delta^{13}C$ values for sediments (−21.2) than is observed at sites further south (−18.7 to −19.6) (Blair et al., 1994). The composition of fatty acids and sterols are typical of refractory shelf and estuarine sediments (Harvey, 1994). The concentrations of chlorophyll a in sediments at depths from 530 m to 2003 m averaged 19.9 mg m^{-2}, a value much higher than observed elsewhere on the eastern continental slope of the United States. Viable diatoms present in cores up to 14 cm below the surface suggest high rates of bioturbation (Cahoon et al., 1994). Observations of rapid subduction of diatoms by maldanid polychaetes at this site support this idea (Levin et al., 1997, 1999), as do other experimental studies of particle mixing (DeMaster et al., 1994; Blair et al., 1996; Fornes et al., 1999). Analyses of fatty acids and sterols suggest that diatoms and dinoflagellates are the principal source of labile organic matter to the sediments, with a minor input of vascular-plant material (Harvey, 1994).

The Cape Hatteras margin supports extraordinarily large numbers of megafauna (Hecker, 1994) and dense infaunal assemblages with unusually low species diversity (Schaff et al., 1992; Blake and Grassle, 1994; Blake and Hilbig, 1994). The abundant megafauna includes large populations of brittle stars and asteroids, the foraminiferan *Bathysiphon filiformis*, three demersal fish, two eelpouts and a large anemone (Fig. 5.5) (Hecker, 1994). These taxa attain much higher population densities off Cape Hatteras than at any other site on the eastern margin of the United States (Hecker, 1994).

Macrofaunal densities at depths between 530 and 850 m off Cape Hatteras are also extraordinarily high (46 000–89 000 individuals m^{-2}), about 2–9 times higher than at comparable depths elsewhere on the eastern United States slope (Blake and Hilbig, 1994; Blake and Grassle, 1994; Schaff et al., 1992). These densities are typical of those found in shallow water, and some of the species are characteristic of shelf depths (Schaff et al., 1992; Blake and Grassle, 1994). Bioturbation activity in this area is much higher than in other regions of the Northwest Atlantic margin (Schaff et al., 1992; Diaz et al., 1994; DeMaster et al., 1994; Levin et al., 1997; Fornes et al., 1999).

The diversity and evenness of benthic foraminiferal assemblages (the fraction >63 μm – i.e., within the meiofaunal size range) at depths between 600 m and 2000 m off Cape Hatteras are reported by Cutter et al. (1994) to be high ($H' = 4.02$–4.42, $\log_e$). About 9% of the species present are those characteristic of shelf environments (Cutter et al., 1994), comparable to values from the metazoan macrobenthos. These data, however, refer to 'total' assemblages – that is, there was no discrimination between 'dead' and 'live' individuals (the 'live' being those stained with rose Bengal). Gooday et al. (2001) found that large Foraminifera (the fraction >300 μm – i.e., within the

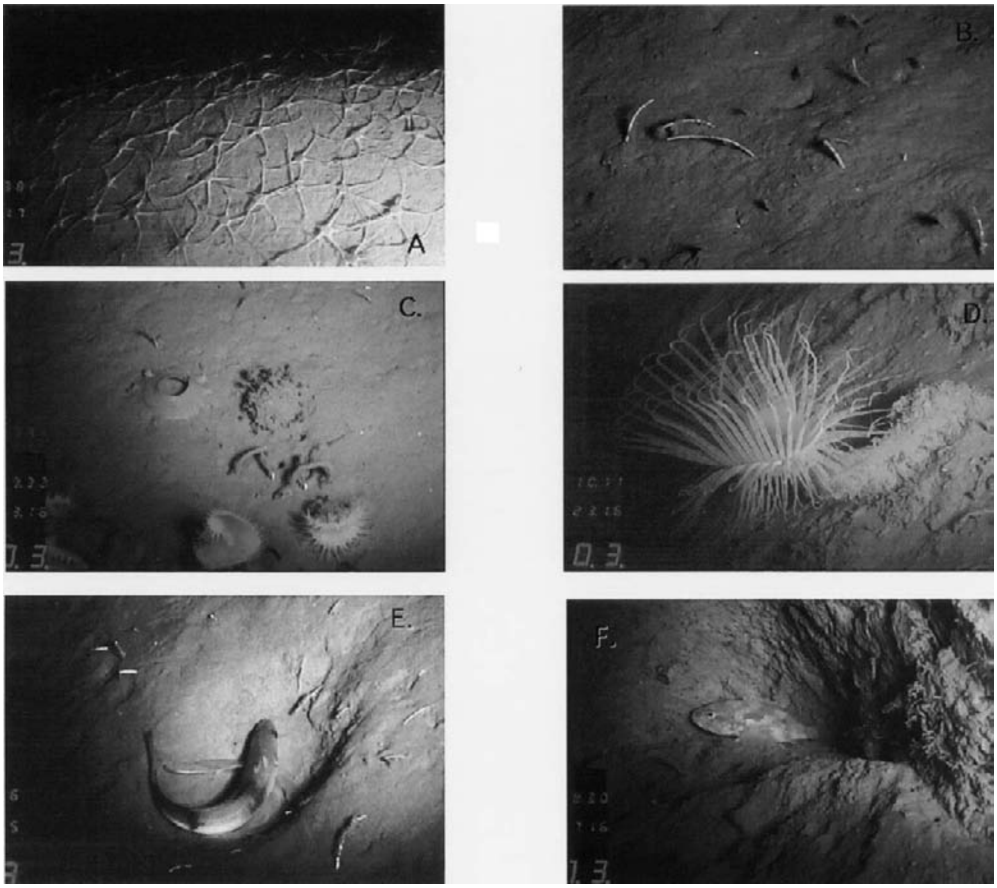

Fig. 5.5. Photographs of epifauna on the North Carolina continental margin off Cape Hatteras, NW Atlantic Ocean. (a) Aggregation of brittle stars (*Ophiura sarsi*) and unidentified asteroids atop a ridge, 600 m; (b) the foraminiferan *Bathysiphon filiformis* (white tubes) and polychaete tubes, ~800 m; (c) anemones (*Actinauge verrillii*), eel pout (*Lycenchelys verrillii*), and egg case at 850 m; (d) anemone on steep gully wall, 850 m; (e) *Phycis chesteri* (hake) and *Bathysiphon filiformis* tubes at 850 m; (f) *Helicolenus dactylopterus* off Cape Hatteras at 350 m. Note dense polychaete tubes protruding from the gully wall.

macrobenthic size range) were more abundant (15.7–24.0 stained individuals cm^{-2}) at Site III of Schaff et al. (1992) off Cape Hatteras (850 m) than at Sites I (4.3–8.7 individuals cm^{-2}) and II (8.6 individuals cm^{-2}) off Cape Fear and Cape Lookout, respectively. However, the faunas were substantially less diverse at Site III (31–42 species) compared to Sites I (64–90 species) and II (67 species). In all cases, these data are derived from the 0–15 cm layer.

Blake Plateau and Spur: It is clear from bottom photographs that certain areas of the deep ocean are eroded by strong near-bottom currents. Substrata in these high-energy regions can be sediment-covered, where particles are periodically resuspended and deposited, or moved as bedload (Hollister et al., 1984) or sediment-free rock, as sometimes found on seamounts, in canyons and at the base of plateaus (Genin et al., 1992).

Genin et al. (1992) studied the benthic fauna at depths between 3300 and 3900 m on the flanks of the Blake Escarpment off the southeastern United States. Here the bottom has steep, exposed limestone cliffs covered with manganese oxide alternating with sediment-covered slopes. The Western Boundary Undercurrent passes along the face of the escarpment and is associated with a southward flow at a speed sometimes exceeding 30 cm sec^{-1} (Lai, 1984). Analyses of over 2000 photographs revealed domination of the community by massive demosponges (Lithistidae), several species of gorgonian corals, and brisingid asteroids. Megafauna cover averaged 10% on hard substrata, and sometimes covered as much as 25% of the bottom. Megafaunal abundance at this site is several orders of magnitude higher than that reported for other sediment-free (non-reducing) sites of comparable depth. Genin et al. (1992) attributed these high abundances to an increased rate of food supply resulting from the high particle flux generated by the current, as surface productivity in the area is not known to be especially large.

Northwest Atlantic Abyss and trenches

The abyssal and hadal environments of the Northwest Atlantic have received minimal attention. By far the best-studied are the Hatteras Abyssal Plain (Fig. 5.2) and the Puerto Rico Trench, but even for these areas there are only a handful of reports, with the emphasis largely on meiofauna.

Hatteras and Nares abyssal plains

The relations between metazoan meiofaunal abundance and biomass, bacterial abundance and particulate flux were examined at a depth of 5411 m on the Hatteras Abyssal Plain (32ºN, 70ºW) (HAP), and compared to values in the Puerto Rico Trench (PRT) (Tietjen et al., 1989). Meiofaunal abundance on the Hatteras Abyssal Plain was 11.4±2.6 individuals cm^{-2}, and the biomass was 3.84 micrograms C cm^{-2}. Although nematodes comprised 75% of the individuals, harpacticoid copepods made up 85% of the biomass. Most of the meiofaunal biomass was present below the 0–2 cm layer. Comparisons with the Puerto Rico Trench indicate higher meiofaunal densities, biomass and even bioturbation rates on the Hatteras Abyssal Plain than in the Puerto Rico Trench (7460–8189 m). Nematode faunas at the same two sites, and at a bathyal silty-sand site in the Puerto Rico Trench (2217 m), were largely dominated by species of *Acantholaimus, Halalaimus* and *Theristus,* with some additional genera (*Camaicolaimus, Desmodora, Greeffiella, Leptolaimus, Setoplectus* and *Tricoma*) also important at the bathyal silty-sand site (Tietjen, 1989). Many species were endemic – 67% in the Hatteras Abyssal Plain area and 77% in the Puerto Rico Trench area.

Foraminiferal faunas on the Nares Abyssal Plain have been described by Schröder (1986) and Schröder et al. (1989). The assemblage at a 5800 m site located below the calcium compensation depth is dominated by fragile agglutinated taxa, komokiaceans being particularly abundant and diverse. More than 70% of the 54 species (komokiaceans excluded) recognized here are also present in the central North Pacific, reflecting the wide occurrence of many abyssal agglutinated foraminiferal species (Schröder et al., 1988).

Puerto Rico Trench

Early, non-quantitative reports of the fauna of the Puerto Rico Trench focused on taxonomic descriptions and provided little general information about the benthic community (Nybelin, 1951; Bruun, 1957; Pérès, 1965; Staiger, 1972). Recent sampling has demonstrated that, in contrast to the typical view that trenches support abundant, low-diversity assemblages, the Puerto Rico Trench has a depauperate benthic assemblage (Richardson et al., 1995). Three 0.25 m^2 boxcores collecting macrofauna (>297 μm) along the central axis of the trench (8371–8376 m) collected only 21 specimens (= 28 individuals m^{-2}) belonging to 13 species, with a biomass of only 0.079 g wet wt m^{-2} (Richardson et al., 1995). Polychaetes and tanaids accounted for 54% of the individuals and 96% of the wet biomass. Slightly higher faunal biomass (0.3–0.42 g m^{-2}) was estimated for the Puerto Rico Trench by Pasternak et al. (1975) using dredge samples. Metazoan meiofaunal abundance also was extremely low: 69±10.8 individuals 10 cm^{-2}. Nematodes made up 95% of the total meiofauna; harpacticoid copepods were 2.3% and ostracods were 1.0%. George and Higgins (1979) reported even lower meiofaunal densities of 17.1–17.3 individuals 10 cm^{-2} from 8560 m in the Puerto Rico Trench, but used a 63 μm rather than 42 μm mesh net. Their otter trawls contained deposit-feeding holothurians, isopods, amphipods and cumaceans. The presence of depositional laminae of fine silt visible in *x*-radiographs is considered indicative of low sediment mixing in the Puerto Rico Trench (Richardson et al., 1995). This observation is in agreement with the very low biomass of bioturbating taxa.

The faunal values for the Puerto Rico Trench are among the lowest reported for abyssal or hadal environments. This is attributed to low food flux and poor nutrient value (0.74% organic C) of the food supply. Disturbance by turbidity flows may also contribute to the depauperate nature of the benthic assemblages (Richardson et al., 1995).

Northeast Atlantic

The deep-sea fauna along the northeast Atlantic continental margin, first sampled during the 1860s and

1870s, is perhaps better known than that of any other deep-sea region in the world. Recently, this margin and the adjacent abyssal plains have been the focus for a number of national (e.g., British, Dutch, French and German) programs, and international ones, mainly funded by the European Union (Table 5.1) which have influenced the development of modern themes in deep-sea biology.

Le Danois (1948) provided a valuable synoptic account of early studies of larger animals along the northwest European margin (Bay of Biscay, Porcupine Seabight, Rockall Trough). Comprehensive reviews of meiofauna in the deep northeast Atlantic (their abundance, faunal composition, bathymetric and latitudinal patterns, vertical distribution within the sediment, temporal patterns) have been compiled by Thiel (1983) and Vincx et al. (1994). Gooday et al. (1998) have provided a synopsis of Northeast Atlantic foraminiferal diversity data.

Norwegian–Greenland Sea (NGS)

The benthic systems of this subarctic region have been investigated as part of a large-scale interdisciplinary study ('Sonderforschungsbereich 313') by the University of Kiel of particle flux to the seafloor and its transformation into the paleoceanographic record. Multiple corer samples taken over a wide area of the Norwegian–Greenland Sea were used to analyze the pigment content (chlorophyll equivalents) of the sediment (Graf et al., 1995). The highest concentrations were encountered close to the ice edge off Greenland, in samples from the Kolbeinsey Ridge (800–950 m), and particularly at the 'FLUFF' station, southwest of Jan Mayen Island, where a phytodetritus layer 1 to 2 cm thick was observed during 1989. Pigment concentrations on the Barents Sea slope (380–2500 m) were also high, probably owing to lateral advection from the adjacent shelf, but they were lower on the Vøring Plateau (950–1450 m), and particularly at two deep stations in the East Greenland Basin (3000 m) and the Lofoten Basin (3300 m).

The Vøring Plateau, a bathyal (1200–1600 m) terrace on the Norwegian continental margin, was a particular focus of interest during this project. A site in this area, 1240-m deep, was visited on eight cruises; samples were obtained during seven different months (February, May to October), albeit in different years (Graf et al., 1995, table 1 therein). Chlorophyll equivalents were unmeasurable during mid-May, but increased dramatically in late May and June 1986 before declining during July. A second, lower peak occurred in September 1988. Pigment concentrations were puzzlingly high in February 1987, possibly as a result of some unusual sedimentation event. Data for sediment oxygen demand (SOD) are available for the period from May to September and show two peaks of activity in June and August. Graf et al. (1995) pointed out that fluctuations in the pigment concentrations and sediment oxygen demand match patterns of organic-matter flux, as determined from sediment-trap records. The July peaks correspond to the spring input of particulate organic carbon (POC) and the August/September peaks to the maximum flux of particulate organic nitrogen (PON). A pulse of copepod fecal pellets at the end of May 1986 at a somewhat deeper site (1430 m) led to a rapid increase in concentrations of chlorophyll a in the sediment. Within a period of only 11 days (May 24th to June 4th), the chlorophyll had been incorporated to a depth of 9 cm by the sipunculan *Golfingia (Nephasoma)*. Correspondingly enhanced metabolic activity was indicated by increased ATP concentrations, with subsurface peaks reflecting the feeding activities of *Golfingia (Nephasoma)* and the enteropneust *Stereobalanus canadensis*. These and other large infauna are discussed below.

Sibuet (1985) studied megafaunal echinoderms from the Norwegian, Lofoten and Greenland Basins (depth range 2500–3700 m) where holothurians were exceptionally abundant, occurring in densities of 5779, 4971 and 7232 individuals ha^{-1}. Populations were dominated by *Elpidia glacialis,* a small species <25 mm in size.

Romero-Wetzel and Gerlach (1991) have presented an overview of macrofaunal abundance, species composition, and biomass on the Vøring Plateau based on the >500 μm fraction of 17 boxcores collected from depths between 1200 and 1500 m. Of the 70 species recognized, only the following were present in half or more of the samples: *Malletia obtusa* (bivalve), *Aricidea abranchiata*, *Chaetozone setosa*, *Myriochele* sp. 1, *M. fragilis*, *Notomastus latericeus*, *Paramphinome jeffreysii* (polychaetes), *Golfingia (Nephasoma)* sp. 1 (sipunculan), *Ophiocten gracilis* (ophiuroid), and *Stereobalanus canadensis* (enteropneust). They recognized three categories of macrofauna: smaller and larger infauna, and epifauna (all sizes), which have mean densities of 531, 34 and 56 individuals m^{-2} and biomass values of 1.28, 2.26 and 0.52 g wet weight m^{-2}, respectively (Romero-Wetzel and Gerlach, 1991). These authors also emphasized the contribution of large (10–1000 mg individual biomass) and very large macrofauna (1–100 g) to benthic biomass on the Vøring Plateau. The very large animals in particular were rarely caught in core samples, but were estimated to contribute as much as 70% of total macrofaunal biomass.

Burrowing organisms may play an important role in geochemical processes and sediment bioturbation on the Vøring Plateau. Romero-Wetzel (1987) described a network of very narrow (0.2–0.5 mm diameter), predominantly vertical burrows which penetrated to a depth of 50 cm and intersected the sediment surface as tiny, inconspicuous openings. These are constructed by the sipunculan *Golfingia (Nephasoma)* and may be extremely abundant (up to 20 000 m^{-2}). The sipunculan draws organic matter down into its burrow and ejects feces back onto the sediment surface. Elaborate burrow systems are constructed within the top 10 cm of sediment by the enteropneust *Stereobalanus canadensis* (Romero-Wetzel, 1989). The burrows are 5–6 mm in diameter, and include vertical shafts to the surface as well as extensive, dichotomously branched horizontal galleries. Individual burrow systems may contain several individuals of *S. canadensis* as well as masses of their fecal pellets (Jensen, 1992b). Like its shallow-water relatives, *S. canadensis* secretes brominated phenols. These toxins deter colonization of the burrow wall by metazoan meiofauna, although foraminifers (mainly *Lagena* sp.) appear resistant to their effects (Jensen et al., 1992a). Another large infaunal inhabitant of the Vøring Plateau (at depths of 1244–2926 m), the anemone *Cerianthus* (Anthozoa), occupies a horizontal, branched tube 12–40 cm below the sediment surface in densities of up to 3.5 individuals m^{-2}(Jensen, 1992a). Jensen suggested that the tube systems act as a 'gas pipeline' for methane and hydrogen sulfide derived from deeper in the sediment column. He speculated that the gases might support endosymbiotic bacteria or bacteria living in the tube lining.

Jensen et al. (1992b) discovered distinct difference between the meio- and macrofauna on opposite sides on a ridge on the Vøring Plateau. The side exposed to sediment advection (Expo-stations) had generally higher oxygen consumption rates, lower meiofaunal biomass and lower maximum depth of penetration of meiofauna than the other side where sediment was being accumulated (Impo-stations). Taxa which were more abundant at the Impo-stations included larger nematodes (e.g., *Pararaeolaimus rumohri* and various desmoscolecids) and several pogonophore species (i.e. infaunal worms); those found mainly at the Expo-stations included smaller nematodes (*Acantholaimus elegans, Desmodora pilosa*, *Rhabdodemania* sp. and *Sabatieria* sp.), sipunculans, sponges and hydroids (i.e. suspension and deposit-feeders). Jensen et al. (1992b) concluded that a distinctive pogonophore and nematode fauna occupies areas of the Vøring Plateau which experience high levels of sediment and organic-carbon accumulation.

Foraminifera are an important component of the Norwegian–Greenland Sea benthos. On the Vøring Plateau, Romero-Wetzel and Gerlach (1991) estimated that they constituted 41.6% of the biomass of 'larger meiofauna' (wet weight 1–100 micrograms), in addition to an unknown proportion of the 'small meiofauna'. Thies (1991) described 'live' (Rose Bengal stained) and dead foraminiferal faunas (>250 μm fraction) in 81 box cores from areas between Greenland and Spitzbergen (Svalbard) and between Greenland and Norway (depth range 81 to 3695 m). A total of 102 species were recognized, but the faunas were of low diversity, particularly in the deep basins where only 3–5 species were present in the >250 μm fraction. Thies (1991) recognized a low-diversity fauna on the lower slope and in the basins, dominated by *Cibicidoides wuellerstorfi, Cribrostomoides subglobosa, Crithionina hispida* and *Pyrgo rotaliaria.* This contrasts with a more diverse fauna (up to 19 species) on the upper slope and shelf characterized by *Cibicides lobatulus, Cribrostomoides subglobosa, Reophax difflugiformis* and *R. scorpiurus* She concluded that food supply exerted a decisive influence on the foraminiferal faunas. This is in accordance with the observations of Heeger (1990; reviewed by Gooday et al., 1992) that many of the Foraminifera in the Norwegian–Greenland Sea feed on fresh phytodetritus. Moreover, ingested food can be converted into biomass very rapidly (Heeger, 1990), within a period of days in experimental systems (Altenbach, 1992; Linke et al., 1995). Some species (*C. subglobosa, Pyrgo murrhina*, *Rhabdammina abyssorum*), show corresponding physiological adaptations to a fluctuating food supply. Rapidly fluctuating ATP content and heat production indicate that they can survive periods of starvation by metabolizing their own protoplasm, while the ability to phosphorylate adenosine monophosphate (AMP) to adenosine triphosphate (ATP) allows a rapid physiological reawakening to occur when the Foraminifera are presented with a sudden food pulse (Linke, 1992; Linke et al., 1995).

British continental margin

Recent work has concentrated in three main areas of the Celtic margin of Britain: the Rockall Trough, the Porcupine Seabight, and the Goban Spur – localities which are convenient to reach from British ports and relatively easy to sample.

Rockall Trough (RT): This elongate basin lies between Scotland and the northern part of Ireland on the one hand, and the Rockall Bank on the other, and deepens from the Wyville Thomson Ridge in the north to the Porcupine Abyssal Plain in the south. It has been intensively studied for over 20 years by J.D. Gage and his colleagues at the Scottish Marine Biological Association/Scottish Association for Marine Science in Oban. They have compiled a data set from two deep Permanent Stations, one situated at 2200 m depth, the other at 2900 m – the longest time series available anywhere in the deep ocean. Mean standing crop of macrofauna (>420 μm, excluding Foraminifera), sampled using replicate 0.25 m^2 box cores, was 1716 individuals m^{-2}, with a wet weight of 14.92 g m^{-2} (Gage, 1979). Polychaetes (59.1% of the individuals) were the dominant taxon followed by tanaids (10.3%), bivalves (10.1%), isopods (4.4%), scaphopods (3.9%), amphipods (3.3%) and nemertines (3.3%). The proportions of various taxa were remarkably similar in box cores taken at 1800 m, 2000 m, 2500 m and 2900 m in other parts of the Rockall Trough; only isopods tended to be relatively more abundant at the Permanent Station. The isopod fauna includes 79 species, dominated by the Eurycopidae, Haploniscidae, Ilyarachnidae, and Ischnomesidae (Harrison, 1988). The bivalves consist predominantly (80%) of members of the Nuculanidae. The macrofauna at the Permanent Station was also sampled using an epibenthic sledge fitted with a 500 μm-mesh net (Gage et al., 1980). These catches were dominated by polychaetes, bivalves and ophiuroids, although there was considerable variation between individual catches, caused in particular by summer recruitment of juveniles of the ophiuroid *Ophiura ljungmani.*

Gage (1986) reviewed knowledge of the invertebrate megafauna of the Rockall Trough based on catches from Agassiz trawls or large, single- or twin-warp trawls. The faunas are generally similar to those found in the Bay of Biscay and Porcupine Seabight. Echinoderms predominate at all depths, and species are zoned bathymetrically, the greatest rates of faunal change occurring between 800 and 1200 m and (particularly in the case of ophiuroids) around 1800 m. Other invertebrates, particularly cnidarians and crustaceans, are also important. The cnidarians include the deep-water coral *Lophelia pertusa*, a widespread inhabitant of the upper slope along the European continental margin, and associated with areas of steady current around the Rockall Trough (Wilson, 1979). The influence of currents on the megafauna is particularly evident on the Feni Ridge on the western flank of the Rockall Trough, where suspension feeders are more common than they are at tranquil sites on the eastern side of the Trough. As well as bathymetry and current velocity, megafaunal composition seems to reflect sediment type and bottom water-mass distribution. Thus, the zone of rapid change in the echinoderm fauna between 800 and 1200 m occurs within a distinctive water mass of Mediterranean origin, and also spans the permanent thermocline. Gage (1986) attributed differences in the depths of zones of maximum faunal change between the Rockall Trough and sites in the Northwest Atlantic and Northeast Pacific to such local influences superimposed on bathymetric and other trends which apply globally.

The availability of extensive time-series material allowed Gage and his colleagues to analyse the demography and reproductive dynamics among animals in the Rockall Trough (reviewed by Tyler, 1988; Gage, 1991; Gage and Tyler, 1991). This has led to the recognition of taxa displaying seasonal reproduction, leading to the production of juveniles in the spring, coincident with phytodetrital pulses (Gage and Tyler, 1991). Seasonally breeding taxa include isopods, the protobranch bivalves *Ledella pustulosa* and *Yoldiella jeffreysi,* and the echinoderms *Echinus affinis, Ophiura ljungmani, Plutonaster bifrons* and possibly *Dytaster insignis, Ophiocten gracilis* and *Ophiomusium lymani.* Other echinoderms have non-seasonal (continuous) reproduction with large or intermediate egg size and low or intermediate fecundity. Classical growth-rate studies based on size distributions have been carried out for *E. affinis, L. pustulosa*, *Ophiomusium lymani*, *Ophiura ljungmani* and *Y. jeffreysi.* In the case of *Ophiomusium lymani,* it was impossible to disentangle the individual cohorts present within the single unimodal size peak. In this species, and in *Ophiura ljungmani* and the crinoids *Annacrinus wyvillethomsoni* and *Bathycrinus carpenteri,* growth rates have been determined by analyzing growth zones in skeletal plates (Duco and Roux, 1981). These studies suggest that the two crinoid species have growth and mortality patterns similar to those of near-shore species. The echinoid *Echinus affinis*, however, appears to live longer (up to 28 years) and grow more slowly than related shallow-water species, although some other echinoderm species may grow faster (Gage and Tyler, 1985).

Porcupine Seabight (PSB): This embayment of the continental slope, lying southwest of Ireland and south of the Rockall Trough, is bounded by the Porcupine Bank to the west, the Irish shelf to the east and the Goban Spur to the south (Fig. 5.1). It is connected to the Porcupine Abyssal Plain by a narrow southwestern opening. An excellent general account of the topography, sedimentology, geology and hydrography of the Porcupine Seabight has been given by Rice et al. (1991). To the north and west the slopes are fairly gentle but the eastern side is cut by canyons; this makes conventional sampling gear difficult to use. An important feature is the Gollum Channel System, which runs through the axis of the Seabight and out onto the Porcupine Abyssal Plain. Recent submersible observations suggest that the upper part of the channel system (down to at least 940 m depth) is active, but that at 3000 m depth bottom currents are too weak to resuspend fine-grained sediments (Tudhope and Scoffin, 1995).

Between 1977 and 1986, the Porcupine Seabight was subject to an extensive sampling program by the Institute of Oceanographic Sciences (U.K.), summarized by Rice et al. (1991). The main focus was on the megafauna, but the meiofauna (including the Foraminifera) was also studied. This program yielded some important results, the most notable being the discovery of phytodetritus deposition (Billett et al., 1983), described elsewhere in this chapter (p. 121).

The invertebrate megafauna was sampled with a semi-balloon otter trawl and an epibenthic sledge, and photographed *in situ* using a camera attached to the sledge. Rice et al. (1982) used an epibenthic sledge fitted with an odometer wheel, and simultaneously obtained seafloor photographs, to quantify the megafauna in the Porcupine Seabight. Despite various shortcomings, a combination of sampling and photography provided reasonably accurate estimates of densities for some non-sessile taxa such as the larger echinoderms. For example, the holothurian *Benthogone rosea* had a mean density of 0.098 and 0.114 individuals m^{-2} (photographic and catch data respectively) in a haul taken at 1400 m. Dense aggregations of the small holothurian *Kolga hyalina* are occasionally observed in the Porcupine Seabight. Billett and Hansen (1982) counted 50 individuals m^{-2} in photographs taken around a depth of 3700 m, and 34 individuals m^{-2} around 4000 m depth, these high densities being associated with the Gollum Channel System. Specimens caught at particular stations were small and had a narrow size distribution, suggesting periodic synchronous reproduction and other opportunistic life-history characteristics. Large numbers of possibly opportunistic holothurians have also been observed in some Northwest Atlantic canyons (Rowe, 1971b).

Megafaunal biomass in the Porcupine Seabight is between two and five times greater than in the Bay of Biscay (Billett, 1991). Despite considerable scatter, total biomass values (whether measured as wet weight, dry weight, or ash-free dry weight [AFDW]) show a clear logarithmic decrease between 500 and 4100 m depth, with echinoderm biomass decreasing less steeply with depth than the biomass of crustaceans and ‘other phyla’ (Lampitt et al., 1986). On the upper slope (200–1000 m), the main megafaunal animals are crustaceans (particularly the crab *Geryon tridens* and other decapods), sponges and cnidarians. Echinoderms predominate at greater depths, constituting >75% and sometimes >90% of the invertebrate megafaunal AFDW at 1500 m, 2000 m, 2500 m, 3500 m and 4000 m depth (Billett, 1991). Holothurians are always the most important taxon, except around 2500 m depth in the center of the Seabight where the megafauna is dominated by asteroids. Billett (1991) has summarized the bathymetric distribution of holothurian species in the Porcupine Seabight based on epibenthic sledge catches (Fig. 5.6). He recognized three zones: the upper and middle slope where species occupy relatively narrow depth bands related to changing hydrographic conditions, the middle and lower slope, where holothurians are uncommon for poorly understood reasons, and areas beyond the base of the slope where bathymetric distributions are relatively broad.

Lampitt et al. (1986) repeatedly sampled a station at a depth of 1300 m using an epibenthic sledge. Differences in megafaunal biomass between samples collected at this site on a single cruise spanned an order of magnitude, from $<0.1\ g\ m^{-2}$ to $>1\ g\ m^{-2}$ ash-free dry weight. These disparities were due entirely to variations in the abundance of *Pheronema carpenteri.* This hexactinellid sponge is abundant along parts of the Northwest European margin and forms dense aggregations between 1000 m and 1300 m in the Porcupine

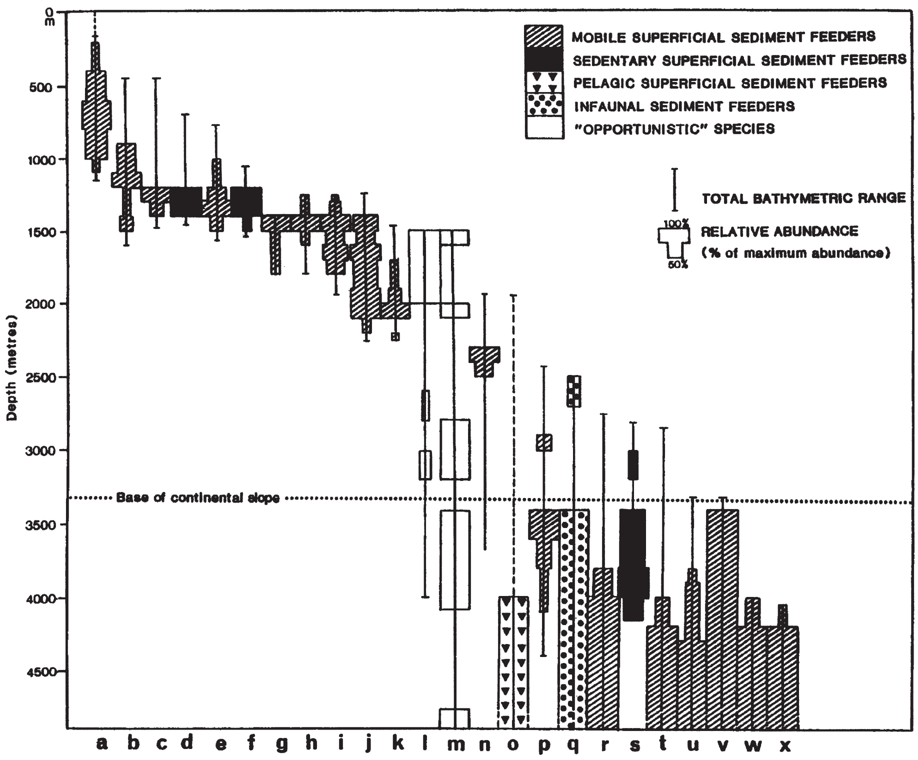

Fig. 5.6. Bathymetric distribution of the 24 most common holothurians in the Porcupine Seabight showing total range and relative abundance of each species at various depths. Feeding types are also indicated. From Billett (1991).

Seabight (Rice et al., 1990). The density and biomass of these populations were analysed from photographs by Rice et al. (1990). Maximum sponge densities in 10-m depth horizons ranged from 0.8 to 1.6 individuals m^{-2} (biomass 199–453 $g\,m^{-2}$) but reached values of 2.5 to 5.0 individuals m^{-2} (biomass 498 to 1131 $g\,m^{-2}$) in single photographs. These dense populations lie below a zone on the upper slope where near-bottom tidal current velocities are enhanced by topographic effects. Rice et al. (1990) suggested that *Pheronema* avoids the regions of highest current velocity but populates nearby downslope areas in order to benefit from the availability of an enhanced load of suspended material. Mats of *Pheronema* spicules cover about a third of the seafloor in the sponge zone. Macrofaunal densities were an order of magnitude higher in a spicule-dominated box core from 1250 m than in box cores from outside the sponge zone (Bett and Rice, 1992).

Meiofauna in the Porcupine Seabight was sampled using the Barnett–Watson multiple corer. Pfannkuche (1985) studied samples taken at 500-m intervals along a transect of the Seabight extending from a depth of 500 m to 4850 m. Metazoan meiofaunal abundance (individuals 10 cm^{-2}) decreased rapidly from 2604 to 1492 between depths of 500 and 1500 m, but more gradually from 828 to 315 below 2000 m. Biomass (AFDW), declined correspondingly from 1.16 mg 10 cm^{-2} at 500 m to 0.61 at 1500 m, and then from 0.6 at 2000 m to 0.35 at 4850 m. Both biomass and abundance were closely related to the concentrations of chloroplastic pigments measured in a parallel set of samples. The foraminiferal meiofauna at a bathyal station 1320–1340 m deep has been described by Gooday (1986). Foraminifera accounted for 46–59% of all the meiofauna, and were highly diverse (95–124 species). This was one of the earliest studies to describe the vertical distribution of foraminiferal species within the sediments. Some species were more or less restricted to the upper 1 cm, while others lived infaunally. In a later study, Gooday and Lambshead (1989) and Lambshead and Gooday (1990), described population fluctuations among foraminiferal species in relation to phytodetritus deposition. Some species, particularly those associated with phytodetrital aggregates, were substantially more abundant during July, when phytodetritus was present on the seafloor, than during April before its arrival. In contrast, few seasonal changes were observed among the metazoan meiofauna at this site (Gooday et al., 1996).

Goban Spur: The Goban Spur is a gently sloping stepped platform which, together with the Meriadzek Terrace (a plateau-like feature on the continental margin to the southeast of the Goban Spur; see Fig. 5.1), forms the southeastern flank of the Porcupine Seabight. This region was studied intensively as part of the OMEX project funded by the European Union, which addressed the role of the Northwest European continental margin in the global carbon cycle (van Weering et al., 1998).

Total benthic biomass on the Goban Spur was dominated by small organisms: Bacteria, Fungi, flagellates, Foraminifera, and small metazoan meiofauna. The percentage contribution of these groups to the total benthic biomass increased with water depth from 90% on the shelf to 97–98% at bathyal and abyssal depths (Pfannkuche and Soltwedel, 1998). Soltwedel et al. (1996) studied trends in the metazoan meiofauna along a transect extending down the Goban Spur and onto the Porcupine Abyssal Plain (182–4470 m). Abundances (individuals cm^{-2}) varied as follows: 33.5 (182 m), 38.1 (410 m), 19.1 (1013 m), 6.6 (2084 m), 4.3 (3552 m), 6.4 (3889 m), 12.4 (4470 m). Nematodes made up between 66% (at 182 m) and 93% (at 3552 m) of the fauna and, below depths of 2000 m, showed a clear decrease in size with increasing bathymetric depth, as observed previously by Pfannkuche (1985) in the Porcupine Seabight and Soetaert and Heip (1989) in the Mediterranean. These observations support the hypothesis of Thiel (1975) that organisms tend to become smaller with increasing bathymetric depth as a result of food limitation.

Flach and Heip (1996a) analysed macrofauna (>500 μm; no. ind. m^{-2}) in box cores taken along a similar transect (208–4470 m) during October 1993, May 1994 and August 1995, and related the differences observed to seasonal and interannual variations in organic-matter inputs. Flach and Heip (1996b) have reported on the vertical distribution of macrofauna within the upper 15 cm of sediment in the May 1994 samples. One of the main findings of these studies is that there are clear seasonal and interannual variations in the macrofauna on the Goban Spur only above about 1500 m depth. Macrofaunal densities decreased exponentially with increasing bathymetric depth, but they also showed substantial seasonal and interannual differences. In particular, densities were significantly higher on the upper part of the slope (down to 1500 m) during May than in August and October, mainly as a result of the presence of large numbers of juvenile echinoderms including the echinoid *Echinus affinis* and the ophiuroid *Ophiocten gracilis,* both seasonal breeders. These fluctuations probably reflect interannular differences in the intensity of phytodetrital pulses. Polychaetes were always the most important macrofaunal taxon. Their numbers declined fairly regularly along the transect, and were significantly higher at the two shallowest stations (208–231 m, 670–693 m) during May. Crustaceans were most abundant at mid-slope depths (670–2256 m), significantly more so in August. Biomass (mg m^{-2}) also tended to decline with depth, but was consistently higher (1021) at 1034 m (station B), owing to the predominance of relatively large animals, and low (1425) at 1457 m (station II) where the animals were relatively small. Sedimentary organic carbon peaked at station B, suggesting that this site received substantial inputs of labile phytodetritus. Biomass values were somewhat higher in May at the three shallowest stations (208–1034 m) and higher in August at mid-slope stations (1425–2256 m), but these seasonal differences were not significant. Macrofaunal community respiration rates, estimated from individual weights and biomass values, were high in May between 208 m and 1034 m, but much lower at the deeper stations. At mid-slope depths (2200 m), however, rates were higher in August than in May. Between 40% and 80% of the macrofauna occurred in the 0–1 cm layer of sediment and the stations of intermediate depth (670 m, 1034 m and 1425 m) showed the highest proportions within this upper layer.

The numerical density of the megafauna undergoes a steady decrease along the OMEX transect, but biomass values are more irregular (Duineveld et al., 1997). Low values are found around the shelf break (200 m) and upper slope (700 m) (1913 and 1914 g wet weight 1000 m^{-2}, respectively) and Pendragon Escarpment (2200 m; 1188 g 1000 m^{-2}), while the highest values occur at 1450 m (4076 g 1000 m^{-2}) and 3650 m (3789 g 1000 m^{-2}). These irregularities reflect the changing taxonomic composition of the megafauna, which is dominated at different depths by crinoids (200 m), echinoids (700 m), holothurians (100 m, 3650 m, 4500 m) and poriferans (1450 m).

Among the megafauna, macrofauna and Foraminifera (>150 μm fraction), the proportion of deposit feeders generally increased with increasing water depth across the Goban Spur transect (Flach et al., 1998). The densities of suspension feeders, however, were particularly high within a zone on the upper slope (1000–1500 m water depth) subject to high current velocities. Submersible observations indicate that suspension-feeding megafauna are also common on hard steep substrates (<1000 m depth) to the west of the Porcupine Bank and Goban Spur (Tyler and Zibrowius, 1992). The most common taxa observed by Tyler and Zibrowius (1992) were sponges, cnidarians (actiniarians, corals, zoantharians, ceriantharians, antipatharians, alcyonarians and particularly gorgonians) and echinoderms (mainly crinoids, asteroids and ophiuroids). A crinoid-dominated zone between 2100 and 2600 m depth was associated with a northward-flowing water mass reaching velocities of 7 cm s^{-1}.

French and Iberian margins

Bay of Biscay: There has been a long history of French research along the Bay of Biscay continental margin and on the adjacent abyssal plain, starting in the 1880s with the *Travailleur* and *Talisman* campaigns (Le Danois, 1948; Rice, 1980). A century later, the eleven cruises organized by Biologie Gascogne (BIOGAS) between 1972 and 1981 yielded a considerable body of quantitative information on many aspects of the Biscay benthos (Sibuet, 1977; Laubier and Sibuet, 1979; Laubier and Monniot, 1985). The megafauna was sampled using a large beam trawl and evaluated photographically; macro- and meiofauna and bacteria were sampled using an epibenthic sled, and Reineck and USNEL box corers. The extensive BIOGAS collections were studied by numerous scientists from many countries, resulting in a long list of publications. In particular, the volume edited by Laubier and Monniot (1985) includes data on different faunal groups (from bacteria to megafauna), necrophages, and particular higher taxa, as well as processes such as sediment recolonization and particle fluxes. Laubier and Monniot (1985) have also given a comprehensive list of BIOGAS publications, which include both taxonomic and ecological studies.

The BIOGAS program centered around six intensively worked stations, four located in the northern part of the Bay (stations 1–4: 1920–4825 m depth) and two in the southern part (stations 5–6: 1894–4475 m depth), extending from the continental slope out onto the continental rise and abyssal plain (Laubier and Sibuet, 1979). Sibuet and Segonzac (1985) reported on the 'megafauna' from trawl samples, although they examined the fraction >1 mm and therefore included animals more appropriately considered as macrofauna. The megafauna show greater heterogeneity, both across the Bay and at particular stations, than do the meiofauna and macrofauna. Densities decreased by a factor of 9 from the shallowest to the deepest station along the northern transect (2924 individuals m^{-2} to 321 individuals m^{-2}). The shallowest station (#1: 1920–2245 m), on the Meriadzek Terrace was particularly rich and diverse, with cnidarians (actiniarians) and echinoderms making up about two-thirds of the fauna. Molluscs were abundant (34%) at station 3 (4134–4240 m), and ascidians became fairly important (up to 14% of the fauna) at the deepest station (#4: 4706–4825 m). Fewer animals were present at the two southern stations; for example, at station 5 on the continental slope (1894–1995 m) the faunal density was 440 individuals ha^{-1}, much lower than at comparable depths on the Meriadzek Terrace (2924 individuals ha^{-1}). In the south, too, echinoderms (mainly holothurians), were relatively more important than on the northern margin (Sibuet, 1977; Sibuet and Segonzac, 1985). These north-to-south differences in assemblages of larger invertebrates within the Bay of Biscay probably reflect the greater terrigenous input (including plant material) in the southern area, much of it presumably channeled down submarine canyons.

Biogenic traces visible in seafloor photographs showed a good correlation with abundance of animals (>1 mm) across bathymetric gradients, and, in agreement with animal densities, were more prevalent at the northern than at the southern sites (Mauviel and Sibuet, 1985). Trace densities were greatest on the Meriadzek Terrace, but their diversity was highest at station 3, close to the lower end of the Shamrock Canyon, where 23 of the 29 categories recognized by Mauviel and Sibuet (1985) occurred. The traces included a wide variety of tracks, burrows, and mounds, as well as holothurian fecal casts.

Data on the macrofauna, both *sensu strictu* (>250 μm fraction, macrofaunal taxa only) and *sensu lato* (>250 μm fraction, all taxa), from BIOGAS stations 1–3 in the northern Bay of Biscay (2100–4100 m) are given by Dinet et al. (1985). At 2800 m and 4150 m, the macrofauna appears to be fairly abundant. Although the comparison is complicated by differences in mesh sizes, densities at the 2800 m BIOGAS station (4635 individuals m^{-2}, for the >250 μm fraction) are most similar to values from 1800 m (4320 individuals m^{-2}, for the >420 μm fraction) and 2000 m

(4156 individuals m^{-2}, for the >420 μm fraction) in the Rockall Trough (Dinet et al., 1985, table 5). More data are available for the metazoan meiofauna, particularly the nematodes, from the six BIOGAS stations. Dinet and Vivier (1977) found that total meiofaunal densities declined with increasing bathymetric depth, as did the proportion of the fauna present in the upper 1 cm of sediment. Densities also showed considerable spatial variability at both bathyal and abyssal sites, and particularly at stations 1, 2 and 4 to the north and station 5 to the south. Dinet and Vivier (1977) attributed this variability to the physico-chemical heterogeneity of the sediments. Interestingly, they could find no seasonal variation in total meiofaunal densities, or any correlation between densities and the organic-carbon content of the sediments. In a second study, Dinet and Vivier (1979) investigated the nematode fauna at the species level. The populations were very diverse, most species being represented by only one or a few individuals. The minimum and maximum diversity values occurred at the two southern sites (from about 50 species at station 5 to about 128 species at station 6) with the four stations of the northern transect yielding approximately 82–115 species (Dinet and Vivier, 1979, fig. 5 therein). Analysis of faunal similarity indicates an approximate separation between stations on the continental slope and those on the continental rise. However, there were no consistent differences between northern (1–4) and southern (5–6) sites; stations 1 and 6 showed a fairly close affinity, while station 5 showed little similarity to other sites. According to Soetaert and Heip's (1995) analysis of these and other literature data, the nematode faunas of the continental rise and the abyssal plain in the Bay of Biscay closely resemble those from the Hatteras Abyssal Plain, the HEBBLE site and the Puerto Rico Trench at the generic level. In terms of trophic groups, they are dominated by selective and non-selective deposit feeders and epistrate feeders; predatory/scavenging forms are uncommon (<10%).

Iberian margin: Gage et al. (1995) and Lamont et al. (1995) described macrofaunal sediment communities at two contrasting localities off Portugal, a presumed high-energy site in the Setubal Canyon (3356–3776 m), which is believed to experience periods of elevated current activity, and a tranquil site on the adjacent Tagus Abyssal Plain (5038 m). In both cases, the samples were dominated by agglutinated Foraminifera, and the metazoan fauna comprised nematodes, polychaetes, peracarid crustaceans, molluscs and echinoderms in descending order of numerical importance. Mean macrofaunal densities (300 μm individuals m^{-2}) were an order of magnitude higher in the canyon (mean 459.2, s.d. 208.6) than on the Tagus Abyssal Plain (mean 10.55, s.d. 22.24). On the other hand, species diversity for bivalves, tanaids and agglutinated Foraminifera was higher on the abyssal plain. There is some evidence that the fauna is more aggregated on the scale of tens of meters (between cores) in the canyon than on the abyssal plain, although the evidence for this is not conclusive. In general, the results of these studies suggest that hydrodynamic disturbance tends to diminish species diversity and increase the spatial heterogeneity of assemblages.

Northwest African margin

Studies carried out during the 1970s by the Institut für Hydrobiologie und Fischereiwissenschaft (IHF), Hamburg, and the Institute of Oceanographic Sciences (IOS), Wormley, have contributed greatly to knowledge of the benthos under the upwelling region and in other areas of the Northwest African margin. Downslope transects were worked by IHF off Cap Blanc (21ºN), near the center of the main upwelling area where primary production reaches 200 g C m^{-2} yr^{-1}, as well as off Morocco (Cape Mazagan, 35ºN) and Western Sahara (Cabo Peña Grande, 24–26ºN) to the north and off the Mauretanian coast (17ºN) to the south. General results have been reviewed by Thiel (1978, 1979, 1982, 1983); Pfannkuche et al. (1983) presented data from the Moroccan transect where upwelling intensity is low.

In general, the benthic system is strongly influenced by upwelling intensity, and hence surface primary production, and by hydrographic conditions (Thiel, 1978; Pfannkuche et al., 1983). Concentrations of chloroplastic pigments (chlorophyll breakdown products), which indicate organic-matter inputs, are two orders of magnitude higher off Cap Blanc than off Morocco; the Western Saharan transect yielded intermediate values (Thiel, 1978, fig. 4 therein). Along the Cap Blanc transect, pigment concentrations are high on the shelf, low on the upper slope (200 m) and then increase to much higher values between 400 and 1500 m before diminishing gradually with increasing depth. The low values at 200 m are believed to reflect the influence of a high-energy benthic boundary layer on the sedimentation of organic matter. Off Morocco, there is no increase on the lower slope. Instead, pigment intensities peak at the shelf edge, decline rapidly to 1200 m, and then remain relatively constant down to 3000 m.

Meiofaunal densities are higher at all depths off Cap Blanc (21ºN) than off Morocco (35ºN), presumably reflecting the increased organic-matter input in this highly productive region. Moreover, the abundance profiles along these transects are distinctly different, corresponding fairly closely to pigment concentrations. At 21ºN, meiofaunal abundances are highest on the shelf, drop to a distinct minimum at 200 m, followed by maximum values between 400 and 1000 m and declining numbers in deeper samples. At 35ºN, high abundances are also found on the shelf (2656 individuals m^{-2}) and at 400 m (2480 individuals m^{-2}) with a minimum at 200 m (1778 individuals m^{-2}). However, below 400 m, meiofaunal numbers fall fairly steeply down to 1200 m (631 individuals m^{-2}), below which they decline only slightly down to 3000 m (557 individuals m^{-2}). Meiofaunal biomass along the Moroccan transect follows a similar trend. Macrofaunal densities and biomass are also much higher at 21ºN and 17ºN than they are at 35ºN. The difference is particularly apparent above a depth of 1000 m. Along the deeper parts of the two southerly transects, the decrease in macrofaunal abundance is much steeper than off the Moroccan coast. Pfannkuche et al. (1983) also determined rates of benthic respiration and the activity of the electron transport system (ETS) (a measure of metabolic activity) along the Moroccan transect, in both cases using a shipboard technique. Respiration was highest at 130 m and 400 m, fell sharply between 400 and 800 m and then decreased slightly down to 3000 m. Electron transport activity also decreased with depth, and was substantially lower than values reported by Christensen and Packard (1977) from 21ºN, particularly at the shelf and slope sites above 500 m.

Sibuet et al. (1993), Cosson et al. (1997), and Galéron et al. (2000) have presented faunal data for their eutrophic, mesotrophic and oligotrophic EUMELI stations (sites E, M and O) located at 1700 m depth on the slope off Cap Blanc, 3100 m on the continental rise southwest of Cap Blanc, and 4700 m on the Cape Verde Abyssal Plain, respectively (Fig. 5.1). Densities of macrofauna (>500 μm) were 5403 individuals m^{-2} at site E and 1856 individuals m^{-2} at site M – high values which reflect the substantial organic-matter inputs at these stations. In contrast, only 231 individuals m^{-2} were recovered at site O. Polychaetes were the most abundant macrofaunal group (56% at site E, 67% at site M and 64% at site O) but tanaidaceans (12.7%, 10.0%, 11.9%), isopods (10.6%, 8.6%, 7.6%) and bivalves (8.2%, 1.9%, 6.5%) were also important. The spatial distribution of macrofauna tended to be patchy at the two shallower stations and particularly at site E, but much more homogeneous at site O. Cosson et al. (1997) attributed the aggregated faunal distributions at site E to the heterogeneous deposition of organic matter associated with upwelling, strong near-bottom currents, and the generation of small-scale sedimentary structure by macrofaunal activity. There was no evidence for temporal (seasonal) variability among the macrofauna at either station, although this may have reflected inadequate sampling. The densities of other faunal categories followed trends similar to those for the macrofauna (Sibuet et al., 1993). Densities of meiofauna (>40 μm; multiple and box-core samples) were 55.2±4.6, 27.7±2.3, 6.9±0.5 cm^{-2}, and those of megafauna (>2 mm; trawl samples) were 8624, 702 and 33 ha^{-1} at sites E, M and O, respectively. Xenophyophores (giant protists) were an important component of the megafauna in photographs from site M (Auffret et al., 1992).

Megafauna on the Northwest African margin have been sampled using various types of trawl, including an IOSDL epibenthic sledge equipped with a camera (Aldred et al., 1976; Rice et al., 1979). Unusually large populations of megafaunal organisms occur at various places on the continental slope and rise. At 2000 m off Cap Blanc (21ºN), sledge catches were dominated numerically by the suspension-feeding anemone *Actinoscyphia aurelia* and the irregular spatangoid echinoid *Pourtalesia miranda* (Rice et al., 1979). The anemone is abundant (>1 m^{-2}) in both the catches and photographs obtained between 1000 and 2000 m in this area (Aldred et al., 1979). At 4000 m off Cap Blanc, virtually the only organism visible in bottom photographs was the xenophyophore *Reticulammina labyrinthica* (Rice et al., 1979; Tendal and Gooday, 1981). Individual specimens reached 6 cm maximum dimension (Gooday and Tendal, 1988), considerably larger than specimens of the same species from the Porcupine Abyssal Plain (Gooday, 1996a). Further north, off the Moroccan coast, the hexactinellid sponge *Pheronema carpenteri* occurs in overall densities of up to 0.17 individuals m^{-2} at depths between 740 and 820 m (Barthel et al., 1996). Although considerably lower than the *Pheronema* densities recorded in the

Porcupine Seabight (Rice et al., 1990), local densities off Morocco may reach up to 6 individuals m^{-2} in single photographs. Of particular interest was the distribution of live and dead sponges, which suggested a progressive upslope movement of the population, possibly in search of a richer food supply.

Galéron et al. (2000), observed that total metazoan density and biomass (megafauna, macrofauna, and meiofauna) decreased with increasing depth and decreasing food supply across the EUMELI stations. However, each faunal component studied responded differently to the variation in food input. Overall, the megafauna dominated biomass at the most eutrophic site, macrofauna dominated at intermediate food conditions, and meiofauna dominated at the most oligotrophic site. However, within metazoan size groups, some taxa (e.g., sponges, tunicates and holothuroids) did not follow this pattern, implying that food availability is not the sole control on community structure.

A close relation between benthic foraminiferal biomass and surface primary production exists along the Northwest African margin (Altenbach, 1988; Altenbach and Sarnthein, 1989). The species composition of foraminiferal assemblages is also controlled, at least partly, by organic-matter fluxes (Lutze, 1980; Lutze and Coulbourne, 1984). In particular, a *Uvigerina peregrina* biofacies predominates in areas to the south of 22ºN (near Cap Blanc) where the annual flux rate exceeds 2–3 g C m^{-2}, whereas a *Cibicidoides wuellerstorfi/C. kullenbergi* biofacies occupies lower-productivity areas to the north (Lutze and Coulbourne, 1984; Altenbach, 1988). Other factors influencing foraminiferal faunas along this margin include bathymetry, sediment granulometry and bottom-water oxygen concentrations.

Northeast Atlantic abyssal plains

The faunas of Northeast Atlantic abyssal plains are known in varying degrees of detail as a result of recent national and international sampling programs (Table 5.1). The Porcupine Abyssal Plain has been particularly well studied within the framework of BENGAL and earlier projects funded by the European Union. Many of the biological and geochemical results of the BENGAL Project have appeared in a recent special volume (Billett, 2002).

Megafauna: Thurston et al. (1994) have provided a detailed account of the megafauna (>4 mm) of the Porcupine Abyssal Plain, Madeira Abyssal Plain (MAP) and Great Meteor East region (GME) and have summarized comparable published data (derived from net catches and *in situ* photographs) from other abyssal plains (Table 5.3). One of the most striking conclusions of this analysis is that megafaunal biomass is much greater (16–39×) at 48ºN on the Porcupine Abyssal Plain than it is in the Madeira Abyssal Plain and the Great Meteor East region areas (both at 31ºN); there is a corresponding but much smaller disparity in density values. The biomass differences are mirrored in the taxonomic composition of the megafauna in regions to the north of 40ºN and south of 33ºN. Holothurians, actiniarians, and to a lesser extent asteroids, constitute a major proportion of the invertebrate megafauna, both in terms of abundance and (particularly for holothurians) biomass, on the Porcupine Abyssal Plain (Thurston et al., 1994) and Iberian Abyssal Plains (Feldt et al., 1989). On the Madeira Abyssal Plain and in the Great Meteor East area (i.e. to the south of 33ºN) the megafauna is dominated by asteroids and natant decapods, with holothurians constituting a relatively small proportion of the fauna. Similarly, the Cape Verde Abyssal Plain (CVAP) harbors a sparse megafauna (0.00052 individuals m^{-2}) (Bett et al., 1995). One may note that values for megafaunal density from the Cape Verde Abyssal Plain given by Sibuet et al. (1993), which are an order of magnitude greater than those of Bett et al. (1995), are based on the >1mm fraction and therefore include animals normally considered as macrofauna. Thurston et al. (1994) have suggested that the large holothurian-dominated biomass on the Porcupine Abyssal Plain is supported by the phytodetritus flux which occurs in this area but not to the south of 33ºN.

Sibuet (1985) has presented a survey of the echinoderm fauna of deep Atlantic basins, mainly abyssal plains but including some continental-margin regions. Echinoderms constitute a highly variable proportion of the total megafauna in samples from >4000 m: 12% (Angola Basin, 5250 m), 33% (Cape Basin, 4650 m), 63% (Demerara Plain near the Amazon cone, 4420 m), 19% (Demerara Plain, 4850 m), 20% (Vema fracture zone, 5100 m), 3% (Cape Verde Abyssal Plain, 5190 m), 48% (southern Bay of Biscay, 4450 m), 20% (northern Bay of Biscay, 4750 m), 17% (northern Bay of Biscay, 4200 m), 75% (Porcupine Abyssal Plain, 4820 m). The dominant classes are always either holothurians (Angola Basin, Demerara Abyssal Plain, Vema fracture zone, Cape Verde Abyssal Plain, northern Bay of Biscay) or ophiuroids (Cape Basin, southern Bay of Biscay, Porcupine Abyssal Plain). Maximum

Table 5.3
Biomass and abundance of selected benthos in the deep Atlantic Ocean[1]

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	
NORWEGIAN–GREENLAND SEA								
Vøring Plateau	1200–1500	110000	0.89	610 (500 µm)	3.28	4 (top 3 taxa)	7	Romero-Wetzel and Gerlach (1991)
export stn	1325–1424		0.20–0.57		13.06–25.48			Jensen et al. (1992b)
import stn	1325–1424		0.6–1.00		17.21–32.10			Jensen et al. (1992b)
	1245	172000	0.007 (C)					Jensen (1988)
	1255	204000	0.006 (C)					Jensen (1988)
	1426	107000	0.010 (C)					Jensen (1988)
Norwegian Basin	2725			6440				Dahl et al. (1976)
	2992			1848				Dahl et al. (1976)
	2998			1026				Dahl et al. (1976)
	3665			54–74				Dahl et al. (1976)
	2600–3600	71000		740		0.61		Sibuet et al. (1989)
	3062	200000	0.010					Jensen (1988)
SE Jan Mayen	2133	60000	0.004					Jensen (1988)
Lofoten Basin	2957			187–264 (250 µm)				Dahl et al. (1976)
	3213			422				Dahl et al. (1976)
	3294	20000	0.003					Jensen (1988)
Spitzbergen Basin	3203			355				Dahl et al. (1976)
	3209			3188				Dahl et al. (1976)
Greenland Basin	2465			288				Dahl et al. (1976)
	2492			829				Dahl et al. (1976)
	2904			1944				Dahl et al. (1976)
	2941			759				Dahl et al. (1976)
	3294			1292				Dahl et al. (1976)
	3306			4509				Dahl et al. (1976)
	3606			388				Dahl et al. (1976)
	3718			4654				Dahl et al. (1976)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	
Norwegian Shelf	970	138 000	0.073					Jensen (1988)
NORTHEASTERN ATLANTIC								
Iceland Basin	2880					0.91–9.38	1.27–15.56	Christiansen and Thiel (1992)
Rockall Trough	1800			4320 (420 μm)	4.80 (wet)			Gage (1978)
	1800			1636 (420 μm)	3.72 (wet)			Gage (1978)
	2000			4156	4.156			Gage (1978)
	2500			1332	3.08			Gage (1978)
	2900			3052	4.08			Gage (1978)
	2875			2903 (297 μm)	0.92 (dry)			Gage (1977)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	
Porcupine Seabight	2650	54 500		1180		1.0		Sibuet et al. (1989)
	4820	50 000		420		0.31		Sibuet et al. (1989)
	300	502 000 (42 μm)						Vanreusel et al. (1995b)
	600	1 410 000						Vanreusel et al. (1995b)
	900	1 523 000						Vanreusel et al. (1995b)
	1200	1 500 000						Vanreusel et al. (1995b)
	1500	1 283 000						Vanreusel et al. (1995b)
	500					1	5.0	Lampitt et al. (1986)
	500	2 604 000 (42 μm)	1160 (AFDW)					Pfannkuche (1985)
	510	1 963 000	0.093					Pfannkuche (1985)
	960	1 593 000	0.075				Pfannkuche (1985)	
	1492	943 000	0.061					Pfannkuche (1985)
	2000	828 000	0.060					Pfannkuche (1985)
	2510	744 000	0.059					Pfannkuche (1985)
	2785	900 000	0.063					Pfannkuche (1985)
	3567	663 000	0.055					Pfannkuche (1985)
	4167	528 000	0.051					Pfannkuche (1985)
	4500	362 000	0.036					Pfannkuche (1985)
	4850	315 000	0.036					Pfannkuche (1985)
	4100					0.01	0.05–0.07	Lampitt et al. (1986)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 (g m^{-2})	Density (m^{-2})	Biomass^2 (g m^{-2})	Density (m^{-2})	Biomass^2 (g m^{-2})	
Porcupine Abyssal Plain	4850					0.014 (4.5 mm)	0.169	Thurston et al. (1994)
	4850					0.008 (otter trawl)	0.189	Thurston et al. (1994)
	4000–4800					0.004 (10 mm)	0.081	Rutgers van der Loeff and Lavaleye (1986)
	??					0.002 (30mm)	0.054	Feldt et al. (1989)
	4500–4550					0.194 (>20 mm)		Christiansen and Thiel (1992)
	4350–4750					0.093 (>30 mm)		Sibuet and Coic (1989)
Bay of Biscay (BIOGAS)	2100			2783 (250 µm)				Dinet et al. (1985)
	2900	[39 000]		4635 (250 µm)		0.020		Tietjen (1992)
	4100			3612				Tietjen (1992)
Bay of Biscay (NW)	2150			2783	0.21 (dry)			Tietjen (1992)
	1920–2245					0.292 (1 mm)		Sibuet and Segonzac (1985)
	2878–3380					0.069		Sibuet and Segonzac (1985)
	4134–4240					0.048		Sibuet and Segonzac (1985)
	4706–4825					0.032		Sibuet and Segonzac (1985)
Bay of Biscay (SE)	1895–1995					0.044		Sibuet and Segonzac (1985)
	4434–4475					0.021		Sibuet and Segonzac (1985)
BIOTRANS Site	3800–4590	320 000	0.007 [C]	2000	0.106	1.07–4.14	0.20–2.18	Pfannkuche (1992)
Madeira Abyssal Plain	5400–5450					0.0035 (>4.5 mm)	0.004	Thurston et al. (1994)
	5400–5450					0.002 (>18.5 mm)	0.011	Thurston et al. (1994)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	Density (m^{-2})	Biomass[2] (g m^{-2})	
Iberian Abyssal Plain	5200					0.001 (>30 mm)	0.007	Feldt et al. (1989)
NORTHEAST TROPICAL ATLANTIC								
EUMELI	1700	1 041 514 (40 µm)		2568 (500 µm)		0.8624 (>2 cm)		Sibuet et al. (1993)
	1700			5403 (250 µm)				Cosson et al. (1997)
	3100	479 247		1124 (500 µm)		0.0702		Sibuet et al. (1993)
	4600	130 189		88 (500 µm)		0.0033		Sibuet et al. (1993)
	3100			1856 (250 µm)				Cosson et al. (1997)
	4600					5.2 ha^{-1}		Bett et al. (1995)
Vema Fracture Zone	5100			860	0.08 (dry)			Khripounoff et al. (1980)
	5100	130 000		200		0.033		Sibuet et al. (1989)
Demerara Abyssal Plain	4420	278 000	0.010 [C]	2159	0.09 (dry) 0.039 [C]	0.011	0.010 [C]	Sibuet et al. (1984, 1989)
	4800		0.005 [C]		0.014 [C]		0.0265 [C]	
Off N. Morocco	400	2 480 000		1265	1.12			Pfannkuche et al. (1983)
	600	1 465 000		1546	1.99			Pfannkuche et al. (1983)
	800	1 175 000		1132	1.76			Pfannkuche et al. (1983)
	1200	631 000		932	1.75			Pfannkuche et al. (1983)
	1500	620 000		1004	1.30			Pfannkuche et al. (1983)
	2000	570 000		832	0.82			Pfannkuche et al. (1983)
	2435	550 000						Pfannkuche et al. (1983)
	3000	447 000		352	0.45			Pfannkuche et al. (1983)
Cape Verde Basin (Cape Verde Abyssal Plain)	4950	62 000		95		0.012		Sibuet et al. (1989)
	5190	87 000		100		0.007		Sibuet et al. (1989)
	4700			232				Cosson et al. (1997)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] ($\mathrm{g\,m}^{-2}$)	Density (m^{-2})	Biomass[2] ($\mathrm{g\,m}^{-2}$)	Density (m^{-2})	Biomass[2] ($\mathrm{g\,m}^{-2}$)	
WESTERN ATLANTIC								
Hatteras Abyssal Plain	5300		0.038 [C]		0.0064 [C]			Tietjen et al. (1989)
Venezuela Basin	3450	131 000	0.0394 [C]	678	0.0152 [C]	0.0025	0.0010 [C]	Tietjen (1992)
(Caribbean Sea)	3950	81 000	0.0173 [C]	263	0.0026 [C]	0.0031	0.0012 [C]	Tietjen (1992)
	5050	49 000	0.0132 [C]	238	0.0053 [C]	0.0016	.0064 [C]	Tietjen (1992)
NORTHWEST ATLANTIC								
Gayhead–Bermuda Transect	1110–1180			3070–4430	0.845–1.216 (420 μm)			Rowe et al. (1974)
DOS-1	1850			3218	9.45			Smith (1978)
	1900			2020	15.60			Rowe et al. (1974)
	2080			700	0.325			Rowe et al. (1974)
DWD	2200			22 988	0.556			Smith (1978)
	2425			1344	0.871			Rowe et al. (1974)
	2710			1089; 742	0.485, 0.529			Rowe et al. (1974)
ADS	2750			8764	2.143			Smith (1978)
	2885–2950			309–1150	0.154–1.485			Rowe et al. (1974)
HH	3000			2143	0.653			Smith (1978)
DOS-2	3650			1632	0.771			Smith (1978)
	3923			466	0.158			Rowe et al. (1974)
JJ	4670			753	0.220			Smith (1978)
KK	4830			285	0.180			Smith (1978)
	4901–4950			175	0.218			Rowe et al. (1974)
NN	5080			117	0.078			Smith (1978)
MM Sargasso	5200			259	0.142			Smith (1978)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	Density (m^{-2})	Biomass^2 ($g\,m^{-2}$)	
Cape Hatteras								
1985	500–1599					0.88		Hecker (1994)
	604			46 255 (300 µm)				Blake and Grassle (1994)
1988–91	850			55 500 (300 µm)	54.52			Schaff et al. (1992)
1985	2003			8950				Blake and Grassle (1994)
1992	500–1599			37 282 (300 µm)		2.65		Hecker (1994); Blake and Hilbig (1994)
	580–2000					9.93–12.41 (>2 mm)		Brown (1991)
	3000					1.015		Brown (1991)
	3500					0.786		Brown (1991)
Long Bay	600–1799					0.93		Brown (1991)
Cape Lookout	700–1599					0.49		Brown (1991)
1983–4	583			16 337 (300 µm)				Blake and Grassle (1994)
1988–91	850			21 400 (300 µm)	8.16			Schaff et al. (1992)
	1000			9130 (300 µm)				Blake and Grassle (1994)
	1500			5017				Blake and Grassle (1994)
	2000			5622				Blake and Grassle (1994)
	3006			870				Blake and Grassle (1994)
	3494			1000				Blake and Grassle (1994)
Cape Fear	850			9439 (300 µm)	7.19			Schaff et al. (1992)
Hatteras canyon	800–1599					0.29		Hecker (1994)

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Table 5.3, *continued*

Location	Water depth (m)	Meiofauna		Macrofauna		Megafauna		References
		Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	Density (m^{-2})	Biomass[2] ($g\,m^{-2}$)	
New Jersey	600–1499					0.46		Hecker (1994)
	600–1499					0.24		Hecker (1994)
	1263				1.47 (300 μm)			Hathaway (1971)
	2132				5.5 (300 μm)			Hathaway (1971)
Carson canyon	1129			370.4	3.61 (520 μm)			Houston and Haedrich (1984)
U.S./Canada boundary	500–1300					2.61		Hecker (1994)
Scotian rise	4620	23 500		2215				Thistle et al. (1985)

[1] Mesh size is given between parentheses where available.

[2] Biomasses are wet wt unless indicated otherwise.

densities for individual classes do not exceed 64 individuals m^{-2}, except at the Porcupine Abyssal Plain site where holothurian and ophiuroid densities reach 363 and 965 m^{-2}, respectively. Holothurian abundance was found to correlate well with organic-carbon flux.

Variations in megafaunal composition may have a temporal as well as a spatial aspect. Results from the BENGAL Project suggest that a striking and persistent shift in the composition of the megafauna occurred on the Porcupine Abyssal Plain during the 1990s (Billett et al., 2002). The holothurian *Amperima rosea* exhibited a massive increase in abundance, and *Ellipinion* cf *molle* (holothurian) and *Ophiocten hastatum* (ophiuroid) also showed substantial increases between 1989–1994 and 1996–1999. Billett et al. (2002) have argued that long-term changes in the quantity and/or quality of the organic-matter supply to the seafloor may underlie these fluctuations.

Megafaunal behavior can be addressed by means of seafloor photography. Examples of this approach being used in the Atlantic include determination of rates of movement in echinoderms in the Porcupine Seabight and Porcupine Abyssal Plain areas (Lampitt and Billett, 1985; Smith et al., 1997b), and feeding activities in an echiuran on the Cape Verde Abyssal Plain (Bett and Rice, 1993). In addition, a BATHYSNAP sequence obtained on the Madeira Abyssal Plain has provided remarkable documentation of test development in giant testate protists. The sequence shows three specimens of the xenophyophore *Reticulammina labyrinthica* undergoing a 3–10-fold increase in volume over an 8-month period. Growth occurred episodically and in distinct phases, each lasting about two days, during which sediment was collected and incorporated into the test. The growth phases were separated by periods of about two months during which the external appearance of the tests changed little. Gooday et al. (1993) suggested that the xenophyophores used the accumulated sediment as a source of both food and particles for test construction, thereby combining growth with deposit feeding.

Macrofauna: Macrobenthic density and biomass are also substantially higher on the Porcupine Abyssal Plain than on the Madeira Abyssal Plain, by factors of approximately 5 and 35, respectively (Rice, 1993). Macrofaunal densities on the Cape Verde Abyssal Plain are very low, only 88 individuals m^{-2} of which 59% are polychaetes (Sibuet et al., 1993). Apart from protobranch bivalves (Allen and Sanders, 1996), polychaetes are the only macrofaunal group to have been studied in any detail. Paterson et al. (1994a,b) compared polychaete populations at sites on three Northeast Atlantic abyssal plains (Porcupine, Madeira, Tagus) with those from other regions in the Atlantic and Pacific Oceans. Polychaetes were more abundant on the Porcupine Abyssal Plain (302 individuals m^{-2}) than on the Tagus Abyssal Plain (169 individuals m^{-2}) and Madeira Abyssal Plain (178 individuals m^{-2}); these densities represented 17%, 27% and 25%, respectively, of all metazoans >300 μm and 35%, 58% and 49% of the macrofaunal taxa >300 μm. The Porcupine Abyssal Plain yielded 32 species and the Tagus Abyssal Plain only 11 species. Several undescribed species of *Aphelochaeta, Prionospio* and *Sigambra* were represented at all three sites. The five most abundant families on the Porcupine Abyssal Plain were the Spionidae (25%), Cirratulidae (22%), Sabellidae (10%), Ophelliidae (8%) and Paraonidae (8%); on the Tagus Abyssal Plain the Cirratulidae (24%), Spionidae (17%), Pilargidae (11%), Ophelliidae (11%) and Paraonidae (9%); on the Madeira Abyssal Plain the Sabellidae (24%), Flabelligeridae (20%), Paraonidae (16%), Spionidae (8%) and Pisionidae (6%). Rarefaction curves indicated that family richness was higher on the Porcupine Abyssal Plain and the Tagus Abyssal Plain than on the Madeira Abyssal Plain.

Meiofauna: Vincx et al. (1994) provides an overview of meiofauna from the Northeast Atlantic, including the Porcupine Abyssal Plain, the Madeira Abyssal Plain, the Cape Verde Abyssal Plain, the Iberian Abyssal Plain and the BIOTRANS area (Figs. 5.1, 5.2); additional data on the nematode component are provided by Vanreusel et al. (1995a) and Lambshead et al. (1995). Total meiofaunal and nematode densities are higher at northern abyssal sites (e.g., BIOTRANS, Porcupine Abyssal Plain; 45–48ºN) than on the Madeira Abyssal Plain (30ºN) and Cape Verde Abyssal Plain (21ºN); for example, total densities are almost five times higher on the Porcupine Abyssal Plain than on the Cape Verde Abyssal Plain (Vanreusel et al., 1995a). Other differences are apparent among the nematode fauna. In particular, there is a substantially higher proportion of nematodes inhabiting the upper centimeter of sediment on the Madeira Abyssal Plain compared to the Porcupine Abyssal Plain (Lambshead et al., 1995), and mean individual nematode body weight is significantly lower on the Cape Verde Abyssal Plain compared to the Porcupine Abyssal Plain, mainly due to the greater abundance of large nematodes at the more northerly site (Vanreusel et al., 1995a). These contrasts are believed to reflect differences in the supply of organic matter to the seafloor, in particular the fact that the deposition of aggregated phytodetritus is restricted to the northern part of the Northeast Atlantic (Porcupine Abyssal Plain and BIOTRANS area).

Gooday (1996b) has given a detailed analysis at the species level of foraminiferal assemblages in multiple-corer samples (top 1 cm of sediment) collected from the Porcupine Abyssal Plain, Madeira Abyssal Plain and Cape Verde Abyssal Plain during August, 1989. Foraminifera accounted for 61–76% of the total meiofauna in these samples. Densities were higher on the Porcupine Abyssal Plain than at the two southern sites, and part of the difference is accounted for by specimens inhabiting the phytodetrital layer, present only at on the Porcupine Abyssal Plain. The phytodetrital foraminiferal populations were of low diversity and dominated by a few apparently opportunistic species (e.g., *Epistominella exigua*). These species are typically much less common in the underlying sediment, so that the phytodetrital assemblages can be regarded as being to some extent 'decoupled' from those in the underlying sediment. Total populations, from the phytodetritus plus the 0–1 cm sediment layer, are highly diverse (123–167 species) and broadly similar in their species composition. However, in addition to the phytodetritus-exploiting species, some sediment-dwelling species of *'Hyperammina'*, *Lagenammina, Leptohalysis* and *Reophax* were more abundant at the Porcupine Abyssal Plain site whereas a few, such as *Lagenammina tubulata* and *Subreophax aduncus*, were more abundant at the southern sites.

Northeast Atlantic Seamounts

Seamounts are abundant in the deep Atlantic (Epp and Smoot, 1989), but there have been few ecological descriptions of their benthic communities (Rogers, 1994). The best studied are the Meteor and Vema Seamounts, but even here the papers are few, and mostly are taxonomic in nature (citations within Rogers, 1994). Thiel (1970, 1975) studied the meiofaunal communities of the Great Meteor Seamount, 1600 km from the coast of Africa, and the Josephine Seamount, 300 miles west of southern Portugal in a region of higher primary productivity. Samples taken from the summit plateaus at depths of 206–355 m and 292–350 m yielded mean densities of 40.3±14.0 individuals cm^{-2} and 22.7±7.4 individuals cm^{-2} on Josephine and Meteor, respectively. Samples taken by Rachor (1975) just southwest of the Josephine Seamount were much lower. The Meteor data suggest little difference in meiofauna between the shallow seamount and the Iberian Abyssal Plain 5000 m deeper, although primary productivity may be twice as much above the Iberian deep sea. Heavy predation pressure by fishes and strong currents above the Great Meteor Seamount may have reduced meiofaunal densities (Thiel, 1975). In the South Atlantic, Russian investigations have contributed to knowledge of the seamount faunas, for example, on the Valdivia Seamount (Kamenskaya, 1988).

North Atlantic necrophages

Necrophages (animals which scavenge dead carcasses) play an important role in the cycling of organic matter on the deep-sea floor (Haedrich and Rowe, 1977; Smith, 1985a). Megafaunal necrophages usually congregate around large carcasses within hours of the carcass reaching the seabed, and are capable of consuming all but the bones within days (Hargrave, 1985). Among the commonest necrophages in the deep Atlantic are fish (particularly macrourids, ophidioids and synaphobranchiid eels), natantian decapods, and amphipods (almost entirely lysianassids). These highly mobile benthopelagic animals appear to be concentrated within, at most, a few meters of the deep-sea floor, but can swim up hundreds or even thousands of meters into the overlying water column (Smith et al., 1979; Thurston, 1990; Sainte-Marie, 1992). In particular, the amphipod *Eurythenes gryllus* undergoes an ontogenetic migration hundreds of meters up into the water column (Charmasson and Calmet, 1987; Christiansen et al., 1990; Christiansen, 1996). It is notable that dominant scavengers in the Pacific, such as hagfish, sablefish and ophiuroids (Smith, 1985a), are not observed at bait in the deep Atlantic.

The existence of necrophages in the deep sea was first revealed in the Northeast Atlantic when amphipods were caught in baited traps deployed from the Prince of Monaco's yacht *L'Hirondelle* during its campaign of 1888 (Chevreux, 1900; Richard, 1934). Baited traps are the most effective means of sampling scavenging amphipods (Thurston, 1979; Hargrave, 1985; Hargrave et al., 1995), whereas larger animals such as fish and decapods are best documented by means of baited cameras (Isaacs, 1969). Both fish and amphipods attracted to bait include opportunistic generalist feeders as well as the more specialized scavengers (Thurston, 1979; Thurston et al., 1994). However, in the case of both amphipods and fish, the scavengers which are abundant around bait represent only a small proportion of the species known to be present in the deep sea (Thurston, 1979, 1990; Merrett and Haedrich, 1997).

Although still limited, information on the taxonomic composition, distribution and ecology of Atlantic necrophage faunas is growing. Many species are widely distributed in the Northeast and Tropical Atlantic. According to Thurston (1990), the region between 8ºN and 50ºN supports a 'single faunal entity'. Most of the amphipods caught and photographed on the Iberian Abyssal Plain (4885 m) by a baited fish trap equipped with a camera belonged to the genera *Orchomene* and *Paralicella*. The photographic record revealed a slow increase in numbers of amphipods present on the bait, and subsequent fluctuations in abundance which may have been related to the presence of fish in the trap and to current activity. These interactions were examined further by Lampitt et al. (1983), who used methods similar to those of Thurston (1979) at a site 4009 m deep close to the mouth of the Porcupine Seabight. Fluctuations in the numbers of amphipods visible on the bait could be related to tidal cycles and to the presence of small black fish (probably *Paraliparis bathybius*). Amphipods were most abundant when current velocities were low. However, appearances of the black fish coincided with the flood tide (i.e., higher current velocities) and also with a marked decline in numbers of visible amphipods, suggesting that the fish preyed on the amphipods.

In situ studies of feeding and digestion by *Eurythenes gryllus*, conducted on the Nares Abyssal Plain (3421 m) using time-lapse photography, revealed rapid consumption of bait (1.8 g individual^{-1} h^{-1}) by large amphipods (3–6 cm). These crustaceans ingested 30–60% of their body weight within 12 h (Hargrave, 1985). From studies on the Nares and Sohm Abyssal Plains using traps which allowed timed exposure to bait, it was established that, once *E. gryllus* starts to feed on carrion, digestion is rapid, with 0.4–1.0% of the gut contents lost per hour and 95% digested in 1–10 days (Hargrave et al., 1995). *Eurythenes* has mandibles and a gut adapted to rapid gluttonous feeding; it apparently can survive long periods between meals. Other lysianassid scavengers (e.g., *Orchomene*) have smaller guts and seem to process food in a more continuous manner (Sainte-Marie, 1992). Sainte-Marie (1992) suggested that none of the deep scavenging amphipods are completely obligate necrophages, and that foraging in the water column is required to compensate for scarce resources (see also Thurston, 1990).

Photographic records obtained on the Porcupine and Madeira Abyssal Plains using a baited time-lapse camera system (BATHYSNACK) revealed that decapods are also common scavengers in the deep Atlantic (Thurston et al., 1994). On the Porcupine Abyssal Plain, the dominant necrophages identifiable in photographs were fish, mainly *Coryphaenoides (Nematonurus) armatus* and *Pachycara bulbiceps*, and the decapod *Munidopsis* spp. Another decapod, the shrimp *Plesiopenaeus armatus*, dominated necrophages photographed on the Madeira and Cape Verde Abyssal Plains but was very rarely photographed at bait on the Porcupine Abyssal Plain, despite being present in trawl samples taken at this site. These latitudinal differences between necrophages on Northeast Atlantic abyssal plains are striking, and possibly linked to differences in food availability. The greater abundance of scavenging fish on the Porcupine Abyssal Plain than on the Madeira or and Cape Verde Abyssal Plains may reflect higher densities of large animals present in the pelagic community, and hence of carrion on the seafloor, on the Porcupine Abyssal Plain (Merrett, 1987). *Plesiopenaeus armatus* appears to be a facultative necrophage which is deterred from scavenging on the Porcupine Abyssal Plain by the presence of large fish, but is able to do so at the southern sites where fish are scarcer (Thurston et al., 1994). A species of *Plesiopenaeus* was also attracted, together with macrourid and ophidiid fish, to a baited camera system deployed at 4850m on the Demerara Abyssal Plain (Rowe et al., 1986).

As part of the BIOGAS program, Desbruyères et al. (1985b) studied necrophages with baited traps along a bathymetric transect between 200 m and 4700 m across the continental margin in the northern Bay of Biscay. They also deployed baited cameras 7 m, 100 m and 200 m above the seafloor at three stations deeper than 4000 m. Necrophages caught in the traps were dominated by reptant decapods (*Geryon, Munida*) and isopods (Gnathiidae) between 200m and 1800 m and by fish and amphipods below this depth. Fish were not observed at all above 1800 m. Among the fish, sharks were the main group attracted to bait on the Meriadzek Terrace (1800–3000 m) and the Le Danois Bank (1980 m), while rattails (macrourids) dominated below 4000 m. Desbruyères et al. (1985b) noted a correlation between maximum current velocities and the highest abundances of macrourids at their 4700 m station. They also observed that an attack on the bait by a single fish provoked an immediate concentration of congeneric individuals around the bait.

Unique information about the biology of abyssal scavenging fish in the Atlantic and Pacific Oceans has been obtained using AUDOS, a free vehicle which attracts fish to bait in which small transponders are embedded (e.g., Priede et al., 1990, 1991, 1994a,b; Armstrong et al., 1992; reviewed by Merrett and Haedrich, 1997). The fish readily ingest these transponders along with the bait. The transponders report back acoustically to a sonar on the central AUDOS vehicle, allowing the movements of the fish on the ocean floor to be tracked over a range of up to 500 m. The AUDOS experiments have demonstrated that benthopelagic species living in the water near the seafloor do not sit and wait for carcasses, as previously believed, but actively search for them. The first fish to arrive at bait in the Northeast Atlantic were *Coryphaenoides armatus* and *Histiobranchus bathybius.* Having ingested the bait (and transponder), the fish generally wandered slowly away from the food source, usually disappearing from the range of the AUDOS sonar within a period of twelve hours. Recent observations made on the Porcupine Abyssal Plain suggest that there were no significant differences in the arrival times or swimming speeds of fish before and after the arrival of phytodetritus at this site (Smith et al., 1997a). These results contrast with the observation that macrourids arrived more slowly at bait in the North Pacific Ocean before the spring bloom than they did later in the year following a pulsed input of organic matter (Priede et al., 1994a).

Equatorial and South Atlantic

Compared with the North Atlantic, the deep-sea benthos of the Equatorial Atlantic, and particularly the South Atlantic, is rather poorly known. Most studies have concerned the abundance, diversity and distribution of particular groups, in some cases as part of an ocean-wide study of distribution and diversity patterns. Examples include ascidians (Monniot and Monniot, 1978; Monniot, 1979), protobranch bivalves (Allen and Sanders, 1996) and echinoderms (Sibuet, 1979, 1985). Russian expeditions have also contributed much to knowledge of the taxonomy and distribution of animals in the deep South Atlantic (e.g., volumes edited by Vinogradova, 1990, 1993; see also Vinogradova, 1997). A synthesis of meiofaunal, macrofaunal and megafaunal densities in the Angola and Cape Basins (Southeast Atlantic), the Demerara Abyssal Plain and the Vema Fracture Zone (Equatorial Atlantic) as well as in North Atlantic basins has been presented by Sibuet et al. (1989). More recently, Rex et al. (1993) have analyzed latitudinal trends in diversity among macrofaunal bivalves, gastropods and isopods from the Greenland–Norwegian Sea in the north to the Argentine Basin in the south. Southern Hemisphere sites include the Brazil, Angola and Cape Basins in addition to the Argentine Basin.

Relatively few studies, however, have addressed smaller-size fractions of the benthic fauna at particular sites in the South Atlantic. One of the few is that of Sanders (1969), who presented data for macrofauna (>420 μm) from a transect through the oxygen minimum zone (OMZ) off Walvis Bay, Namibia. At depths of 100 m, where the oxygen content of the bottom water was <2% saturation, faunal density was low (125 individuals m^{-2}). Species richness was low as well, comparable to that found at 5000 m under the oligotrophic Sargasso Sea. At 200 m (11% oxygen saturation), densities were exceptionally high (30 000 individuals m^{-2}), but diversity was only slightly increased. At 300 m (15% saturation) diversity remained low, but densities dropped to 8000 individuals m^{-2}. Densities at 450 m, 630 m, 975 m and 2140 m were 2300, 5400, 4750, and 4140 individuals m^{-2}, respectively. Diversity, estimated by rarefaction, increased with depth and increasing oxygen saturation through the 975 m station, but declined again at 2140 m. Sanders (1969) noted that macrofaunal patterns along the Walvis Bay transect, a gradient of oxygen stress, resemble those observed along gradients of organic or chemical pollution. Maximal densities combined with low diversity are observed at the edge of the stressed conditions.

In a recent study, Soltwedel (1997) described meiofauna on the shelf, slope and abyssal plains (27–4601 m) off the tropical West African coast between Guinea (10ºN) and Angola (17ºS). This part of the eastern equatorial Atlantic is subject to coastal upwelling, which varies seasonally and geographically but is never sufficiently intense to result in the formation of an oxygen minimum zone. Meiofaunal abundance and biomass generally decrease fairly regularly with increasing water depth. However, the rate of increase varies in different parts of the margin, and is usually fairly well correlated with upwelling intensity, as indicated by concentrations of chloroplastic pigments in the sediments. In some regions away from the main upwelling centers, densities are relatively low, despite fairly high pigment concentrations. This discrepancy may be due to the degradation of phytodetrital fluxes during lateral advection by subsurface currents.

MICROBIAL PROCESSES

The earliest direct observations of bacterial populations in the deep sea were made in the nineteenth century on samples taken at 5100 m in the Mediterranean by the French vessel *Talisman* (Certes, 1884), while the first quantitative data on the rates of microbial activity were obtained in the Pacific Ocean during the 1950s (Morita and Zobell, 1955; Zobell and Morita, 1957a,b). During the last three decades, however, work carried out in the North Atlantic has contributed enormously to the rapid development of ideas about deep-sea bacterial ecology (Deming and Baross, 1993). In this section we highlight some of these advances.

A landmark event in the history of modern deep-sea microbiology was the sinking of the DSV[7] *Alvin* off New England at a depth of 1540 m in 1968, and the subsequent recovery of its relatively undegraded lunch nearly a year later. Microbiologists interpreted the lack of decomposition in the lunch to indicate that metabolic rates of deep-sea microbes were much slower than those in shallow water (Jannasch et al., 1971). To a great extent, the results of this ‘experiment’ were misleading. The lack of substantial decomposition can be largely explained by the way in which the lunches were sealed, and therefore insulated from the deep-sea scavengers and bacteria, rather than to slow rates of deep-sea microbial activity (Sieburth and Dietz, 1972). Nevertheless, the *Alvin* lunch incident strongly influenced the direction of deep-sea biology, and initiated a generation of microbiological experiments based on work with *in situ* free vehicles or submersibles (Jannasch and Wirsen, 1973, 1983; Wirsen and Jannasch, 1986).

An important theme in deep-sea microbiological studies has been quantification of the abundance and ecological role of bacteria. Much of this work has been conducted in the North Atlantic (e.g., Deming, 1985; Lochte and Turley, 1988; Turley and Lochte, 1990; Meyer-Reil and Köster, 1992; Lochte, 1992; Deming and Yager, 1992; Deming and Baross, 1993; Boetius and Lochte, 1994, 1996; Turley et al., 1995; Turley, 2000; Turley and Dixon, 2002). Bacterial densities and production tend to decrease with water depth, but the correlation is weak. Flux of particulate organic matter (POC) to the seafloor seems to exert a stronger influence on bacterial populations. Both biomass and the rate of utilization of dissolved organic carbon (DOC) are particularly high at high latitudes, where organic-matter inputs are substantial and seasonally variable. The highest bacterial densities ever recorded in deep-sea sediments were near the HEBBLE site in the Northwest Atlantic, an area which receives an abundant food supply from the activity of currents (Thistle et al., 1985, 1991). The relation observed between bacterial abundance and POC flux is consistent with evidence which emerged during the 1980s that microbial processes can operate at much faster rates than suggested by earlier studies, such as the *Alvin* lunch ‘experiment’ (Deming, 1985; Lochte and Turley, 1988; Gooday and Turley, 1990; Turley and Lochte, 1990).

Microbial decomposition rates are often substantially enhanced in food-rich microhabitats such as those provided by vertebrate and invertebrate carcasses, phytodetrital aggregates, benthic feces, animal burrows and particularly within animal guts which are hot-spots of barophilic activity. For example, experiments and observations conducted within the past decade in the North Atlantic (notably the BIOTRANS area), indicate that freshly deposited phytodetritus is subjected to intense microbial activity, and that remineralization of the labile component occurs rapidly within a period of about 5 days (e.g., Gooday and Turley, 1990; Poremba, 1994). Degradation is carried out by extracellular hydrolytic enzymes (Boetius and Lochte, 1994), which originate from a mixture of barotolerant bacteria conveyed from the upper water column on sinking aggregates and from indigenous barophilic bacteria (Lochte and Turley, 1988; Turley and Lochte, 1990; Turley et al., 1995). Small (3.5–6.0 μm long) barophilic bodonid flagellates are also associated with decomposing phytodetritus both in natural systems (Lochte and Turley, 1988) and in experimental systems (Turley et al., 1988), and may help to regulate the size of associated bacterial populations.

Remineralization rates depend on the quality or

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[7] *DSV*: Deep Submergence Vehicle.

freshness of the sedimenting organic matter, which depends in turn on the rapidity of transport from the euphotic zone. Seasonal variation in bacterial numbers and biomass have been recorded at the BIOTRANS area, presumably in response to seasonal phytodetritus deposition (Lochte, 1992), although such increases do not always accompany microbial degradation of phytodetritus (Boetius and Lochte, 1994). Insights derived from naturally or experimentally enriched samples, however, are not applicable to bacterial populations in oligotrophic deep-sea regions where activity is likely to be much slower.

ANIMAL TRACES

The Atlantic seabed is covered with surficial sediment features such as pits, burrows, mounds, tracks, fecal casts and resting traces. Many of these result from movement, burrowing, feeding, defecation or dwelling-construction by benthic invertebrates and fishes (Hollister et al., 1975). Detailed surveys of these features have been carried out in the Bay of Biscay (Mauviel and Sibuet, 1985), on the Northwest Atlantic continental margin (Hecker, 1994; Diaz et al., 1994), in the Porcupine Seabight (de Vaugelas, 1989), the Porcupine Abyssal Plain (Bett and Rice, 1993), the Cape Verde Abyssal Plain (Bett et al., 1995) and the Bahama Outer Ridge (Hollister et al., 1974).

Lebensspuren (traces of animal activity) often provide the main evidence for large organisms on abyssal plains and elsewhere in the deep sea, and may be particularly useful for quantifying buried megainfauna (large animals living within the sediments). These organisms, which are very difficult to sample using conventional methods, potentially play a major role in deep-sea community ecology and in the structuring of the deep-sea sedimentary environment (Romero-Wetzel and Gerlach, 1991; Bett et al., 1995). Bett et al. (1995) have provided a survey of *Lebensspuren* photographed on the Cape Verde Abyssal Plain using a wide-angle survey photographic system (WASP) and a camera attached to the epibenthic sledge. They found that the density of traces on this oligotrophic abyssal plain were two orders of magnitude greater than animal densities estimated from the same photographic records (8.72×10^{-2} traces vs 5.2×10^{-4} individuals m^{-2}). The traces were dominated by various kinds of spoke burrows, similar in form to those generally attributed to echiurans. Bett et al. (1995) estimated that the abundance of the spoke-burrow producers is of the order of 0.001 individuals m^{-2}, considerably greater than the density of surface-dwelling megabenthos. Similar traces occur on the Madeira Abyssal Plain (Huggett, 1987). Young et al. (1985) found no strong correlation of megafaunal diversity and trace diversity in the deep Caribbean. However, because the persistence of these features varies with both the physical environment and biological activity (Gage and Tyler, 1991), it is difficult to interpret animal densities directly from quantification of *Lebensspuren.*

Sediment properties can influence the composition of *Lebensspuren*. Huggett (1987) observed striking differences in categories of feeding traces present between areas of the Madeira Abyssal Plain underlain by turbidite deposits and those underlain by pelagic deposits. In particular, meandering traces, and small spokes, were virtually confined to the turbidites, while irregular traces were more common on the pelagic deposits. Huggett (1987) attributed these differences to the greater amounts of organic matter contained within turbidite deposits. Thus, *Lebensspuren* may have the potential to provide geologists with a simple visual method for mapping the distribution of turbidites and pelagic deposits.

DEMERSAL FISH

Merrett and Haedrich (1997) have provided an excellent overview of the biology of deep-sea demersal fish; Haedrich (1997) described their distribution and population ecology. Because some species are familiar and commercially important, the biology of demersal fish (e.g., their diets, reproduction and growth rates) is better understood than that of megafaunal invertebrates, particularly in the continental-slope settings that are now accessible to fisheries. The abundance of fish and invertebrates is not often compared. In the Porcupine Seabight they have roughly comparable biomass values and show a similar decrease with bathymetric depth (Merrett and Haedrich, 1997, figs. 4.3, 4.4 therein). On the Cape Verde Abyssal Plain, the density of the invertebrate megafauna is about three times the density of the fish (Bett et al., 1995).

The taxonomy and biogeography of bottom-dwelling fish are probably better known in the North Atlantic than in any other ocean. Regions like the Rockall Trough are particularly well studied (e.g., Gordon and Duncan, 1985, 1987a,b). Overall, the dominant deep-sea families are the Alepocephalidae (slickheads), Macrouridae (grenadiers) and Ophidiidae (cusk eels). The macrourids are particularly well represented at all depths from the upper slope to the abyss, and the ophidiids are unusual because the number of species increases with bathymetric depth, both absolutely and relative to the total number of fish species (Haedrich and Merrett, 1988; Merrett and Haedrich, 1997). The 505 species belonging to 72 families recorded from areas beyond the 200 m contour in the North Atlantic represent 39% of all deep-sea species (Merrett, 1994). Taxonomically, the North Atlantic fauna is most similar to the Indian Ocean fauna (40% of genera in common) and least similar to the Northeast Pacific fauna (14% of genera in common) (Merrett and Haedrich, 1997). As in the case of many invertebrate taxa, fish diversity is greatest on the middle and lower parts of the slope. In the North Atlantic, the species/family ratio, a useful measure of diversity, is lowest in the depth ranges 200–399 m (species/family ratio = 2.5) and >4000 m (species/family ratio = 2.9) and highest between 400 and 1999 m (species/family ratio = 6.0) (Merrett and Haedrich, 1997, table 2.1 therein). However, it is useful to be reminded (Merrett and Haedrich, 1997) that deep-sea fish are not a particularly diverse group compared with the small invertebrates on which perceptions of high deep-sea diversity are based.

Haedrich and Merrett (1988) have summarized the distribution of species in different bathymetric zones at a series of localities around the North Atlantic continental margin (slope and rise), the region where most demersal fish species occur. Their compilation indicates that two species, the synaphobranchiid eel *Synaphobranchus kaupi* and the grenadier *Coryphaenoides armatus,* are particularly widespread. On the other hand, many other species have restricted geographical ranges, leading Haedrich and Merrett (1988, 1990) to conclude that it is impossible to recognize real demersal fish communities in the deep North Atlantic. Like some invertebrate megafauna (e.g., Billett, 1991), fish species have well-defined bathymetric ranges on North Atlantic continental margins. However, these ranges are often different in different parts of the North Atlantic, and the impression they convey of vertically zoned communities are merely artifacts of species replacement patterns (Haedrich, 1997; Merrett and Haedrich, 1997). Most demersal species probably do not interact ecologically with each other to any great extent.

Truly oceanic abyssal demersal fish faunas (4000–6000 m) are less well documented than those from the continental margin. Nevertheless, the faunas of the Northeast Atlantic basins are reasonably well sampled, and their characteristics can be related to the structure of the overlying water column and patterns of primary production. Merrett (1987) recognized a northern assemblage (Porcupine Abyssal Plain, 49ºN) dominated by three grenadier species (two in the subgenus *Coryphaenoides* (*Chalinura*) and one in the subgenus *C.* (*Nematonurus*)) and the synaphobranchiid *Histiobranchus bathybius,* and a southern assemblage (Madeira Abyssal Plain, 30ºN) dominated by ipnopids (*Bathymicrops regis* and *Bathypterois longipes*) and the rattail *Echinomacrurus mollis*. The northern species are large benthopelagic fish with functional swim bladders and robust musculature, which imply considerable mobility and hence the ability to catch relatively large prey. Limited data suggest that fecundity is high. The southern species are small, microphagous fish which are either negatively buoyant, or able to maintain neutral buoyancy only by reducing ossification and musculature and therefore mobility. Limited data suggest that fecundity is low. Merrett (1987) advanced the hypothesis that these characteristics reflect the switch from the seasonal deposition of phytodetritus at the Porcupine Abyssal Plain site to the more oligotrophic, non-seasonal system which prevails on the Madeira Abyssal Plain. Subsequent sampling has modified this picture somewhat, with the recognition of two assemblages between 31–38ºN and another southern assemblage off the Northwest African margin around 20–22ºN (Merrett, 1992; Merrett and Haedrich, 1997). The latter appears to be related to high productivity associated with the main upwelling zone off Cap Blanc, referred to above (p. 139). Merrett and Haedrich (1997) suggested that, in abyssal open-ocean settings, trophic inputs derived from primary production in the overlying photic zone usually exert a strong influence on the distribution of demersal species. On the other hand, along continental margins, vertical water-column fluxes are obscured by food inputs derived from upwelling, terrigenous sources, currents, shelf production, and interactions between horizontally distributed pelagic organisms and the continental slope. In such areas, these factors have the most decisive effect on distribution patterns.

BASIN-WIDE BIOLOGICAL PATTERNS AND PROCESSES

Though many studies of deep-sea benthos are regional in nature, a few have tried to draw global or basin-wide comparisons in an attempt to evaluate the relative importance of factors controlling biological pattern in the deep sea. In the sections below we review the conclusions of such studies, and, because we found large gaps in treatment of these issues, have attempted to create our own syntheses. We focus on patterns of density and biomass, community respiration, bioturbation and succession, in the belief that much, though certainly not all, of the accumulated knowledge about the deep Atlantic fauna addresses these issues.

Density and biomass

Most early investigations of density and biomass patterns of Atlantic benthos examined the effects of water depth. Investigators usually treat meiofauna, macrofauna, or megafauna, but rarely all three (Table 5.3; but see Galéron et al., 2000). In most places monotonic, sometimes exponential, declines in density and biomass were observed with increasing water depth for each group (Thiel, 1983; figs. 6, 7 therein; Rowe, 1983; fig. 3 therein; Vincx et al., 1994; table 3 therein). Lampitt et al. (1986) reported a logarithmic decline in megafaunal biomass along a depth gradient in the Porcupine Seabight, with a reduction by a factor of 30 between 500 and 4100 m. They observed no significant change in average body weight with depth. Declines in macrofaunal density with depth are also evident along most depth transects in the Northwest Atlantic (Hessler and Sanders, 1967; Rowe et al., 1974; Smith, 1978; Blake and Grassle, 1994; Blake and Hilbig, 1994).

Less regular patterns have been reported beneath upwelling regions, where oxygen minima at intermediate depths depress density (Sanders, 1969; Thiel, 1978; Pfannkuche et al., 1983), where fluxes of organic matter to deep water are very high, as in the Norwegian–Greenland Sea (Thiel, 1983: fig. 9 therein), and in regions subject to hydrodynamic disturbance (Hecker, 1990b). Where hydrodynamic reworking is intense, as in the Rockall Trough and Goban Spur, maximal densities and biomass sometimes occur at mid-slope depths (Gage, 1978; Flach and Heip, 1996b). These patterns may be modified by seasonal and interannual variation (Flach and Heip, 1996b).

A more recent emphasis has been on the comparison of abundance and biomass at sites differing in organic-matter flux (Sibuet et al., 1989, 1993; Rowe et al., 1991; Thurston et al., 1994; Paterson et al., 1994a,b; Vanreusel et al., 1995a; Gooday, 1996b; Cosson et al., 1997; Galéron et al., 2000). These studies have invariably found that flux of particulate organic carbon (POC) is the first-order parameter controlling macrofaunal and meiofaunal abundances in the deep Atlantic (Thiel, 1983; Sibuet et al., 1989; Rowe et al., 1991). Regions of the Atlantic with highest organic flux support the greatest infaunal densities and biomass. Particularly notable hot-spots in this regard are the Norwegian–Greenland Sea (Romero-Wetzel and Gerlach, 1991), the continental margin off Cap Blanc, Northwest Africa (Cosson et al., 1997; Galéron et al., 2000), and off Cape Hatteras, North Carolina. In the latter area, macrofaunal densities at 850 m depth exceed 40 000 individuals m^{-2} (Schaff et al., 1992; Blake and Hilbig, 1994).

A similar correlation is often apparent along bathymetric transects. Work by Pfannkuche et al. (1983) off Morocco (35ºN) and Pfannkuche (1985) in the Porcupine Seabight indicates that meiofaunal abundances are strongly linked to surface productivity regimes and sediment chloroplastic pigments, but do not necessarily decrease exponentially downslope. For example, on the Moroccan transect, meiofaunal maxima were observed between 400 and 1200 m. Thiel (1978) reported meiofaunal densities to be fairly constant with depth at sites beneath upwelling areas off Northwest Africa, with densities sometimes exceeding 10^{6} m^{-2}. Vanreusel et al. (1995a) documented lower nematode density and biomass in oligotrophic waters off Mauritania (EUMELI 3) than at the Porcupine Abyssal Plain site, which experiences seasonal phytodetrital pulses. Larger nematode body size was observed on the Porcupine Abyssal Plain. In some cases, the macrofaunal and meiofaunal trends appear linked to patterns of bacterial biomass and density (Rowe et al., 1991; Vanreusel et al., 1995b), which are in turn dependent on the primary productivity of overlying waters (Morita, 1979; Tan and Ruger, 1989). Rowe et al. (1991) suggested that the importance of bacteria in the pool of living carbon (relative to macro and meiofauna) increases with depth.

Patterns of density and biomass generally track one another; regions of highest density often exhibit high biomass. However, for macrofauna, biomass declines more rapidly with depth than does abundance because body size declines with depth (Rowe et al., 1974;

Thiel, 1975). Based on a comparison of data for macrofauna in the Northwest with data for meiofauna in the Northeast Atlantic, Thiel (1983) reported that the slope of density decline with water depth is steeper for macrofauna than for meiofauna by a factor of 2. A reasonable explanation is that smaller-sized organisms (the meiofauna) are better able to cope with declining food inputs at greater depths. However, east–west differences in patterns of carbon flux with depth may have influenced the outcome of this analysis.

Several authors have suggested that megafauna are more sensitive to changes in food supply than are smaller organisms (Sibuet et al., 1984; Lampitt et al., 1986). Sibuet et al. (1989) have reported that there is a constant proportional relationship between metazoan meiofauna, macrofauna, and megafauna, but that the relation of particulate organic matter to abundance of megafauna differs from that of the other groups. Galéron et al. (2000) found that megafaunal biomass in the tropical Northeast Atlantic exceeded that of macrofauna and meiofauna only at the most eutrophic of the three EUMELI sites. Grassle et al. (1975) estimated that, in the Northwest Atlantic, megafauna were three orders of magnitude less abundant than the macrofauna at 1850 m, whereas biomass for the two size groups was about equal (Haedrich and Rowe, 1977). Megafauna appear to dominate where food input is high (e.g., off Cape Hatteras, off Northwest Africa, or on the Amazon Cone), or where advective transport enhances particle flux (e.g., the Rockall Trough). They appear less important in systems where food supply is lower, although their role in these ecosystems may not be accurately reflected by counts (Lampitt et al., 1986).

There have been no systematic comparisons of the western and eastern Atlantic Ocean in terms of benthic abundance or biomass in deep waters. Too few meiofaunal data exist, and methods are too variable to draw valid comparisons between the two sides of the Atlantic, although they have been discussed by Thiel (1983).

Regressions of macrofaunal density against water depth reveal higher densities in the Northwest than Northeast Atlantic at bathyal depths (Fig. 5.7A). The Northwest Atlantic macrofauna show a strong exponential decline in density with depth (exponential fit: $r^2 = 0.70$; $P < 0.0001$); this relationship is much weaker in the Northeast Atlantic (exponential fit: $r^2 = 0.16$; $P = 0.007$), where the density relationship with depth is more linear ($r^2 = 0.31$; $P < 0.0001$). The regression lines for the two areas cross just below 4000 m (Fig. 5.7A), suggesting that, at abyssal depths, the macrofauna may be more abundant in the Northeast than the Northwest Atlantic. It is possible that these differences, driven largely by high margin densities in the South Atlantic Bight, are due to activities of the western boundary current (Gulf Stream) in focusing organic-matter inputs. However, the same trends are not evident for macrofaunal biomass which, on the basis of limited data (Fig. 5.7B, Table 5.3), appears to be greater in the Northeast than in the Northwest Atlantic.

Strong regional variation is evident in the Atlantic. The Porcupine Seabight yielded invertebrate megafaunal biomass eighteen times and ten times higher, respectively, than depths of 500 m and 4000 m on the slope off southern New England, prompting Lampitt et al. (1986) to suggest that there is higher megafaunal biomass in the Northeast than in the Northwest Atlantic. Megafaunal biomass on the Demerara Abyssal Plain (4.5 mg dry wt. m^{-2}) was less than half that on the Porcupine Seabight (11.7 mg m^{-2}), while the margin off the Amazon had more than twice as much biomass as the Porcupine Seabight. Ocean-wide comparisons of megafaunal biomass, of the sort carried out above for the macrofauna, are made difficult by the broad range of methods and variable minimum body sizes considered in megafaunal investigations (Thurston et al., 1994) (Table 5.3).

Community respiration

Sediment community respiration, also termed sediment community oxygen consumption (SCOC), is of interest because it represents a highly integrated measure of activity levels of aerobic bacteria, protozoans and metazoans. This activity is believed to be strongly controlled by the flux of particulate organic carbon (i.e., food availability) at the sea floor. Sediment community oxygen consumption has been measured using several approaches (Smith and Hinga, 1983). These include (a) *in situ* respirometry, which is based on loss of dissolved oxygen in water overlying enclosed sediments, with measurements made within the seabed or in cores suspended just above the bottom; (b) shipboard core incubations, which also measure changes in dissolved oxygen; (c) biochemical assay of the respiratory electron-transport system (ETS) activity in the laboratory; and (d) calculations of oxygen consumption derived from oxygen concentration gradients in sediment pore-waters. Several other approaches

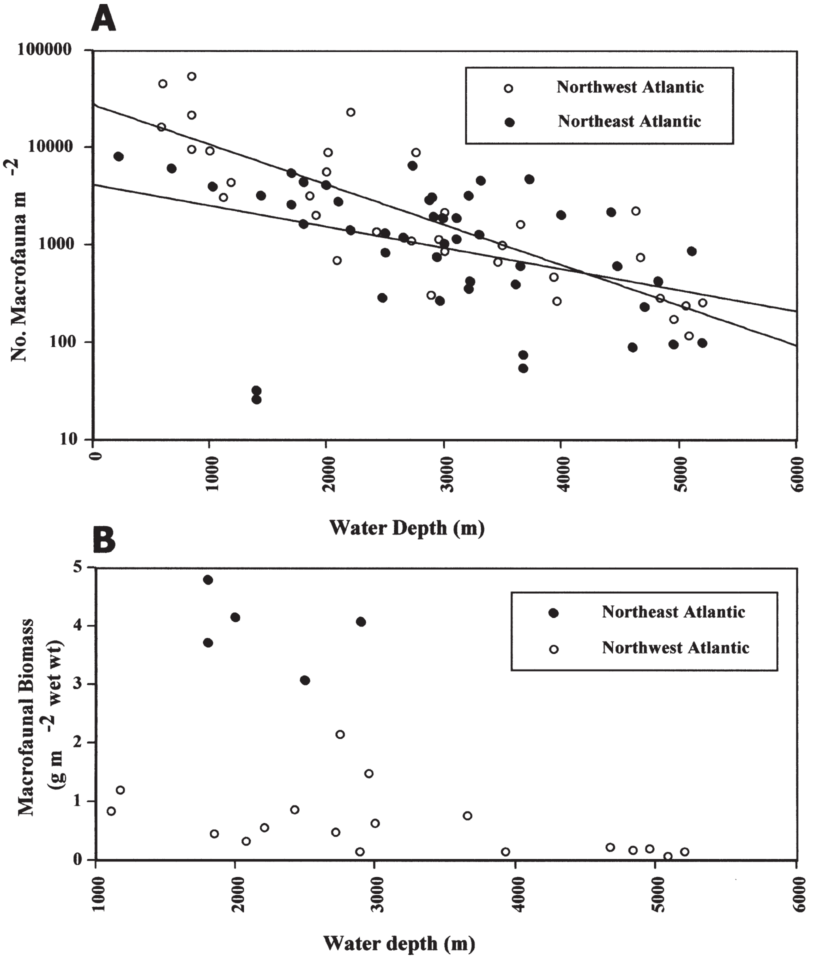

Fig. 5.7. Regression of macrofaunal standing stock against depth for NW and NE Atlantic stations. A, densities; B, biomass.

include measurement of chemical oxygen demand with inhibitors and poisons, and ATP analyses (Graf and Linke, 1992). Data collected to date indicate a strong link between surface primary production and *in situ* measures of sediment oxygen consumption. This link is mediated by water depth and distance from shore, which, in concert with seasonality and mass transport, control the proportion of surface production that reaches the seabed – that is, organic-carbon flux.

Western Atlantic

Total SCOC in the Northwest Atlantic spans three orders of magnitude, from a low of 0.02 ml O_2 m^{-2} hr^{-1} at 5200 m in the Sargasso Sea near Bermuda to 1.31 ml O_2 m^{-2} hr^{-1} at 1345 m on the continental slope north of the Blake Plateau. On the Blake Plateau at a depth of 1345 m (Hinga et al., 1979), SCOC was twice that at the shallowest slope station (1850 m) along the Gay Head–Bermuda transect (Smith, 1978). Smith and Hinga (1983), using data from nine stations along the Gay Head–Bermuda transect, were able to account for 96% of the variation of *in situ* SCOC with the following regression equation:

$$Y = 0.9421 - 0.0001621D - 0.001252PP,$$

where Y = SCOC in ml O_2 m^{-2} hr^{-1}, D = water depth in meters, and PP = annual primary productivity in g C $m^{-2}y^{-1}$.

In situ measurements of SCOC were reported by Smith and Hinga (1983) in the western tropical Atlantic, in the Straits of Florida at the base of the Blake Plateau (675 m) and in the Tongue of the Ocean station (TOTO) (2000 m) near the Bahamas. Values were 2.95 and 3.10 ml O_2 m^{-2} h^{-1}, respectively – much higher than any reported in the Northwestern Atlantic. Smith and Hinga (1983) suggested that these high respiration rates might result from proximity to land, both to the west and east, and associated channeling into the sites of organic matter from terrestrial and shallow marine sources. Respiration requirements exceeded measured fluxes of particulate organic carbon in the Straits of Florida and the TOTO site by a factor of 5, leading various investigators to suggest that macrophytic algae and seagrass may have supplied some of the missing material (Wiebe et al., 1976). A time series of nine SCOC measurements made by benthic lander at an abyssal station 83 km southeast of Bermuda (BATS), during a period of three years, indicated remarkable constancy ($0.030\pm0.0035\ \mu\mathrm{mol\,cm^{-2}\,d^{-1}}$) with no seasonal variation.

Eastern Atlantic

Measurements made in the Gulf of Guinea off Northwest Africa indicate very high SCOC ($3.93\ \mathrm{ml\,O_2\,m^{-2}\,h^{-1}}$) at 278 m and much reduced values at 4000 m ($0.65\ \mathrm{ml\,O_2\,m^{-2}\,h^{-1}}$). Both are probably elevated by upwelling, and the shallow site may be influenced by terrigenous input from nearby rivers (Hinga et al., 1979). Patching et al. (1986) measured SCOC at depths of 2880 m in the Rockall Trough and 4980 m on the Porcupine Abyssal Plain. Mean values were 2.2 times greater in Rockall Trough (99–$203\ \mu\mathrm{mol\,O_2\,m^{-2}\,h^{-1}}$) than on the Porcupine Abyssal Plain (58–$77\ \mu\mathrm{mol\,O_2\,m^{-2}\,h^{-1}}$). The high rates observed might be related to the timing of the measurements, which were taken just after the spring phytoplankton bloom in surface waters, or to methodology bias (Patching et al., 1986). Seasonal measurements made *in situ* in the Porcupine Seabight (2000 m) by Lampitt et al. (1995) yielded SCOC values between those in the Rockall Trough and on the Porcupine Abyssal Plain (74–$125\ \mu\mathrm{mol\,O_2\,m^{-2}\,h^{-1}}$), but indicated no evidence of seasonal variation. Cores with phytodetritus visible on the surface did not yield SCOC values different from those lacking this material, indicating either degradation so rapid that it was missed or very long community response times (Lampitt et al., 1995). Measurements in June 1985 of around $30\ \mu\mathrm{mol\,O_2\,m^{-2}\,h^{-1}}$, made on the Porcupine Abyssal Plain by Lampitt et al. (1995), were half those made earlier in the year (May 1980, April 1982) by Patching et al. (1986) in the same region. Pfannkuche (1992, 1993) obtained comparable SCOC values slightly further south at the BIOTRANS site (4590 m), where values ranged from 15 to $38\ \mu\mathrm{mol\,O_2\,m^{-2}\,h^{-1}}$ during spring and summer. He reported higher SCOC values in July and August than in spring.

Overview

In general, bathyal and abyssal SCOC data from the eastern Atlantic seem to be higher than *in situ* values at equivalent depths from the northwestern Atlantic, although SCOC measurements made on the Hatteras Abyssal Plain were comparable to those on the Porcupine Abyssal Plain and at the BIOTRANS Site (Table 5.4). The Northwest Atlantic margin off Cape Hatteras experiences extremely high carbon flux (Blair et al., 1994), and this influence may extend to the adjacent abyssal areas. The few data available suggest that the organic-carbon input to the Northeast Atlantic seabed may be subject to more seasonal variation than in the Northwest Atlantic. Both the increased SCOC rates and greater variability may be related to heavy, pulsed input of phytodetritus to the seabed during spring blooms in the northeastern section of the Atlantic. Seasonality of SCOC has been documented in both the Atlantic (Pfannkuche, 1992) and the Pacific (Smith et al., 1994). However, the Atlantic and Pacific differ in the extent to which measured fluxes of particulate organic carbon appear to meet the respiratory demands of the benthic community. Evidence to date suggests that this flux in the North Atlantic is more than sufficient to account for the SCOC (Smith and Hinga, 1983), whereas this is not the case in the Pacific (Smith, 1987).

Bioturbation

Most quantitative estimates of bioturbation in deep-sea sediments are based on a diffusive mixing coefficient (D_b) derived from profiles of radiotracers scavenged on particles in the seabed. D_b is calculated from the following steady-state, unidirectional equation as derived by Nozaki et al. (1977):

$$D_b\frac{\partial^2 N}{\partial x^2} - S\frac{\partial N}{\partial x} + P - \lambda N = 0,$$

where N, radiotracer concentration in bulk sediment (atoms $\mathrm{g^{-1}}$); ∂, bulk sediment density ($\mathrm{g\,cm^{-3}}$); S, sedimentation rate ($\mathrm{cm\,sec^{-1}}$); D_b, mixing coefficient ($\mathrm{cm^2\,sec^{-1}}$); P, production rate of radiotracer (atoms $\mathrm{g^{-1}\,sec^{-1}}$); λ, decay constant of tracer ($\mathrm{sec^{-1}}$).

Most estimates of D_b for sediments of the continental rise and abyss in the Atlantic have been based on $^{210}\mathrm{Pb}$ profiles with a half life of 22 years (Boudreau, 1994). Values determined for marine sediments at depths between 1410 and 5160 m consistently fall between 0.02 and $1.0\ \mathrm{cm^2\,yr^{-1}}$ (Table 5.5, Fig. 5.8A). These values are several orders of magnitude lower

Table 5.4
In situ measurements of sediment community oxygen consumption (SCOC) in the Atlantic ocean[1]

Station	Water depth (m)	SCOC		Reference
		ml O_2 m^{-2} h^{-1}	µmol O_2 m^{-2} h^{-1}	
WESTERN ATLANTIC				
Gayhead–Bermuda Transect	1850	0.50	22.8	Smith and Teal (1973)
	2200	0.46	20.5	Smith (1978)
	2750	0.35	15.6	Smith (1978)
	3000	0.20	8.9	Smith (1978)
	3650	0.21	9.4	Smith (1978)
	4670	0.09	4.0	Smith (1978)
	4830	0.04	1.8	Smith (1978)
	5080	0.07	3.1	Smith (1978)
	5200	0.02	0.9	Smith (1978)
Mid Atlantic Bight	2159	1.17[2]	52.41[2]	Hales et al. (1994)
	4236	0.69	30.82	Hales et al. (1994)
	4501	0.54	23.97	Hales et al. (1994)
	5210	0.31	13.70	Hales et al. (1994)
	5380	0.33	14.84	Hales et al. (1994)
North of Blake Plateau	1345	1.31	58.5	Hinga et al. (1979)
Florida Strait	675	2.95	131.7	Smith and Hinga (1983)
Tongue of the Ocean	2000	3.10	138.4	Smith and Hinga (1983)
Bermuda (BATS)	4400	0.28	12.5	Sayles et al. (1994)
EASTERN ATLANTIC				
Rockall Trough	2280	1.50[3]	67[3]	Patching et al. (1986)
Porcupine Seabight	2000	2.12[3]	94.58[3]	Lampitt et al. (1995)
Porcupine Abyssal Plain	4980	1.39[3]	62.00[3]	Patching et al. (1986)
	4000	0.66[3]	29.75[3]	Lampitt et al. (1995)
BIOTRANS	4590	0.40 (April 88)	17.9	Pfannkuche (1992)
	4590	0.86 (July 86)	38.4	Pfannkuche (1992)
	4590	0.81 (Aug 89)	36.3	Pfannkuche (1992)
Gulf of Guinea	278	3.93	175.5	Hinga et al. (1979)
	4000	0.65	29.0	Hinga et al. (1979)

[1] All measurements are based on grab respirometry unless indicated otherwise.
[2] Porewater oxygen profiles made *in situ* by microelectrodes.
[3] Suspended core methods.

than those observed in shallow water. Compilation of mixing-coefficient data from sites in the Northwest, Northeast and South Atlantic suggest several patterns that bear further investigation. The D_b data from the Northwest Atlantic show an exponential decline with water depth ($r^2 = 0.634$) which is not evident in the Northeast Atlantic (Fig. 5.8A), where maximal D_b values were observed on the lower rise in the Cape Verde and Porcupine Seabight regions. The South Atlantic may exhibit lower mixing than the North Atlantic, but the data are few. Latitude appears to have little influence on mixing as estimated from D_b values (Fig. 5.8B).

Recent estimates of diffusive mixing coefficients made in more dynamic environments with ^{234}Th, a shorter-lived radiotracer (24-d half-life), are much

Table 5.5
Estimates of bioturbation rates and mixed layer depth in deep Atlantic sediments

Region	Latitude	D_b (cm^2 y^{-1}) (mixed layer)[1]	Water depth (m)	Tracer	Reference
CONTINENTAL SLOPE					
Northwest Atlantic					
North Carolina (off Cape Hatteras)	35ºN	19±11.0 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		7.4±4.7 (x±1 SD)	850	glass beads	DeMaster et al. (1994)
North Carolina (off Cape Lookout)	34ºN	4.6±5.2 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		0.84±0.65 (x±1 SD)	850	glass beads	DeMaster et al. (1994)
North Carolina (off Cape Fear)	32ºN	6.0±6.2 (x±1 SD)	850	Th-234	DeMaster et al. (1994)
		0.29		glass beads	DeMaster et al. (1994)
Nova Scotian Rise	40ºN	1–33	4800	Th-234	DeMaster et al. (1991)
Newfoundland slope	50ºN	0.1–1.0	1500	Pb-210	Smith and Schafer (1984)
North Atlantic	21ºN	0.25	1410	Pu-230	Guinasso and Schink (1975)
Northwest Atlantic		0.19	2705	Pb-210	Turekian et al. (1975)
	37ºN	0.7–1.2 (8)	1170	Pb-210	Tanaka et al. (1991)
	38ºN	30	2800	Th-234	Aller and DeMaster (1984)
	39ºN	0.42	501	Pb-210	Anderson et al. (1988)
		1.03	553	Pb-210	Anderson et al. (1988)
		0.77	869	Pb-210	Anderson et al. (1988)
		0.45	1126	Pb-210	Anderson et al. (1988)
		0.14, 0.49	1170	Pb-210	Anderson et al. (1988)
		0.92	1275	Pb-210	Anderson et al. (1988)
		0.75	1359	Pb-210	Anderson et al. (1988)
		0.20	1643	Pb-210	Anderson et al. (1988)
		0.71	2362	Pb-210	Anderson et al. (1988)
		0.60, 0.73	2700	Pb-210	Anderson et al. (1988)
Northeast Atlantic					
Northeast Atlantic	51ºN	0.046	2365	Pb-210	Thomson et al. (1993)
BOFS		0.042	4150	Pb-210	Conte et al. (1994)
EUMELI	21ºN	0.142	2050	Pb-210	Reyss et al. (1993)
BIOGAS	47ºN	0.183 (7)	2100	Pb-210	Mauviel and Sibuet (1985)
	47ºN	0.189, 0.167 (6,10)	2800	Pb-210	Mauviel and Sibuet (1985)
Southwest Atlantic	9ºS	0.10	1345	Pu-239	Guinasso and Schink (1975)
Mediterannean		0.8–1.6	1200	Cs-137, luminophores	Gerino et al. (1993)
MID ATLANTIC RIDGE					
Mid Atlantic Ridge		0.19 (8)	2500	Pb-210	Nozaki et al. (1977)

continued on next page

Table 5.5, *continued*

Region	Latitude	D_b (cm^2 y^{-1}) (mixed layer)[1]	Water depth (m)	Tracer	Reference
ABYSSAL PLAINS					
Northeast Atlantic	50ºN 21ºW	0.66	3547	Pb-210	Thomson et al. (1993)
	52ºN 22ºW	0.66	4005	Pb-210	Thomson et al. (1993)
	49ºN 21ºW	0.21	4067	Pb-210	Thomson et al. (1993)
	~45ºN 17ºW	0.1	4000–5000	Pb-210	Smith et al. (1986/87)
Northwest Atlantic: Hatteras	32º	0.022, 0.037 (5)	5200	Pb-210	Stordal et al. (1985)
North Atlantic	39ºN 42ºW	0.220	4810	Pu-239	Guinasso and Schink (1975)
EUMELI	21ºN 31ºW	0.02	4550	Pb-210	Reyss et al. (1993)
Cape Verde Abyssal Plain	18ºN	0.875 (9)	3374	Pb-210	Stordal et al. (1985)
	22ºN	0.040 (5)	4660	Pb-210	Stordal et al. (1985)
	22ºN	0.19, 0.220 (4)	5032	Pb-210	Stordal et al. (1985)
Madeira Abyssal Plain	35ºN 20ºW	0.126 (3.7)	5161	Pb-210	Kershaw (1985)
Southwest Atlantic	41ºS 20ºE	0.04	4910	Pb-120	DeMaster and Cochran (1982)
Southeast Atlantic	29ºS 4ºE	0.14	4920	Pu-239	Guinasso and Schink (1975)
South Atlantic		0.063	4910	Pb-210	Turekian et al. (1975)
TRENCHES					
Puerto Rico Trench	19ºN	0.025	8100	Pb-210	Stordal et al. (1985)

[1] Mixed layer depth in cm, where available, is given in parentheses.

higher. Thorium estimates of mixing rate range from 1 to 33 cm^2 y^{-1}. The most intense mixing has been observed on the continental margin at 850 m off Cape Hatteras (DeMaster et al., 1994), and in a high-energy region on the Scotian Rise at 4800 m subject to benthic storms (the HEBBLE site) (DeMaster et al., 1991). The region off Cape Hatteras is a focus for sediment accumulation, and fluxes of organic carbon are among the highest reported for slope environments. At the HEBBLE site, organic-carbon input to the seabed is elevated by benthic storms. In both cases, benthic macrofaunal densities and biomass are also very high (Thistle et al., 1991; Schaff et al., 1992), supporting the idea that vertical and advective carbon flux, faunal abundance and bioturbation are correlated (Berner, 1980; Aller, 1982; Smith, 1992).

Smith et al. (1993) have suggested that the higher mixing rates associated with ^{234}Th (relative to ^{210}Pb) reflect age-dependent mixing, in which younger particles (associated with ^{234}Th) are mixed preferentially compared to older particles (associated with most ^{210}Pb). Atlantic sites have not yielded strong evidence for this phenomenon. However, at three sites on the Northwest Atlantic margin off North Carolina, reduced mixing of experimentally emplaced sand-sized glass beads relative to fine particles tracked by ^{234}Th suggests that mixing rates may depend on particle quality or size (DeMaster et al., 1994; Fornes et al., 1999).

Diffusive mixing models provide accurate estimates of bioturbation only when radiotracer profiles exhibit exponential declines in activity down-core. However, in

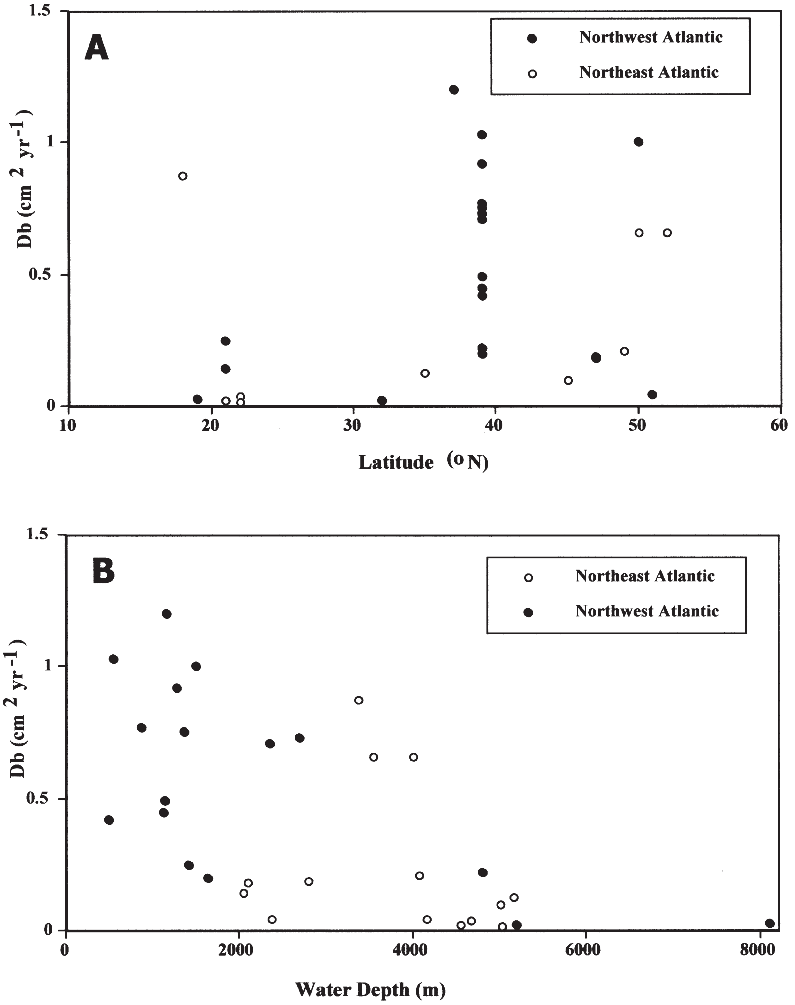

Fig. 5.8. Particle mixing coefficients (D_b) as a function of (A) water depth and (B) latitude.

almost every study of radiotracer profiles in Atlantic slope, rise and abyssal sediments, some cores exhibit subsurface maxima or shoulders underlying sharp surface gradients. These are indicative of non-local transport of surface material by animals to depth in the sediment (Smith et al., 1986/87; Brand and Shimmield, 1991; Thomson et al., 1993; Levin et al., 1997; Fornes et al., 1999). Sometimes, downward transport is so intense that subsurface inventories of Pb-210 can be higher than in surface sediments (Thomson et al., 1993). Significant spatial heterogeneity has been observed in both the Northeast and Northwest Atlantic among profiles generated from subcores within a single box-core (Smith and Schafer, 1984; Smith et al., 1986/87; DeMaster et al., 1991). Significant temporal variation in mixing regimes and non-steady-state conditions have been observed at a very dynamic site (HEBBLE) subject to benthic storms (DeMaster et al., 1991).

Subsurface maxima observed in profiles of chlorophyll (Graf, 1989) and experimentally placed diatoms labeled with ^{13}C (Levin et al., 1997, 1999) reveal that subduction of freshly deposited material can be rapid (within days), and may occur deep within the sediment column (9–13 cm). Deposit-feeding organisms implicated in subduction and generation of subsurface maxima in the Atlantic Ocean include sipunculans (J.N. Smith et al., 1986/87; Romero-Wetzel, 1987; Graf, 1989), maldanid, paraonid, and nereid polychaetes (Blair et al., 1996; Levin et al., 1997, 1999), burrowing anemones and decapods (Smith and Schafer, 1984). It may be that much of the mixing recorded on time scales of 100 days or 100 years by use of particle reactive radiotracers such as ^{234}Th or ^{210}Pb actually occurs within hours or days after reactive particles reach the seabed. Levin et al. (1997), for example, estimated that mixing by maldanid polychaetes observed on the Northwest Atlantic slope (at a depth of 850 m) within 1.5 days after diatom deposition could account for 25–100% of the mixing below 5 cm estimated from naturally occurring ^{234}Th (100-day time scale). Rapid downward transport of particles within the sediment column also can result from infilling of vacant burrows. Trapping of reactive organic matter within burrows on the Nova Scotian Rise (4800 m) was shown by Aller and Aller (1986) to cause intensive decomposition and to generate hot-spots of enhanced microbial, meiofaunal and macrofaunal activity in otherwise organic-poor sediment.

Disturbance, colonization and succession

Present understanding of the responses of macrobenthic communities in the Atlantic to disturbance is derived from experiments in which defaunated sediments (rendered azoic by freezing and thawing), plant material, fish or wood were placed in or on the seabed, and subsequent colonization was observed at varying time intervals (Smith and Hessler, 1987).

Initial investigations of infaunal succession were carried out in the Atlantic by deploying deep-sea sediments in trays lying on the seabed. Grassle's (1977) observations of faunal colonization after 2 and 26 months in trays at a depth of 1760 m (Station DOS-1) in the Northwest Atlantic were the first to suggest that recovery rates following disturbance are very slow for the naturally occurring macrobenthic communities. Numbers of colonizing individuals were low, and most belonged to species not previously reported from the study area. Among the commonest were dorvilleid and capitellid polychaetes, priapulids, wood-boring bivalves and snails ectoparasitic on echinoderms. Later tray recolonization studies in the Northwest Atlantic conducted by Grassle and Morse-Porteous (1987) at DOS-1, and at 3600 m (DOS-2), for periods ranging from 2 to 59 months, supported initial findings of slow recovery. Even after 59 months, faunal densities did not attain those in background sediments. Screening of tray sediments revealed enhanced colonizer densities, and led to the speculation that predation may control rates of succession (Grassle and Morse-Porteous, 1987).

Sediment-tray experiments conducted for 6 and 11 months at depths of 2160 m and 4150 m in the Bay of Biscay also indicated very slow colonization by macrofauna (Desbruyères et al., 1985a). However, in an earlier experiment Desbruyères et al. (1980) reported much more rapid colonization of defaunated sediments at 2160 m after 6 months' exposure, with densities in organically enriched sediments overshooting those of control sediments. As in Grassle's experiments, many of the recruits in the Bay of Biscay belonged to species absent from control samples.

These early sediment-tray experiments were fraught with hydrodynamic artifacts, and deemed unrealistic because the experimental substrata were separated from natural sediments (Smith, 1985b; Snelgrove et al., 1995). However, they were very important in revealing the availability in the deep Atlantic of opportunistic colonizers highly adapted to disturbed or enriched settings. Subsequent deployments of hydrodynamically unbiased colonization trays were made by Snelgrove et al. (1992, 1994, 1996) for 23 days and 28 months at a depth of 900 m near St. Croix, U.S. Virgin Islands in the equatorial West Atlantic. These experiments indicated that colonizing macrofauna can attain or exceed ambient densities in 2+ years, but again the colonists were species relatively rare in background sediments (Snelgrove et al., 1996). This trend was even more evident in organically enriched treatments, which were colonized by large numbers of capitellid and hesionid polychaetes, cumaceans and leptostracans that were not observed in control treatments. The characteristic response of specialized, opportunistic species to disturbance in the deep Atlantic has not been observed in the few comparable colonization studies carried out for Pacific macrobenthos. In the eastern Pacific the initial respondents to non-reducing sediment disturbance appear to be species relatively common in the background community (Levin and Smith, 1984; Kukert and Smith, 1992; Levin and DiBacco, 1995). Opportunists such as *Capitella* have not been reported from deep-water experiments in the Pacific, though *Capitella* and leptostracans are known to colonize detritus in shallow submarine canyons (Vetter and Dayton, 1998). Too few sites and forms of disturbance have been examined to determine whether the Atlantic is really distinct from the Pacific in the distribution of deep-sea opportunists, or to permit speculation about the causes.

Enrichment of experimental sediments deployed in recolonization trays have produced colonizer assemblages distinct from the fauna of surrounding sediments and control trays in all Atlantic studies (Desbruyères et al., 1980; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992, 1996). These experiments, along with those in which direct enrichment of the bottom has been achieved by placement of fish carcasses, wood, or marine algae on the seabed (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994) indicate the importance of patchy organic inputs to the structure of benthic communities. Sediments near experimentally emplaced wood blocks yielded high densities of mussels (*Idasola argentea*) and wood borers (*Xyloredo* sp.), while sediments containing *Sargassum* exhibited elevated densities of amphipods and several polychaetes including *Capitella* spp. and *Ophryotrocha* sp. Patterns of species richness, dominance, taxonomic composition and abundance all seem to be affected by the supply of organic matter to the seabed (Gooday and Turley, 1990; Rice and Lambshead, 1994; Grassle and Grassle, 1994). In recent decades it has become clear that persistent heterogeneity of this supply results from falling carcasses of fish and mammals, macroalgae and phytodetritus, and from the interaction of accumulating particles with biogenic structures such as depressions, tests, mounds, tracks, fecal casts and traces, which impose roughness on the seabed.

CONCLUSIONS

The Atlantic Ocean has, without question, played a focal role in the development of deep-sea biology. Recent discoveries and long-term, time-series investigations have yielded the unexpected, making it clear that the Atlantic is a dynamic ocean whose inhabitants experience environmental variation over a wide range of spatial and temporal scales. The consequences of this forcing, in terms of taxonomic makeup, population dynamics and ecology, are clearly documented for microbial and protozoan forms, but these consequences are less clear for certain higher taxa. Within the Atlantic, the continental margins are among the most heterogeneous and biologically productive settings. They continue to be most heavily studied because of their proximity to population centers and their commercial potential (e.g., exploitation of fisheries, hydrocarbon resources). Despite this, knowledge of species composition and basic functional attributes is lacking for most places within the Atlantic, especially south of the equator. Given that the Atlantic is the best studied of the Oceans, this is true for all of the deep sea. It is evident that the Western and Eastern sides of the Atlantic have been studied independently, with a few notable exceptions. Similarly, the megabenthos, macrobenthos and meiobenthos, as well as the various taxonomic groups of benthic fauna, have been studied in isolation. Often the research focus and methodologies have differed. As a result, except for the issue of species diversity (see Stuart et al., Chapter 10, this volume), there have been only a few whole-basin syntheses for the Atlantic Ocean (see Sibuet et al., 1989; Rowe et al., 1991). Even patterns of species diversity have been addressed primarily for the macrofauna. This should change with increased potential for remote measurement in the deep sea, acquisition of large-scale synoptic data, dramatic technological advances in measurement capabilities *in situ,* and the tremendous improvement in speed and ease of communication between scientists in distant places. As with diversity, ocean-scale considerations of productivity, hydrodynamics, historical, geological, and chemical influences, as well as integration among biological components (micro, meio-, macro- and megafaunal; procaryotic and eucaryotic; microbial, invertebrate and ichthyofaunal) will certainly yield better understanding of the processes underlying biological pattern in this remarkable ocean.

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Chapter 6

THE DEEP PACIFIC OCEAN FLOOR

Craig R. SMITH and Amanda W.J. DEMOPOULOS

INTRODUCTION

The Pacific is a vast ocean, stretching 15 000 kilometers latitudinally from the Philippines to Panama, and 10 000 km longitudinally from the Southern Ocean to Alaska (Fig. 6.1). It is, by roughly a factor of two, the largest of all oceans, covering nearly a third of the Earth's surface. Because of its size, economic importance, and proximity to major oceanographic research centers, scientists have explored the deep Pacific since the *Challenger* Expedition of the 1870s. Portions of the deep Pacific seafloor (for example, the slope of California, USA) are thus well studied by deep-sea standards; nonetheless, many other regions of the deep Pacific are no better known than the surface of the moon.

In this chapter, we first review the general physical characteristics of the deep Pacific Ocean. We then discuss the distribution of key habitat variables, such as substratum type, bottom-water oxygen, and particulate organic-carbon flux, which affect the nature and abundance of life at the ocean floor. We describe the structure and function of a variety of representative habitat types (excluding hydrothermal vents and cold seeps, which are discussed Chapter 4), and speculate on their distribution in the deep Pacific. Finally, we offer some conclusions concerning the processes controlling ecosystem structure and function in the deep Pacific Ocean and identify research needs for the future.

PHYSICAL CHARACTERISTICS OF THE DEEP PACIFIC OCEAN

The Pacific Ocean, excluding its adjacent seas (e.g., the Coral, China and Bering Seas: see Chapter 8) covers roughly 166×10^6 km^2, encompassing 46% of the world ocean. Its average depth is 4190 m, exceeding the average ocean depth by about 12%.

The morphology of the Pacific Ocean differs from that of the other major oceans (the Atlantic and the Indian) in three important ways. (1) The Pacific is largely surrounded by deep ocean trenches abutting on linear mountain chains (e.g., the Andes of South America) or island arcs (e.g., the Aleutians and the Marianas) (Fig. 6.1). The trenches, which range in depth from 6700 to 11 000 m, form the deepest parts of the ocean, and 11 of the worlds' total of 14 trenches occur in the Pacific. Ocean trenches and the marginal seas behind island arcs act as sediment traps, largely isolating the deep basins of the Pacific from the influx of terrigenous (i.e., continental) sediments. Another factor contributing to limited terrigenous sedimentation in the Pacific is a low rate of river discharge; the largest discharges of riverine sediments (e.g., from the Ganges, Yellow, Indus and Amazon) are into the Atlantic and Indian Oceans, or into marginal seas (Berner, 1982; Kennett, 1982). As a consequence, the Pacific lacks the large deposits of terrigenous sediments that form smooth continental rises and abyssal plains in the Atlantic and Indian Oceans. The margins of the Pacific Ocean are instead typified by narrow continental shelves and steep slopes, frequently dissected by submarine canyons. In place of abyssal plains covered by thick sediments, the basin floor in most of the Pacific (85%) consists of abyssal hills with heights of less than 1000 m and widths of 1 to 10 km, blanketed by less than 100 m of sediment (Kennett, 1982).

Other distinctive morphological features of the Pacific include (2) vast, continuous expanses of abyssal seafloor and (3) an abundance of islands and seamounts (Fig. 6.1). Unlike the Atlantic and Indian Oceans, which are subdivided into a number of basins by long

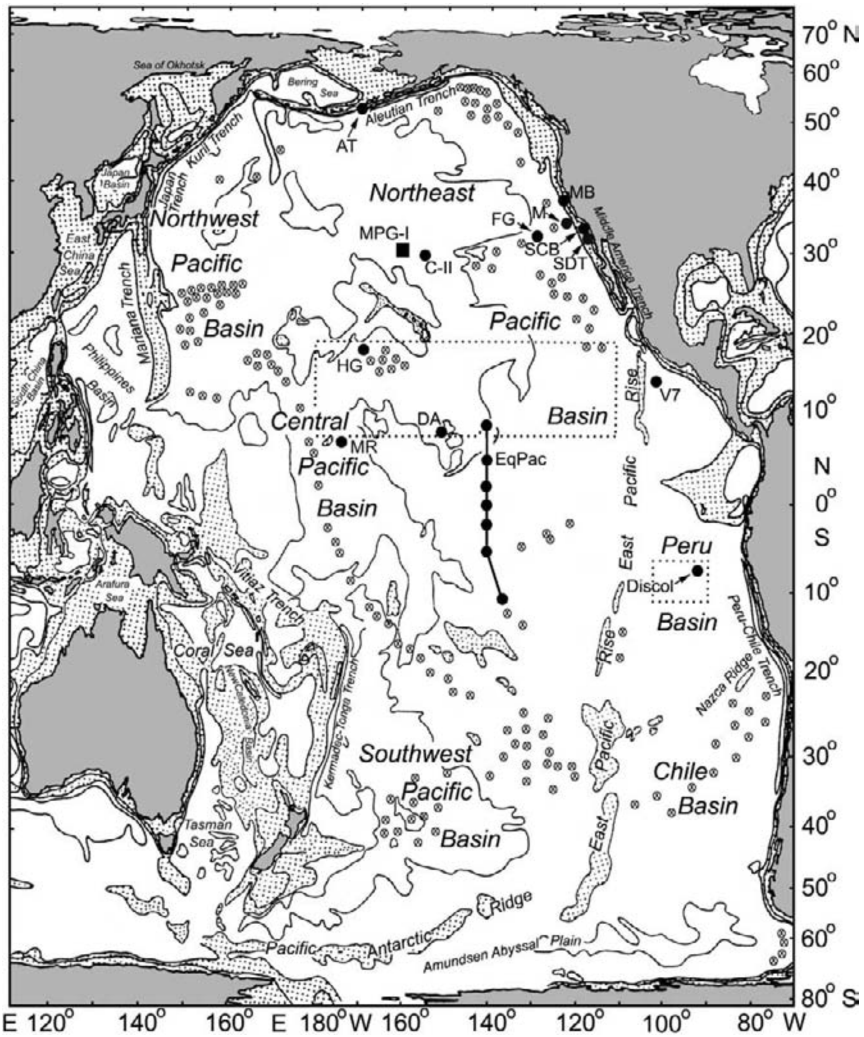

Fig. 6.1. Topography of the Pacific Ocean. The 1000, 3000 and 5000 m isobaths are shown, with regions shallower than 3000 m stippled. Regions of abundant seamounts are indicated by circles with crosses. Dotted boxes enclose areas of maximum commercial and strategic interest for manganese-nodule mining. Also indicated are study sites discussed in this chapter as follows: AT, Aleutian Trench site of Jumars and Hessler (1976); C-II, the Climax II site of Hessler and Jumars (1974); DA, Domes Site A (Paterson et al., 1998): DISCOL (Borowski and Thiel, 1998); EqPac, the US JGOFS Equatorial Pacific Transect (C.R. Smith et al., 1997); FG, Fieberling Guyot; HG, Horizon Guyot; M, Station M of K.L. Smith et al. (1992); MB, California slope site of Reimers et al. (1992); MPG-I, the Mid-Plate, Mid-Gyre area of K.L. Smith (1992); MR, Magellan Rise; SCB, Santa Catalina Basin (e.g., C.R. Smith, 1985); SDT, San Diego Trough (Thistle, 1978); V 7, Volcano 7 (Wishner et al., 1990).

sections of the mid-ocean ridge, only the southeastern corner of the Pacific is fenced off by a ridge system (in this case the East Pacific Rise, 9000 km long that rises roughly 2000 m above the abyssal seafloor to isolate the Peru and Chile Basins). The remainder of the abyssal Pacific basin is essentially continuous, although for convenience portions of this enormous area are called the Southwest, Central and Northeast Pacific Basins (Fig. 6.1). The Pacific abyss is peppered with tens of thousands of islands and seamounts, especially in the central and western regions [in contrast, the entire Atlantic has less than 900 seamounts (Rogers, 1994)]. These seamounts and islands rise at least 1000 m above the seafloor and usually result from vulcanism, testifying to high levels of volcanic activity in the Pacific basin.

The near-surface circulation of the Pacific Ocean has several features of major relevance to deep-

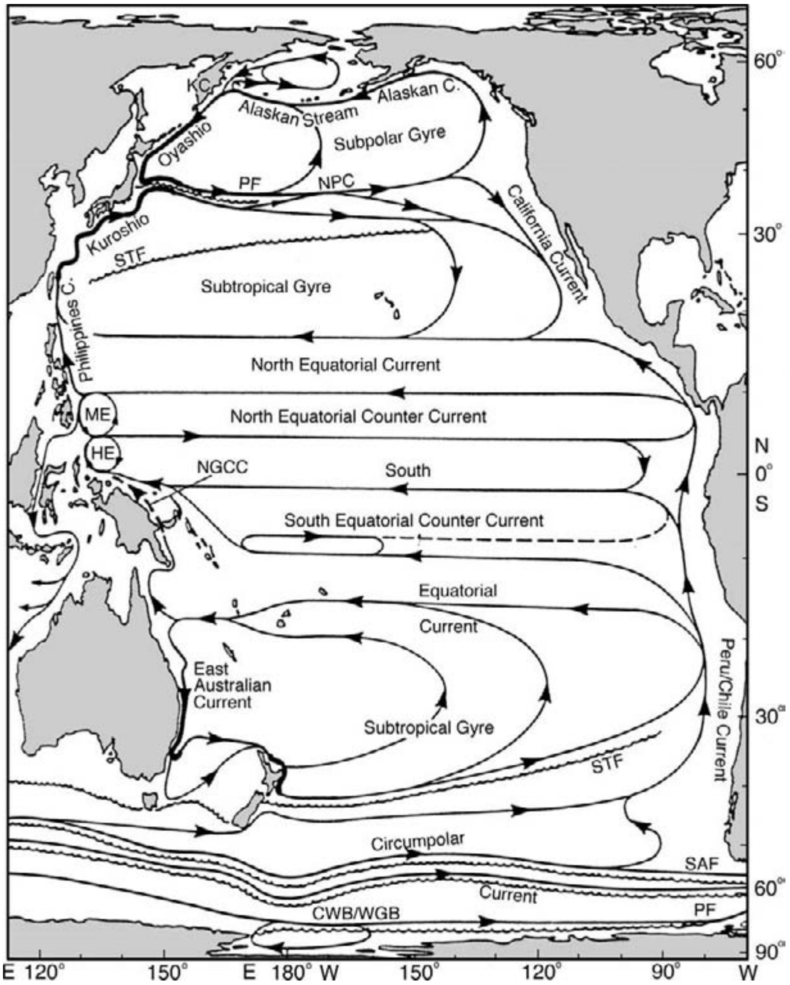

Fig. 6.2. Major surface currents of the Pacific Ocean. Abbreviations are as follows: PF, Polar Front; NPC, North Pacific Current; ME, Mindanao Eddy; HE, Halmahera Eddy; NGCC, New Guinea Coastal Current; STF, Subtropical Front; SAF, Subantarctic Front; CWB/WGB, Circumpolar Water Boundary/Weddell Gyre Boundary. Modified from Tomczak and Godfrey (1994).

sea ecosystems. The presence of large, anticyclonic subtropical gyres between roughly 20 and 40 degrees of latitude in both the North and South Pacific (Fig. 6.2) produces vast downwelling regions. In these "oligotrophic" central gyres, nutrient-bearing waters are suppressed far below the euphotic zone, severely limiting phytoplankton production and yielding a very small flux of particulate organic carbon (or "food") to the deep-sea floor. Another major feature is the presence of western boundary currents (the Kuroshio and the East Australian Current) bounding the western side of each gyre. These currents can flow at relatively high velocity, and scour sediments to ocean depths of ~1500 m along the continental slope. Where the western boundary currents turn eastward into the open Pacific and lose the steering effects of the continental slope, current meanders and high eddy energy are generated to great depths (Tomczak and Godfrey, 1994). In comparable regions of the Gulf Stream in the North Atlantic, such eddy energy intermittently produces currents capable of eroding fine sediments at water depths exceeding 4000 m (Hollister and McCave, 1984; see also Chapter 2). There is good reason to expect similar, high-energy benthic boundary layers to be associated with the Kuroshio and, possibly, the East Australian currents in the Pacific Ocean (Hollister and McCave, 1984).

A third feature of Pacific surface currents that ultimately influences the deep-sea floor is the upwelling of nutrient-rich waters along the equator, and along the eastern boundaries of the North and South Pacific. Near the equator, easterly trade winds impose a westward stress on surface waters. Because of the Coriolis force, this stress is converted to northward water transport in the northern hemisphere and southward transport in the southern hemisphere, producing a divergence of surface waters and upwelling of deep waters laden with nutrients (including iron) along the equator (Tomczak and Godfrey, 1994; Landry et al., 1997). The upwelled nutrients stimulate phytoplankton production, yielding a band of high primary productivity within a few degrees of the equator, extending from 90ºW to 160ºW (Longhurst et al., 1995); the underlying abyss in turn experiences an enhanced flux of particulate organic carbon from biogenic particles sinking from the productive equatorial euphotic zone (Honjo et al., 1995; Smith et al., 1997). In addition to upwelling, the equatorial zone is often characterized by high current velocities (up to 20 cm s^{-1}) to depths of at least 1500 m (Tomczak and Godfrey, 1994).

Similar, but more intense, upwelling occurs along the eastern boundary of the Pacific along the coast of South America from 10 to 43ºS, and along the coast of the American states of Washington, Oregon and California in the northern hemisphere (Tomczak and Godfrey, 1994). This eastern boundary upwelling is caused by equatorward, longshore winds in the coastal zone, which result in offshore transport of surface waters because of Coriolis forces. Surface water transported offshore is replaced by upwelling of nutrient-laden deeper waters, yielding a band of very high phytoplankton production within about 100 km of the coast. The Peru–Chile upwelling system is the most intense in the World Ocean and yields a massive flux of sinking particulate organic carbon to the shelf and slope of South America. Near the equator, the Peru–Chile and equatorial upwelling systems merge to yield high levels of primary production, and a deep flux of particulate organic carbon, throughout the eastern equatorial Pacific. The upwelling system off the west coast of North America is seasonal (occurring from April to September) and is less intense, but it still causes a high flux of particulate organic carbon to the continental slopes of the states of Washington, Oregon and California. Shelf and slope waters beneath these upwelling zones frequently are depleted of oxygen as a result of high rates of degradation of particulate organic carbon, and the underlying sediments typically are organic-rich.

Water masses in contact with the floor of the deep Pacific Ocean consist of three general types. Below depths of 3000 m, the Pacific seafloor is bathed in Antarctic Bottom Water – that is, very cold (0.5–1.5ºC), relatively saline water formed predominantly in the Weddell and Ross Seas during sea ice formation in the Austral winter (Sverdrup et al., 1942; Tomczak and Godfrey, 1994). This bottom water spills down the slope of the Antarctic continent and circumnavigates the globe in the Southern Ocean before moving northward along the western margin of the Pacific and slowly spreading eastward to cover the abyssal Pacific seafloor. Between depths of 1000 and 3000 m, the Pacific is filled with Pacific Deep Water formed by slow mixing of Antarctic Bottom Water, North Atlantic Deep Water advected from the North Atlantic Ocean, and Intermediate Water from depths of less than 1000 m (Tomczak and Godfrey, 1994). In the North Pacific, much of the Deep Water may have last contacted the atmosphere and taken up oxygen more than 1000 years ago; as a consequence, this water mass has relatively low levels of oxygen (although typically not low enough to be biologically stressful). Between depths of 500 m and 1000 m, the Pacific is filled with Intermediate Water formed in either the Antarctic or Arctic polar frontal regions, which occur at roughly 60ºS and 40ºN, respectively. These intermediate waters meet and upwell near the equator, and are characterized by relatively low salinity and temperatures that are warm (>3ºC) by deep-sea standards (Tomczak and Godfrey, 1994). In the northern hemisphere, the intermediate waters are often formed by subsurface mixing (i.e., they are not in atmospheric contact during formation) and thus may be relatively depleted in oxygen, contributing to formation of the oxygen-minimum zone (see below, pp. 184–185).

KEY HABITAT VARIABLES AND THEIR REGIONAL VARIATION IN THE PACIFIC

Several habitat variables play key roles in regulating the nature and abundance of life on the deep-sea floor. These include (1) substratum type (e.g., rocky *versus* soft sediments), (2) near-bottom current velocities, (3) bottom-water oxygen content, and (4) the vertical flux of particulate organic carbon to the seafloor.

Substratum type

Substratum type controls, or at least is correlated

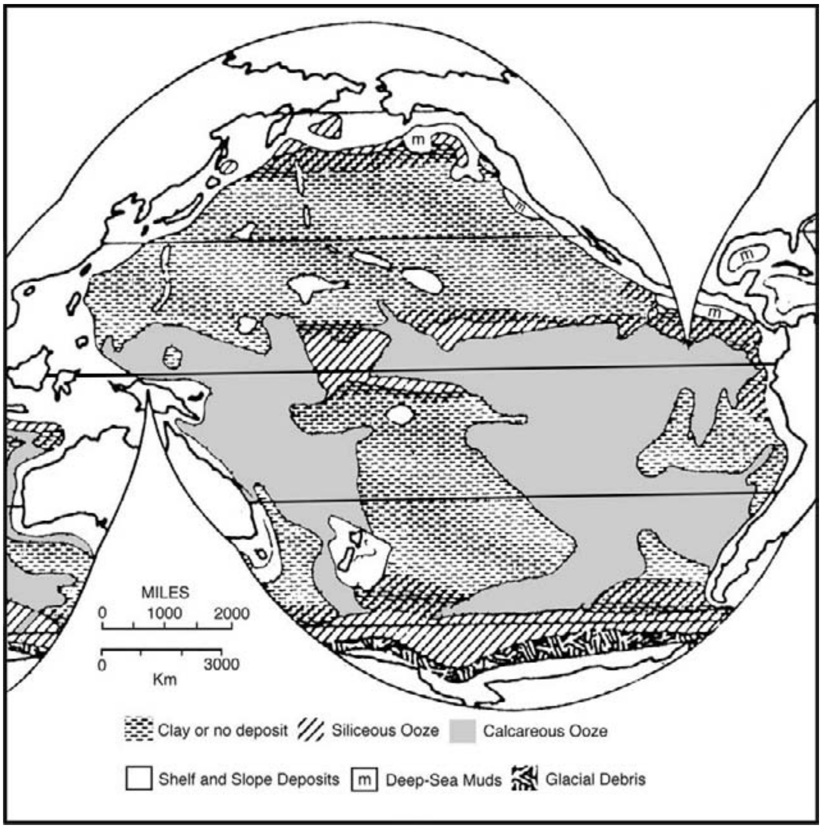

Fig. 6.3. Distribution of surface-sediment types in the deep Pacific Ocean. Modified from Berger (1974).

with, many characteristics of deep-sea benthos, including predominant taxa, mobility patterns and feeding types (see Table 2.3). For example, hard, rocky substrata in the deep sea frequently are dominated by sessile suspension-feeding sponges, cnidarians, and Foraminifera. Organic-poor soft sediments predominantly harbor speciose assemblages of mobile, deposit-feeding polychaetes and nematodes, while organic-rich sediments may contain a few species of tube-dwelling polychaetes (Levin and Gage, 1998).

Most of the deep Pacific seafloor is covered with soft sediments. Along the continental margins, the sediment is mainly terrigenous mud consisting of mineral grains eroded from continents, combined with diatom fragments, the calcareous tests of planktonic Foraminifera, minute pieces of vascular plants, and many other particle types (Fig. 6.3; see also Berger, 1974). Terrigenous muds are relatively high in organic-matter content, typically containing 1–2% organic carbon by weight (Jahnke and Jackson, 1992). Beneath coastal upwelling sites and within oxygen-minimum zones, such sediments may contain much higher levels of organic carbon (2%–18%).

In the open Pacific Ocean, depths less than 4000 m are "snow-capped" – that is, they are covered by white sediments composed largely of the sunken calcareous tests of pelagic foraminiferans and pteropods (Berger, 1974). Calcareous sediments are also found within 5° of the equator to depths of 4600 m. Calcareous sediments often are relatively coarse-grained, containing many more sand-sized particles than most deep-sea sediments, and typically are poor in organic material; the content of organic carbon rarely exceeds 0.3% by weight (Berger, 1974; Jahnke and Jackson, 1992). At depths greater than 4600 m beneath productive waters (e.g., along 50°N at the Arctic Divergence and along the equator west of 170°W), siliceous muds composed of diatom and radiolarian tests predominate, with organic-carbon contents between 0.25% and 0.5%. Red clays are found below depths of 4000 m in the central gyres of the North and South Pacific (Fig. 6.3); these sediments are extremely fine-grained (median grain size <2 µm) and poor in organic material

(<0.25% organic carbon), consisting primarily of clay particles transported by wind from continents and volcanic eruptions (Berger, 1974).

Hard substrata in the deep Pacific Ocean are of three major types. (1) Basalt rocks predominate within 1–2 kilometers of the central valley of the East Pacific Rise, where oceanic crust is too new to have accumulated sediments. (2) Rock faces with slopes >22° typically are bare because they are too steep to allow sediment accumulation. Such faces are most common along continental margins (e.g., in submarine canyons) and on the steep slopes of the islands and seamounts that dot the Pacific. (3) The surfaces of ferromanganese concretions, or manganese "nodules" resting on the sediment surface also typically are sediment-free. Such nodules are found predominantly in red-clay regions of the Pacific, range in size from 0.5 to 20 cm in diameter, and may cover more than 60% the plan area of the seafloor.

Near-bottom currents

Near-bottom currents fundamentally influence the nature of benthic habitats (Nowell and Jumars, 1984; see also Thistle, Chapter 2). Under conditions of very low flow, the horizontal flux of particles near the seafloor may be inadequate to sustain suspension feeders (Jumars and Gallagher, 1982) and chemical exchange between bottom water and the seabed may be limited by molecular diffusion (Archer et al., 1989). At high current velocities, sediments may be eroded and transported, flooding suspension feeders with non-nutritive mineral grains and burying sessile organisms (Aller, 1989; Nowell et al., 1989). At intermediate flow velocities, less dense particles, such as recently settled phytoplankton, may be mobilized by currents and deposited in pits and behind flow obstructions, yielding food-rich patches (Lampitt, 1985; Yager et al., 1993; Smith et al., 1996). In short, near-bottom flow rates and bed shear stress may influence a broad range of ecologically significant physical, chemical and biological processes (see Nowell and Jumars, 1984 for a review).

Currents in the relatively flat areas of the deep Pacific seafloor, such as the vast regions of abyssal hills, are generally sluggish, imposing shear stresses inadequate to transport most sediment types. However, currents of erosive magnitudes may occur in certain deep-sea environments as a consequence of boundary currents, high eddy energy or topographic intensification. The Kuroshio and East Australian western boundary current systems (Fig. 6.2) likely cause intermittent erosion of sediments to water depths of 1500 m along the western margins of the Pacific, although the sites and frequencies of such erosive events are very difficult to predict. In addition, the region of Kuroshio separation from the Japan slope is characterized by high eddy energy (Hollister and McCave, 1984; Hollister et al., 1984); intermittent "storms" at intervals of days to months, which erode and redeposit several centimeters of abyssal sediments, are thus to be expected in this area. Relatively high-velocity currents also occur, at least occasionally, in submarine canyons as a result of storms or tides (Shepard and Dill, 1966; Vetter and Dayton, 1998), and through channels (e.g., transform faults) and around peaks (e.g., seamounts) owing to acceleration of tidal flows (Genin et al., 1986). The frequency and intensity of such high-energy flows are typically very site-specific, and depend on the interactions of local tides, bottom topography and low-frequency flow events (e.g., upwelling and Taylor circulation: Genin et al., 1986; Gage and Tyler, 1991).

Bottom-water oxygen

All deep-sea animals require oxygen as an electron acceptor for oxidative metabolism. When bottom-water oxygen concentrations fall below $0.5\,\mathrm{ml}\,\ell^{-1}$ in the deep sea, oxygen availability becomes an important factor and benthic community structure varies with oxygen concentration (Diaz and Rosenberg, 1995; Levin and Gage, 1998). Above this threshold, other factors control the nature and abundance of seafloor life. On most of the deep Pacific seafloor, bottom-water oxygen concentrations exceed the threshold of $0.5\,\mathrm{ml}\,\ell^{-1}$. However, beneath relatively productive waters, such as the eastern tropical Pacific and in coastal upwelling zones, an oxygen-minimum zone may develop in the water column, with oxygen concentrations approaching zero at depths between 100 and 1000 m (Wishner et al., 1990). This zone results from the oxidation of organic particles sinking through the water column from the highly productive euphotic zone; in the North Pacific the oxygen-minimum zone is often particularly well developed owing to the old "age" (i.e., time since surface ventilation) and consequent low oxygen concentrations of Intermediate and Deep Water masses. Where this oxygen minimum intersects the seafloor, bottom-water oxygen concentrations may drop to zero (Wishner et al., 1990). Oxygen-stressed habitats formed in this manner are common on the California slope between depths of 500 m and 1000 m (Emery, 1960; Reimers et al., 1992; see also Fig. 2.4 in Chapter 2), in the eastern tropical Pacific between roughly 100 and 1000 m (Wishner et al., 1990), and along the Peru–Chile margin at depths of tens to hundreds of meters (Diaz and Rosenberg, 1995). Partially enclosed basins may also contain bottom water with little or no oxygen at depths far below the oxygen-minimum zone if the deepest point of entry into the basin (i.e., its sill depth) falls within this zone; this is because the densest water entering the basin comes from the sill depth, and thus fills all deeper levels. Several such low-oxygen basins (e.g., the Santa Barbara, Santa Monica and San Pedro Basins) occur in the borderland region off southern California (Emery, 1960).

Sinking flux of particulate organic carbon

The primary source of food material for deep-sea communities, excluding hydrothermal vents and cold seeps, appears to be the rain of organic particles, ranging from individual phytoplankton cells to dead whales, sinking from the euphotic zone (Chapter 2). The organic matter in the smaller of these particles degrades and is consumed by midwater animals during transit through the water column, generally yielding a very low flux of food to the deep-sea floor. Consequently, benthic assemblages of the abyss are among those with the poorest supply of food and the smallest biomass on the Earth's solid surface. As might be expected in an energy-poor ecosystem, the total biomass in many size-classes of benthos (e.g., the meiofauna, macrofauna and megafauna) on the deep-sea floor often is correlated with the annual rate of the rain of particulate organic carbon (Fig. 6.4; Rowe et al., 1991; C.R. Smith et al., 1997). In fact, it has been suggested that the biomass in certain benthic size classes, in particular the macrofauna, might be useful as an index of the annual flux of labile particulate organic carbon to the deep-sea floor (C.R. Smith et al., 1997); time series monitoring of abyssal benthic biomass might be employed, for example, to elucidate changes in the deep flux of particulate organic carbon (and the oceanic carbon cycle) in response to global climate change.

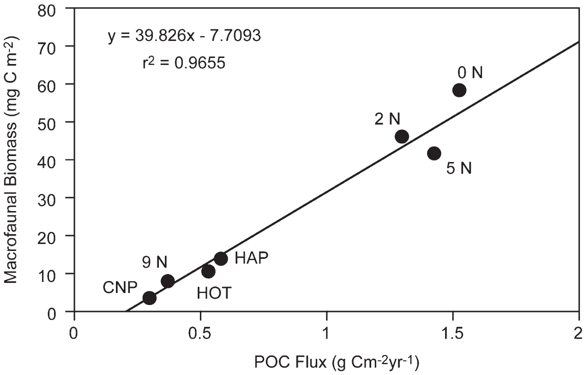

Fig. 6.4. Macrofaunal biomass (wet weight) in underlying sediments plotted against the annual flux of particulate organic carbon to sediment traps moored 600–800 m above the seafloor. Data come from: (1) the equatorial Pacific along the 140ºW meridian at 0º, 2º, 5º and 9ºN (C.R. Smith and R. Miller, unpublished data); (2) the **H**awaii **O**cean **T**ime-Series (HOT) Station just north of Oahu, Hawaii (C.R. Smith and R. Miller, unpublished data); (3) the oligotrophic **C**entral **N**orth **P**acific (CNP) at 31ºN, 159ºW (K.L. Smith, 1992); and (4) the Hatteras Abyssal Plain (HAP) in the North Atlantic (Rowe et al., 1991), included to illustrate that the biomass versus flux pattern is likely to be a general oceanic deep-sea phenomenon. Only stations more than 1000 km from the nearest continent are included, to minimize the influence of downslope transport of organic matter produced in the coastal zone.

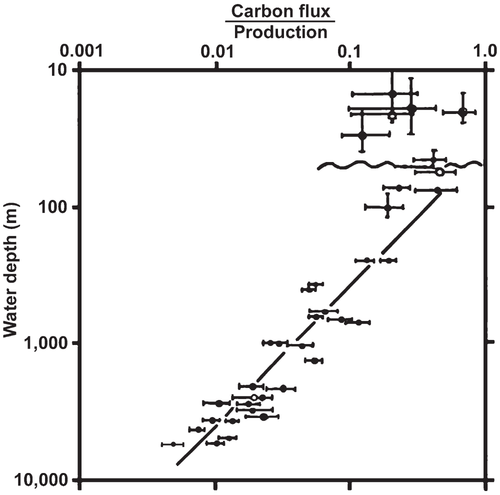

Fig. 6.5. Ratio of the sinking flux of particulate organic carbon to primary production in the euphotic zone (above the wavy line) as related to water-column depth, based on sediment-trap studies in the world ocean (data points). (Figure modified from Suess, 1980.)

Two factors exert primary control on the sinking flux of particulate organic carbon to the ocean floor (Fig. 6.5): these are the annual primary productivity in the overlying euphotic zone and, less importantly, the depth of the water column (Suess, 1980; Smith and Hinga, 1983; Jahnke, 1996). Thus, along continental slopes where coastal productivity is high and the water column relatively shallow, particulate organic carbon rains to the seafloor at high annual rates – for instance, ~10 g C m^{-2} y^{-1} at 1000 m on the California slope (Smith and Hinga, 1983). At abyssal depths (4000–6000 m) beneath productive waters (e.g., the California Current or the equatorial upwelling zone), the annual flux of particulate organic carbon declines to roughly 1–3 g C m^{-2} y^{-1} (K.L. Smith et al., 1992; C.R. Smith et al., 1997). Beneath the vast oligotrophic gyres (see Chapter 2, Fig. 2.13) where the water column is deep (>5000 m) and annual primary production very low, the annual flux of particulate organic carbon may be as little as 0.3 g C m^{-2} y^{-1} (K.L. Smith, 1992).

REPRESENTATIVE DEEP PACIFIC HABITATS

Continental slopes and marginal basins

Continental-slope and marginal-basin habitats surround the Pacific at water depths from 200 m to 4000 m. Habitat conditions vary dramatically over spatial scales of tens to thousands of kilometers along these slopes, yielding a broad array of communities. For example, the sinking flux of particulate organic carbon typically decreases more than three fold as depth increases from 500 m to 4000 m (Martin et al., 1987; Berelson et al., 1996). Substratum and current velocities differ dramatically from depositional fans, where sediments often are muddy and currents sluggish, to submarine canyons, where rocky outcrops and erosive currents abound. In the eastern Pacific, the oxygen minimum is superimposed on this topographically induced complexity, yielding a layer of oxygen-stressed habitats between ocean depths of 100 m and 1000 m. Below we discuss several habitat types found in slope regions: depositional slopes and basins, canyons, and oxygen-minimum zones.

Depositional slopes and basins on the California margin

The best studied slopes and basins occur along the margin of the American state of California, where deep benthic ecosystems have been intensively investigated since the late 1950s (Emery, 1960). The general patterns here are almost certainly representative of Pacific slopes in general, although specific details (e.g., species identities, absolute flux rates of particulate organic carbon, intensity of the oxygen-minimum zone) may vary with geographic location.

Habitat and community description: Along the open California slope, in areas of relatively low current velocity, sediments generally grade from sandy on the upper slope (~200 m to 600 m) to soft muds at greater depths (Emery, 1960; Reimers et al., 1992; Vetter and Dayton, 1998). The borderland basins off southern California, formed by a series of ridges and troughs parallel to the coastline, are floored predominantly by fine muds at depths from 1000 m to 2000 m. Muddy surface sediments in these slope habitats are heavily modified by biological activity, which forms a patina of animal tracks, trails, mounds, tubes and fecal casts on the seafloor (Fig. 6.6a; see also Jumars, 1975; Thistle, 1979b; Smith and Hamilton, 1983). Many of these biogenic structures are surprisingly dynamic, being formed and destroyed by faunal activity rather than by water flow. In the 1240 m-deep Santa Catalina Basin, the fecal mounds of echiurans (5–10 cm high and 30 cm across) can grow several centimeters in height in 100 hours (Smith et al., 1986); when abandoned, the mounds disappear within 11 months as a consequence of sediment reworking by brittle stars and other benthos (Kukert and Smith, 1992). Smaller structures, such as gastropod trails or fecal casts of holothuroids, are erased from the basin floor by brittle stars within a few weeks (Wheatcroft et al., 1989). Thus, much of the biogenic structure of the sediment–water interface appears to change many times during the life spans (years to decades) of macro- and megabenthos on the California margin.

The California slopes and basins harbor richer benthic assemblages than more oligotrophic settings, such as the North Pacific central gyre. Epibenthic megafauna (animals greater than 2 cm in smallest dimension) often are abundant, attaining densities from 0.3 to 17 individuals m^{-2} (Table 6.1; see also Smith and Hamilton, 1983; Bennett et al., 1994; Lauerman et al., 1996). Echinoderms are particularly common, with brittle stars (e.g., *Ophiomusium lymani*, *Ophiophthalmus normani*) and holothuroids (e.g., the “sea pig” *Scotoplanes globosa*) dominating the megafauna (Barham et al., 1967; C.R. Smith and Hamilton, 1983; Lauerman et al., 1996), and at times attaining high biomasses (e.g., a mean of 67±30 g wet weight m^{-2} in the Santa Catalina Basin). In addition to the dominant echinoderms, many other taxa are represented in the megafauna, including gastropods (e.g., neptunids and trochids), hexactinellid sponges, fishes (macrourids, zoarcids, and hagfish), decapods and galatheids (Smith and Hamilton, 1983; Wakefield, 1990; Lauerman et al.

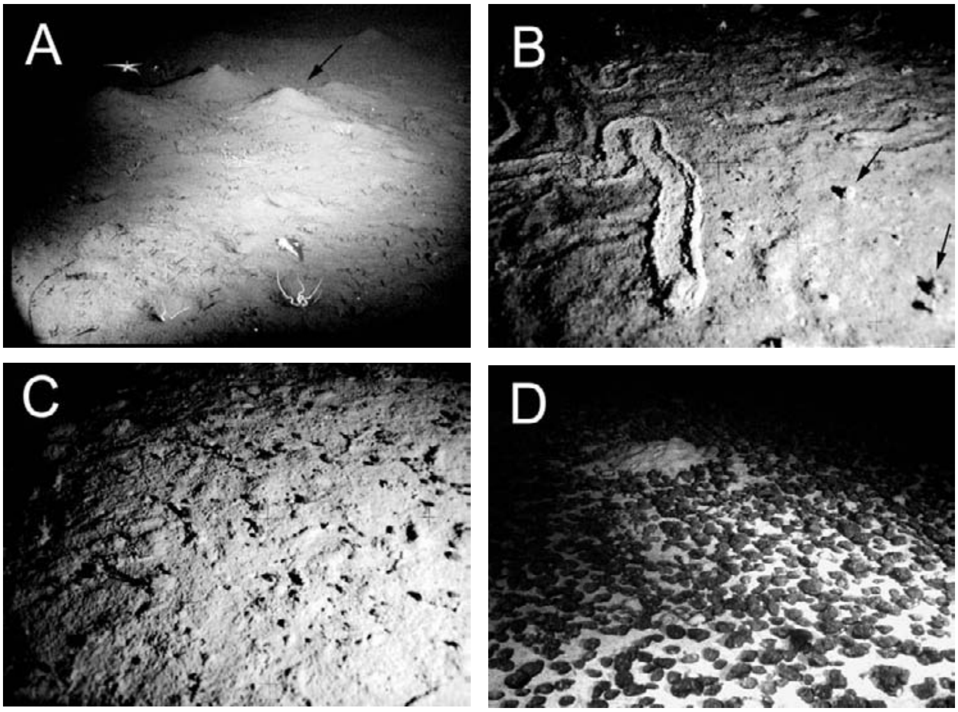

Fig. 6.6. Seafloor photographs from representative deep-sea habitats in the Pacific Ocean. (A) A basin habitat on the continental margin, the Santa Catalina Basin floor at a depth of 1240 m. Note the abundant echiuran mounds (roughly 30 cm in diameter; arrow), ophiuroids (*Ophiophthalmus normani*), and the rockfish (*Sebastolobus altivelis*) in the foreground. Muddy "twig-like" structures are tests of agglutinating foraminiferans. (B) The eutrophic, equatorial-Pacific seafloor at 2°N, 140°W, water depth 4400 m. Note the burrowing urchin and urchin furrow (roughly 10 cm wide) in the left foreground, and the xenophyophores (arrows) visible as "lumps" of sediment. (C) The mesotrophic seafloor at a depth of 5000 m in equatorial Pacific at 9°N, 140°W. Only centimeter-scale worm tubes and centimeter long manganese nodules (black objects) generally are visible. (D) The seafloor of the North Pacific central gyre (depth 5800 m), at approximately 31°N, 158°W. Manganese nodules (roughly 5 cm in diameter) cover much of the sediment surface, and decimeter-scale biogenic structures are rare. Very occasionally, large biogenic sediment mounds (30–50 cm in diameter) are observed, like that in the background.

1996). For those areas studied in detail [e.g., the Santa Catalina Basin (Fig. 6.1) (Smith and Hamilton, 1983) and the base of the central California slope at 4100 m (Station M, Fig. 6.1) (Lauerman et al., 1996; Beaulieu, 2002)], more than 50 megafaunal species have been recorded within a site.

The macrobenthos (i.e., animals passing through a 2 cm trawl mesh but retained on a 300 μm sieve) of the California slopes and basins consists of a high diversity of taxa, especially polychaetes, agglutinating foraminifera, bivalves, cumaceans, tanaids, and enteropneusts (Jumars, 1975; Levin et al., 1991a; Kukert and Smith, 1992). Macrofaunal community abundance (5000 to 10 000 m^{-2}: Table 6.1) and biomass (4 to 8 mg wet weight m^{-2}) (K.L. Smith and Hinga, 1983; C.R. Smith and Hessler, 1987) are low relative to most shelf communities; but local species diversity on the California slope can be extraordinarily high. For example, at 1230 m depth in the San Diego Trough (Fig. 6.1), a sample of 50 macrofaunal polychaetes is likely to contain more than 30 species (Fig. 6.7) and a 0.25 m^2 patch of seafloor typically contains more than 100 species of macrofauna (Jumars and Gallagher, 1982). In contrast, a typical soft-sediment intertidal assemblage includes fewer than 50 species in an area of 0.25 m^2 (Snelgrove and Smith, 2002). In fact, local macrofaunal diversity of California slope sediments is high even by deep-sea standards and rivals that of structurally much more complex, species-rich habitats such as coral reefs (Snelgrove and Smith, 2002).

The meiobenthos (animals passing through a 300 μm sieve and retained on one of 42 μm) are an abundant but relatively poorly studied component of the slope benthos. Nematodes, calcareous and agglutinating Foraminifera, and harpacticoid copepods abound in this size class, with Foraminifera and nematodes probably

Table 6.1

Approximate ranges in the values of some key ecological variables in representative benthic ecosystems in the deep Pacific Ocean

Ecosystem type	Study depths (m)	POC flux ($\mathrm{g\,C\,m^{-2}\,y^{-1}}$)	Sediment C_{org} respiration ($\mathrm{g\,C\,m^{-2}\,y^{-1}}$)	Macrofaunal abundance ($\mathrm{no.\,m^{-2}}$)	Macrofaunal biomass ($\mathrm{g\ wet\ wt.\,m^{-2}}$)	~Median macrofaunal body size (mg)	Megafaunal abundance ($\mathrm{no.\ m^{-2}}$)	Megafaunal biomass ($\mathrm{g\ wet\ wt.\,m^{-2}}$)	^{210}Pb bioturbation coefficient ($\mathrm{cm^2\,y^{-1}}$)	Animal trace disappearance time (months)[26]
Continental Margin										
Oxygenated slopes/basins off California	1000–3500	4–10[14,24]	3–10[3,15,24]	5000–10 000[20,24]	4–8[24]	0.8	7–16[1,2]	68[19]	0.3–0.6[16]	0.5–2[25]
Oxygen minimum zone, Volcano 7	730–1000			1000–14 000[13]			0–8.5[13]			
Base of California slope	3800–4100	3–10[22,24]	3.6–9[15,22,24]		2–24[5,24]		2.7–4.0[12]			~3[23]
Eutrophic Abyss										
Equatorial upwelling zone (5ºS–5ºN, 140ºW)	4200–4450	0.9–1.8[10]	1–3[8]	1200–2000[18]	0.4–0.6[18]	0.3	0.17–0.25[18,27]		0.1–0.9[4,16,18]	> 4[7]
Mesotrophic Abyss										
Equatorial North Pacific (9–10ºN, 140ºW)	4500–5000	~0.4[10]	0.3–1.7[8]	285–290[18]	~0.12[18]	0.4	~0.10[18,28]		<0.1[4,18]	>12[7]
Oligotrophic Abyss										
Central North Pacific (28–31ºN, 155–159ºW)	5600–5800	~0.3[21]	0.3–1.0[21]	84–160[9]	~0.08[21]	0.07	~0.15[21]	~0.6[21]		
Aleutian Trench	7298			1272[11]						

[1] Barham et al. (1967)
[2] Bennett et al. (1994)
[3] Berelson et al. (1996)
[4] Cochran (1985)
[5] Drazen et al. (1998)
[6] Dymond and Collier (1988)
[7] Gardner et al. (1984)
[8] Hammond et al. (1996)
[9] Hessler and Jumars (1974)
[10] Honjo et al. (1995)
[11] Jumars and Hessler (1976)
[12] Lauerman et al. (1996)
[13] Levin et al. (1991b)
[14] Martin et al. (1987)
[15] Reimers et al. (1992)
[16] C.R. Smith et al. (1993)
[17] C.R. Smith et al. (1996)
[18] C.R. Smith et al. (1997)
[19] Smith and Hamilton (1983)
[20] C.R. Smith and Hessler (1987)
[21] K.L. Smith (1992)
[22] K.L. Smith et al. (1992)
[23] K.L. Smith et al. (1993)
[24] K.L. Smith and Hinga (1983)
[25] Wheatcroft et al. (1989)

[26] The time required, in physically quiescent habitats, for animal traces on the millimeter–centimeter scale to disappear due to the sediment-mixing activities of benthos.

[27] 1.9–5.9 with xenophyophores.

[28] ~2.35 with xenophyophores.

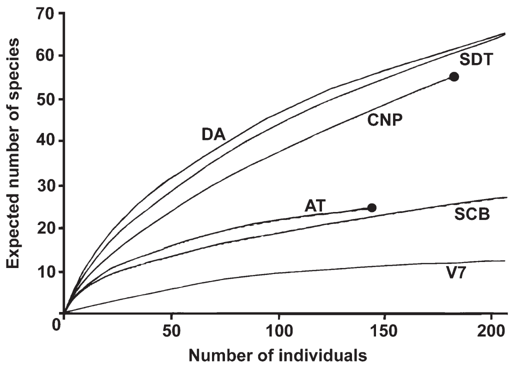

Fig. 6.7. Species rarefaction curves for macrofaunal polychaetes (roughly 50–65% of the total macrofaunal community) from Domes Site A (DA, 5035 m depth in the mesotrophic equatorial Pacific, ~8ºN, 151ºW), San Diego Trough (SDT, 1220 m depth on the California margin), the central North Pacific (CNP, the CLIMAX II site at 5100 m in the oligotrophic central North Pacific), the Aleutian Trench (AT, 7298 m depth), the Santa Catalina Basin (SCB, 1240 m depth on the California margin), and Volcano 7 (V 7, 750 m depth in the oxygen-minimum zone of the eastern equatorial Pacific). Data for SDT, CNP, AT and SCB are from Jumars and Gallagher (1982), for DA from Paterson et al. (1998) and for V 7 from Levin and Gage (1998).

the most abundant. The Foraminifera and Nematoda may contain a significant amount of biomass and undoubtedly a substantial number of species. For example, Bernhard (1992) painstakingly analyzed a small number of core samples and found foraminiferal biomasses ranging from 0.13 to 83 g C m^{-2} on the central California slope at depths of 620 to 3700 m. This is roughly equivalent to a wet-weight biomass between 2.6 and 1700 g m^{-2}, suggesting that foraminiferal biomass may approach, and even substantially exceed, that found in the macrofaunal and megafaunal size categories from similar depths. The agglutinating Foraminifera, which often are macrofaunal in size (Levin et al., 1991a), also contribute markedly to the small-scale physical structure of muddy slope habitats (Thistle, 1983), in some areas producing a "grassy" texture on the seafloor (Smith and Hamilton, 1983; Levin et al., 1991a). The contribution of harpacticoids to community structure also cannot be ignored, for they can attain both high abundances and local species diversity; for example, Thistle (1979a) counted 3940 individuals distributed among 140 harpacticoid species within a total sample area of only 0.14 m^2 at 1200 m depth in the San Diego Trough.

The sediment microbes, or nanobenthos (i.e., organisms <42 μm, including Bacteria, Archaea, yeasts, ciliates, flagellates, and amoebae), clearly constitute an important but poorly evaluated component of the slope benthos (e.g., Burnett, 1979, 1981). Limited studies suggest that California slope sediments harbor microbial biomasses high by the standards of the deep sea, and even of shallow water. For example, in the Santa Catalina Basin, direct bacterial counts using epifluorescence microscopy reveal abundances of about 10^9 per gram of sediment (Smith et al., 1998; A. Jones and C.R. Smith, unpublished data), which are roughly comparable to those at depths of 18 m in the Kieler Bucht (Meyer-Reil, 1987).

Unfortunately, we know of no slope station off California where the biomass distribution of the total benthic community (megafauna, macrofauna, meiofauna and nanobenthos) has been measured (cf., Rowe et al., 1991; K.L. Smith, 1992). The most complete data appear to come from the Santa Catalina Basin (Fig. 6.1), where the ratios of biomass between megafauna, macrofauna, agglutinating Foraminfera and microbial species are roughly 70:6:0.2:1 (based on Smith and Hamilton, 1983 for megafauna; Smith and Hinga, 1983 for macrofauna, Levin et al., 1991a for agglutinating Foraminifera, and Smith et al., 1998 for microbial biomass). The megafaunal biomass in the Santa Catalina Basin consists mostly of ophiuroids, which contain an unusually high percentage of wet weight in inert skeletal material (~80%: Tyler, 1980). Nonetheless, it appears that, at this site, much of the metabolically active benthic biomass is contained in the largest size fraction of organisms. It should be noted that oxygen concentrations in the Santa Catalina Basin bottom water (0.41 ml ℓ^{-1}) lie near the threshold at which oxygen stress begins to influence benthic community structure (e.g., Levin and Gage, 1998; Levin et al., 2000); thus, the biomass distribution patterns in the Santa Catalina Basin may not be typical of more oxygen-rich settings. In particular, in many areas of the California margin, ophiuroids are much less abundant than in the Santa Catalina Basin (Emery, 1960; Lauerman et al., 1996; Reimers et al., 1992; C.R. Smith, personal observations in the San Diego Trough, the San Nicolas Basin, the San Clemente Basin, the Santa Cruz Basin, and on the San Nicolas slope).

Carbon sources and trophic types: The primary sources of organic matter for California-slope assemblages include: (1) very small sinking particles, the flux of which has been evaluated with sediment traps; (2) phytodetrital aggregates (greenish centimeter-scale organic aggregates including fresh phytoplankton remains); (3) the sinking carcasses of nekton (crustaceans, fish, whales, etc.); and (4) sinking parcels of macroalgae such as kelp (e.g., *Macrocystis pyrifera*).

The rain of small particles is the best studied pathway of carbon flux in the northeast Pacific. Based on long-term sediment-trap measurements (K.L. Smith et al., 1992; Thunell et al., 1994; Drazen et al., 1998), the sinking flux of organic carbon in the form of small particles to the California slope varies temporally, with seasonal pulses apparently resulting from enhanced phytoplankton production in the spring and summer (K.L. Smith et al., 1992). These episodic inputs appear to be important to the benthos because sediment-community oxygen consumption, as measured with *in situ* respirometers at 4100 m at the base of the California slope (Station M, Fig. 6.1), tracks the seasonal influx (K.L. Smith et al., 1992, 1994; Sayles et al., 1994; Drazen et al., 1998). The time lag between peaks in flux of small particulate organic carbon and sediment-community oxygen consumption at this site suggest that the mean half-life for the degrading organic carbon is 25–50 days (Sayles et al., 1994) – that is, it is similar in lability to fresh phytoplankton detritus (C.R. Smith et al.,1993). Drazen et al. (1998) also offer some tantalizing evidence that abundance of the macrofaunal community at 4100 m may track the seasonal pulse of particulate organic carbon, in this case with an 8-month time lag; however, the temporal coverage of their study (two years) was too small to be conclusive.

As in the North Atlantic and equatorial Pacific, centimeter-scale aggregates rich in phytoplankton remains ("phytodetritus") also appear to arrive episodically on the deep seafloor along the California margin (K.L. Smith et al., 1994; C.R. Smith, 1994). Off California, as in the North Atlantic, the flux of such phytodetritus appears be related to phytoplankton blooms (Beaulieu and Smith, 1998). Whenever studied in the deep sea, phytodetrital aggregates have proven to be rich in fresh phytoplankton cells, chlorophyll *a* and other labile organic compounds, and to sustain high rates of microbial activity (Rice et al., 1986; Thiel et al., 1988/89; C.R. Smith et al., 1996); thus, it is often conjectured that phytodetritus provides a high-quality food resource for the deep-sea fauna. At a site 4100 m deep at the base of the California slope (Station M, Fig. 6.1), K.L. Smith and co-workers have conducted the most detailed study to date of the significance of phytodetritus to a deep-sea ecosystem. At this station beneath the California Current off central California, phytodetrital aggregates arrive in pulses on the seafloor between July and December (K.L. Smith et al., 1998). Over a two-year period, mean aggregate size at arrival varied roughly between 10 and 150 cm^2, and aggregates could cover up to 4.9% of the seafloor (K.L. Smith et al., 1998). The composition of phytodetrital aggregates was variable, but they included chain-forming diatoms, phaeodarians and/or zooplankton mucus webs (Beaulieu and Smith, 1998); the aggregates were substantially richer in organic carbon (4–5% by weight), total nitrogen and phaeopigments than underlying sediments (K.L. Smith et al., 1998). Based on disappearance times of aggregates in time-lapse photographs (~2 days), and direct measurements of the organic-carbon content of aggregates recovered in cores, the flux of organic carbon in the form of phytodetritus was large, being equivalent to 43–100% of the annual flux of small particulate organic carbon into near-bottom sediments traps deployed at the site. Nonetheless, sediment-community oxygen consumption was only slightly elevated in tube cores 38 cm^2 in cross-section containing phytodetrital aggregates, and the total carbon mineralization in visible aggregates, even during peak phytodetrital abundance, was calculated to constitute only 0.34% of the oxygen consumption of the sediment community (K.L. Smith et al., 1998). Thus, much of the organic carbon in these phytodetrital aggregates appeared to be metabolized over much longer time scales than the two days or so for which individual aggregates remained visible on the seafloor. This is not surprising considering that the mean half-life of metabolized particulate organic carbon at this site appears to be 25–50 days (Sayles et al., 1994). However, sediment protozoans (primarily agglutinating Foraminifera) increased in abundance and density within four weeks of phytodetrital input (Drazen et al., 1998), and mobile epibenthic megafauna appeared to increase their rates of locomotion when phytodetritus was present. In conclusion, phytodetrital aggregates provided a substantial flux of particulate organic carbon to the seafloor, but during the short period of time (~2 days) in which individual aggregates remained coherent enough to be visible on the seafloor they did not appear to be heavily utilized by the benthic assemblage. However, following phytodetritus disaggregation, labile organic matter derived from the phytodetritus may have been preferentially utilized by some components of the benthic community (e.g., Foraminifera, surface-deposit feeding megafauna).

Compared to the rain of fine particles, the flux of organic carbon in the form of animal carcasses and macroalgal parcels has been very poorly studied; the best (and essentially only) flux data for such large organic "falls" come from the California margin. At a depth of 1300 m in the Santa Catalina Basin, C.R. Smith (1983, 1985) used submersible surveys and implantation experiments to evaluate the standing crops and turnover times of nekton carcasses and kelp parcels on the seafloor. The estimated flux of organic carbon in the form of nekton falls was 1.6 g C m^{-2} y^{-1}, while that of kelp was ~0.1 g C m^{-2} y^{-1}.

It is possible to examine the relative importance of various primary food sources in the Santa Catalina Basin because the fluxes of large organic falls and small particles, as well as the respiratory requirements of many components of the seafloor community, have been measured at this site (Table 6.2). The rain of small particles is the largest measured flux component (constituting 70–84% of inputs) and nekton falls also appear to be significant (i.e., 13–23% of influx), while kelp falls comprise only a very small fraction (~1%) of the measured flux. The rain of small particles is roughly comparable to the respiratory demands of the entire benthos studied (not including the benthic-boundary-layer plankton), while the estimated flux of nekton falls could fuel 15–27% of this requirement. The energetic significance of the nekton-fall organic carbon is no doubt enhanced by the high food quality of carrion compared to other sources of detrital carbon (Smith, 1985). Thus, in this bathyal assemblage, the rain of small particles appears to be a major energy input, and nekton falls also appear to contribute substantially.

The California slope biota includes components adapted to exploit all the sources of organic carbon discussed above. Mega- and macrofaunal communities on the sediment-covered California slopes are dominated by scavengers and deposit feeders. Some scavenging species, for example the huge sleeper shark *Somniosus pacificus*, are rarely observed in the absence of carrion. However, a number of megafaunal community dominants are strongly attracted to carrion; these include the brittle star *Ophiophthalmus normani,* which accounts for more than 99% of the biomass and abundance in Santa Catalina Basin (Smith and Hamilton, 1983; Smith, 1985), the hagfish *Eptatretus deani,* with an average density of 0.33 m^{-2} (61% of demersal fish abundance) at depths of 600–800 m on the central California slope (Wakefield, 1990), and the onuphid polychaete *Hyalinoecia* sp. (Dayton and Hessler, 1972), which is the megafaunal dominant in trawl samples from 1800 m in the San Clemente Basin (C.R. Smith, unpublished data). *Ophiophthalmus normani, E. deani*, *Hyalinoecia* sp., and other very abundant species drawn to bait-falls are clearly facultative scavengers which utilize other feeding modes as well, such as predation or deposit feeding (Smith and Hamilton, 1983; Britton and Morton, 1994; Martini, 1998).

Table 6.2
Measured organic-carbon inputs and respiratory demands[1] on the floor of the 1300 m deep Santa Catalina Basin, along the California margin

	Flux (g C m^{-2} y^{-1})	Percentage of total	Ref.
Measured carbon inputs			
Vertical rain of small particles (from sediment traps)	5–10	70–84	1,2
Nekton falls	1.6	13–23	3
Kelp falls	0.1	~1	4
	+	+	
Total carbon influx	7–12	100	
Respiratory demands			
Sediment community	5–10	37–45	5,6
Epibenthic megafauna	0.9	3–9	5
Benthic-boundary-layer plankton	5–11	40–45	5
	+	+	
Total carbon outflow	11–27	100	

References
1. K.L. Smith and Hinga (1983)
2. C.R Smith and D. DeMaster, unpublished data
3. C.R. Smith (1985)
4. C.R. Smith (1983)
5. K.L. Smith et al. (1987)
6. Berelson et al. (1996)

[1] Conversions from oxygen consumption and caloric fluxes to organic-carbon fluxes are based on respiratory quotients (0.8–0.85) and an oxycalorific equivalent (4.86 cal ml^{-1} for nekton falls) given in K.L. Smith et al. (1987) and C.R. Smith (1983, 1985), respectively. It should be noted that all estimates in this table have large associated errors, in most cases $\geqslant$50%. The small degree of overlap between total organic-carbon influx and outflow may be due to unmeasured influxes [e.g., due to phytoplankton blooms, advection of dissolved organic matter, or downslope transport of particles in nepheloid layers (Berelson et al., 1996)] or to large measurement errors (particularly for the benthic-boundary-layer plankton).

The scavenger response on the California slope is very dramatic, with carcass falls (e.g., those of fishes, medusae, cetaceans, etc.) attracting dense aggregations of mobile necrophages within hours (e.g., Dayton and Hessler, 1972; Isaacs and Schwartzlose, 1975;

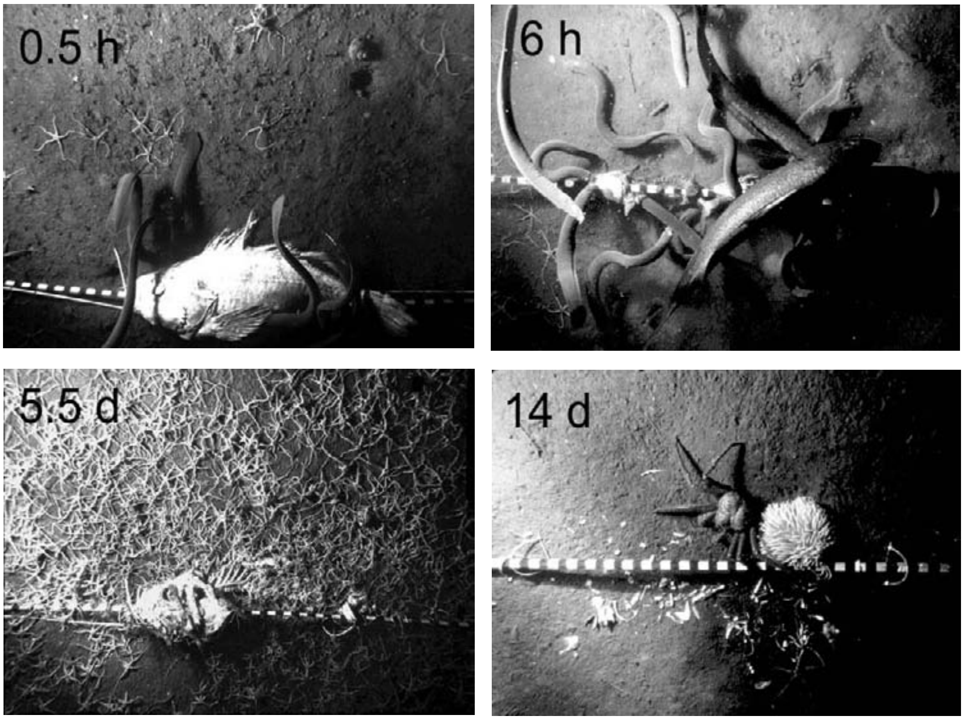

Fig. 6.8. Time series of scavenger aggregations at 1300 m depth on the Santa Catalina basin floor. Scale marks are 1 centimeter. At $t = 0.5$ h, hagfish (*Eptatretus deani*) have already found the 4-kg fish carcass (a cowcod, *Sebastes levis*). After 6 hours, numerous hagfish and the sablefish, *Anoplopoma fimbria*, are actively feeding on the bait parcel, and disturbing surrounding surface sediments. At 5.5 d, the ophiuroid, *Ophiophthalmus normani*, has formed a dense aggregation (hundreds per square meter) around the now stripped fish skeleton, presumably feeding on scraps of tissue left by the more mobile scavengers. At least five shrimps (*Pandalopsis ampla*) festoon the skeleton. After 14 days, only disarticulated bones remain, with a lithodid crab (*Paralomis multispina*) presumably searching for any remaining carrion. The unidentified anemone is likely an accidental visitor to the site.

Smith, 1985; Smith and Baco, 1998; Smith and Baco, unpublished data). The species structure of such aggregations varies with location and depth, but between depths of 600 m and 1300 m there are certain common components including hagfish (*Eptatretus deani*), lithodid crabs, sable fish (*Anoplopoma fimbria*), various species of rattail fish (Fig. 6.8), and often lysianassid amphipods (Dayton and Hessler, 1972; C.R. Smith, 1985; Smith and Baco, 1998). In areas where scavenging brittle stars such as *O. normani* are common, aggregations can achieve megafaunal densities exceeding 700 m^{-2} (Fig. 6.8). Extremely high densities of macrofauna, such as cumacean crustaceans, and dorvilleid and chrysopetelid polychaetes, may also develop around large carrion falls (e.g., dead whales) on time scales of days to months (Smith, 1986; Smith and Baco, 1998; Smith and Baco, unpublished data); for whale falls, the macrofaunal response yields high-density, low-diversity communities reminiscent of the opportunistic assemblages around sewage outfalls in shallow water (Pearson and Rosenberg, 1978; Zmarzly et al., 1994). Macrofaunal attraction to such carrion falls involves both “adult” immigration (e.g., for cumaceans) and, apparently, massive larval recruitment (for dorvilleids and chrysopetalids) (Smith, 1986; Smith and Baco, 1998; Smith and Baco, unpublished data).

The rates at which carrion falls are consumed on the California slope are remarkable. Fifty-kilogram parcels of fish can be “skeletonized” in less than 3 wk, and a 5000-kg whale carcass can be stripped nearly clean of soft tissue within four months (Smith, 1985; Smith and Baco, 1998). This rapid scavenging indicates that the slope ecosystem is adapted to “process” large natural parcels of very labile organic matter, such as carrion, quickly. However, as in shallow water (Mann, 1988), all organic-rich detrital parcels are not consumed in the same way. Accumulations of macroalgae, such as kelp, are utilized much more slowly and by somewhat different “scavengers” than are carrion falls. For example, Smith (1983) found that 0.2 kg parcels of the giant kelp *Macrocystis pyrifera* were consumed in the Santa Catalina Basin by the gastropod *Bathybembix bairdii,* the ophiuroid *Ophiophthalmus normani*, and the shrimp *Pandalopsis ampla* over a period of roughly 24 days, with little feeding occurring until the kelp had aged for 1–2 weeks. The requirement for aging, and presumably microbial colonization, of *M. pyrifera* likely reflects the much lower content of labile protein in kelp relative to carrion (Smith, 1983). The rates and patterns of consumption of anthropogenic materials introduced to slope habitats (e.g., trawl by-catch, sewage sludge, and municipal garbage) also varies with the quality of organic matter contained within these materials. The rapid consumption of whale carcasses does not necessarily indicate that tons of anthropogenic waste deposited at a point on the seafloor will be dispersed and assimilated by slope communities on time scales of months.

While scavenging may be the most dramatic trophic mode for metazoa on the sediment-covered California slope, deposit feeding (i.e., the ingestion of sediment grains and associated organic matter) may be the most prevalent. For example, more than 90% of metazoan macrofaunal individuals in Santa Catalina Basin (Kukert and Smith, 1992; C.R. Smith et al., 1998) and more than 90% of the polychaetes (the dominant macrofaunal group) in the San Diego Trough can be classified as deposit feeders (Jumars and Gallagher, 1982). In the San Diego Trough, the polychaetes are split roughly equally between species feeding within the sediment column (*subsurface deposit feeders*) and those consuming particles at the sediment surface (*surface deposit feeders*), while in the Santa Catalina Basin, subsurface deposit feeders dominate the macrofauna. The predominance of subsurface deposit feeders in the Santa Catalina Basin may be related to the high organic-carbon content of sediments in this basin [5 to 7% organic carbon by weight versus 1.2 to 4% in most other California slope and basin muds (Emery, 1960; K.L. Smith et al., 1983; Reimers et al., 1992)] which may lead to relatively high concentrations of labile organic matter and bacterial biomass within the sediments.

The most abundant California slope megafauna also tend to be deposit feeders. Mobile epibenthic holothuroids such as *Pannychia moseleyi* and *Scotoplanes globosa* in Santa Catalina Basin, and *Abyssocucumis abyssorum* and *Oneirophanta mutabilis* at 4100 m off central California, wander over the seafloor consuming a thin veneer of superficial sediment particles. Studies with naturally occurring radiotracers (^{234}Th) and labile phytoplankton pigments (chlorophyll *a*) indicate that these holothurians are extremely selective, ingesting small sedimenting particles and/or phytodetrital aggregates that have reached the seafloor in the previous 30 days (Lauerman et al., 1997; Miller et al., 2000). Such freshly deposited particles are likely to have a relatively high food value, because any labile organic material they have carried from surface waters will be little degraded by seafloor bacteria (C.R. Smith et al., 1993). Other common megafaunal surface-deposit feeders on the California slope include large gastropods such as *Bathybembix bairdii* and the burrowing chiridotid holothurian *Chirodota* sp. (Miller et al., 2000). These species also consume recently deposited particles on the seafloor, but are substantially less selective than the four epifaunal holothurians mentioned above, consuming sediments that are on average 60–120 days old (Miller et al., 2000). Differences in particle selectivity may result from differences in mechanisms of particle pickup, different mobility (relatively slow burrowers may lose the race to particulate organic carbonkets of young particles), or variations in digestive strategies (Penry and Jumars, 1987; Miller et al., 2000). The megafaunal populations can feed at surprisingly high rates, potentially ingesting ~30% of the daily flux of particulate organic carbon to the seafloor in the Santa Catalina Basin (Miller et al., 2000). Thus, the oft-overlooked megabenthos may play an important role in modifying and redistributing the limited flux of particulate organic carbon reaching slope communities.

Based largely on inferences from studies in other regions, detritivory (which includes scavenging, deposit feeding, and uptake of dissolved organic matter) predominates within the meiofauna of the California slope. For example, deep-sea Foraminifera, as a group, consume phytodetritus and the remains of small animals, sediment grains with associated bacteria and particulate organic carbon, and, possibly, dissolved organic matter (Gooday et al., 1992). The nematodes and harpacticoids similarly appear to feed predominantly on detrital particles, sediment and/or bacteria (e.g., Gage and Tyler, 1991; J. Lambshead, personal communication), although some are certainly predatory. Thus, a very slim data base suggests that the California slope meiofauna predominantly occupy low trophic levels.

In general, specialized predators appear to constitute a very small proportion of the soft-sediment California-slope benthos. For example, less than 0.2% of the epibenthic megafauna in the Santa Catalina Basin belong to taxa likely to include obligate predators (e.g., the rockfish species *Sebastolobus altivelis,* neptunid gastropods, and asteroids: Smith and Hamilton, 1983). Similarly, predators are estimated to constitute no more than 3% of the macrofaunal community in the Santa Catalina Basin and less (probably much less) than 13% of the polychaetes in the San Diego Trough (Jumars and Gallagher, 1982). Based in part on the apparent paucity of specialized predators, it has been suggested that most predation in the deep-sea (including the California slope), is performed by omnivores that ingest a broad range of particle types including live animals, sediments, and/or the remains of dead organisms (e.g., carrion and phytodetritus: Dayton and Hessler, 1972).

Rates of key ecological processes: To understand the biological and geochemical dynamics of sediment communities, it is useful to evaluate the rates of a number of key community processes including respiration, production, bioturbation and recolonization following disturbance. Evaluation of community production in the deep Pacific is extremely problematic because rates of individual and population growth, as well as ratios of production to biomass and production to respiration, are unknown for any major biotic components. However, rates of respiration, bioturbation and recolonization have been evaluated in a number of California-slope communities.

Sediment-community respiration, or organic-carbon mineralization, has been relatively well studied on the California margin, having been evaluated at more than 20 sites with either *in situ* respirometers (e.g., Smith and Hinga, 1983) or porewater measurements and models (e.g., Reimers et al., 1992). These sediment-respiration studies, combined with sediment-trap collections, indicate that the community respiration of organic carbon, as well as the input of particulate organic carbon, declines exponentially with depth along the California margin (Fig. 6.9; see also Jahnke and Jackson, 1987; Reimers et al., 1992; Berelson et al., 1996). In some regions of the margin, for example at the base of the slope at water depths of 3300 to 4500 m and within steep-sided borderland basins such as the Santa Catalina Basin, the total carbon respired and buried at the seafloor exceeds the estimated flux of particulate organic carbon sinking from the overlying euphotic zone (Fig. 6.9; Table 6.2; see also Reimers et al., 1992; Berelson et al., 1996). Some of the "missing" particulate organic carbon flux apparently arrives at the seafloor during infrequent but intense phytoplankton bloom events (K.L. Smith et al., 1992, 1994, 1998), whereas some of it may arrive via pathways poorly sampled by sediment traps. Such pathways include downslope movement of nepheloid layers, debris flows and turbidity currents, and the advection of dissolved organic matter, as well as the sinking of large, relatively rare organic parcels (e.g., phytodetrital aggregates, dead nekton and macroalgal parcels). Downslope transport of particulate organic carbon from shelf habitats to the slope base (~4500 m depth) seems likely to be more important in the Pacific basin than in the Atlantic because of the very narrow continental shelves and steep slopes in the Pacific.

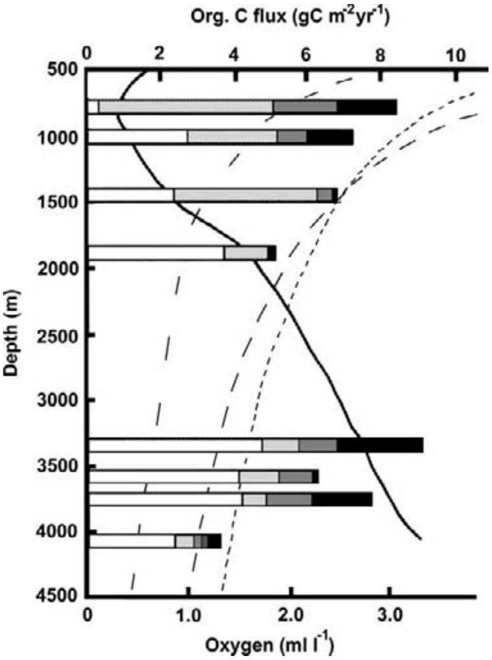

Fig. 6.9. Flux of organic carbon to the seafloor (bars) on the central California margin (Monterey Bay, site MB in Fig. 6.1) overlain by estimated fluxes of particulate organic carbon from sediment-trap studies conducted within the region (the three dashed curves represent separate sediment-trapping efforts), and concentration of dissolved oyygen (solid curve). The five levels of bar shading indicate, from left to right, the amount of organic carbon accounted for by reduction of O_2, reduction of NO_3^-, and reduction of Mn^{4+} (hardly visible except at the deepest station); SO_4^{2-}; and burial of organic carbon. (Figure modified from Reimers et al., 1992.)

It is also interesting to note that, even in areas with well-oxygenated bottom water, microbial anaerobic metabolism, such as denitrification and sulfate reduction, accounts for a substantial proportion (18–54%) of the organic carbon respired by California-slope sediment communities (Fig. 6.6). This reflects the relatively high flux rates of organic carbon, by deep-sea standards, occurring on the California-slope floor, and is direct evidence that microbes (in particular bacteria) mineralize a major fraction of the organic matter reaching slope sediments. Despite a down-slope decline in sediment-community respiration, rates of respiration at the bottom of the California slope are still 3-fold to 10-fold greater than in the oceanic abyssal Pacific (Table 6.1). In addition, at a given water depth, rates of respiration on the California slope substantially exceed those on the northwest Atlantic margin (Jahnke and Jackson, 1987; Jahnke, 1996). This likely results both from high primary productivity along the California margin caused by upwelling (Jahnke and Jackson, 1987) and from the narrowness of the slope, facilitating downslope transport of coastal production.

Bioturbation, or the movement of sediment particles by animals, is a key ecosystem process in low-energy, depositional environments, such as much of the deep sea. Bioturbation results from the sum of deposit-feeding, locomotion and home-building activities of benthos; rates of bioturbation thus provide an integrative measure of the physical activity of sediment assemblages. Biogenic sediment mixing also has an impact on the rates of chemical reactions in sediments, including the recycling and burial of organic carbon and particle-bound pollutants (Officer and Lynch, 1989; C.R. Smith, 1992). Because the rates of bioturbation are generally very high compared to rates of sediment accumulation, sediment mixing also substantially smears the paleontological record preserved in deep ocean sediments.

Rates of bioturbation are typically evaluated using naturally occurring radionuclides, such as ^{234}Th (half-life = 24 days) and ^{210}Pb (half-life = 22 years), that are adsorbed in the water column by sinking particles. These adsorbed radionuclides provide an "excess" signal that disappears from particles, through radioactive decay, after they have been deposited on the seafloor. Occasionally, exotic tracer particles have also been introduced to the deep-sea floor to evaluate mixing rates. Bioturbation is typically parameterized as an eddy-diffusion, or "bioturbation," coefficient (units of $\text{cm}^2\,\text{y}^{-1}$) within a surface-sediment mixed layer ranging from 3 to 20 cm in thickness (C.R. Smith, 1992; Boudreau, 1998; Smith and Rabouille, 2002).

Rates of bioturbation have been evaluated at a number of sites along the California margin, as well as on the nearby Washington slope. The Santa Catalina Basin in particular has served as a test site for mechanistic studies of deep-sea sediment mixing. Several major points have emerged from these margin studies.

(1) Measured rates of sediment mixing vary with the particle type and radiotracer. For example, Wheatcroft (1992) experimentally documented 10-fold faster mixing rates for 10-μm diameter beads than for 100-μm beads at 1240 m depth in the Santa Catalina Basin. This difference was ascribed to *size-dependent* ingestion and mixing of particles by deposit feeders, whose feeding and defecating activities are thought to contribute substantially to deep-sea bioturbation (C.R. Smith, 1992; Wheatcroft, 1992). In addition to size-dependent bioturbation, *tracer-dependent* mixing has been demonstrated in the Santa Catalina Basin (C.R. Smith et al., 1993), where mean bioturbation coefficients for ^{234}Th ($60\,\text{cm}^2\,\text{y}^{-1}$) were a hundred-fold higher than for ^{210}Pb ($0.43\,\text{cm}^2\,\text{y}^{-1}$) in precisely the same sediments. Such tracer-dependent bioturbation, in which tracers with shorter characteristic time scales (e.g., ^{234}Th) are mixed faster than those with longer time scales (e.g., ^{210}Pb), appears to be widespread in the deep sea, and has been thought to result from *age-dependent* mixing (Smith et al., 1993, 1997). According to the age-dependent mixing hypothesis, recently deposited particles relatively rich in excess ^{234}Th, and labile organic matter (e.g., phytodetritus), are preferentially ingested by deposit feeders; the preferential ingestion and defecation of such "young" particles causes the short-lived tracer ^{234}Th to be, on average, mixed faster than its longer-lived counterparts, such as ^{210}Pb. Recent studies on the California slope indicate that deposit feeders do indeed preferentially ingest young particles rich in ^{234}Th (Lauerman et al., 1997; Miller et al., 2000), and that fresh phytoplankton cells often are initially mixed faster into sediments than are food-poor sediments of similar grain size (Smith et al., 2002; Fornes et al., 2002); both results are predicted by the age-dependent mixing hypothesis.

(2) A second generalization to emerge from bioturbation studies on the northeast Pacific slope is that, for a given tracer type, mixing coefficients within and between sites are highly variable. For example, between depths of 500 and 1933 m on the Washington slope, Carpenter et al. (1982) found mixing coefficients for ^{210}Pb spanning more than an order of

magnitude (i.e., 0.47 to 9.6 $cm^2\ y^{-1}$). Similarly, within the relatively homogeneous Santa Catalina Basin, C.R. Smith et al. (1993) measured mixing coefficients for ^{234}Th ranging from 7.9 to 200 $cm^2\ y^{-1}$. This high variability in mixing coefficients undoubtedly reflects the high spatial variability in flux of particulate organic carbon, faunal densities (especially the megafauna), and individual activity rates known to occur in slope habitats.

(3) Despite this high spatial heterogeneity, bioturbation coefficients on the northeast Pacific slope fit into a broad environmental pattern, generally decreasing with ocean depth (Smith and Rabouille, 2002). For example, the maximum bioturbation coefficient measured for ^{210}Pb on the northeast Pacific slope (9.8 $cm^2\ y^{-1}$: Carpenter et al., 1982) is an order of magnitude less than the maximum measured in shallow-water habitats (370 $cm^2\ y^{-1}$: Carpenter et al., 1985) and about 10-fold greater than the maximum in the abyssal Pacific (0.9 $cm^2\ y^{-1}$: Table 6.1). Similarly, the minimum bioturbation coefficient measured on the Pacific slope falls between the minima for the shallow-water and abyssal habitats. Again, this is very likely a function of flux rates of particulate organic carbon, the abundance and biomass of macro- and megabenthos, and presumably the activity rates of animals, which decrease roughly by an order of magnitude from the shelf to the slope, and again from the slope to the oceanic abyss (Table 6.1: see also Smith and Rabouille, 2002).

One final feature of bioturbation is worth mentioning. In low-energy habitats (i.e., those without erosive water currents), animal activities, especially the crawling of epibenthic megafauna, erase the tracks and trails of other animals (Wheatcroft et al., 1989). In the Santa Catalina Basin on the California margin, millimeter-scale animal traces persist for only days to weeks before being erased by an abundant and active megafauna (Wheatcroft et al., 1989). In the abyssal equatorial Pacific, similar structures persist for more than four months (Gardner et al., 1984). Once again, this no doubt reflects the high flux rates for particulate organic carbon, faunal standing crops, and mean rates of animal activity on the Pacific slope relative to the more energy-poor, open-ocean abyss.

Experimental studies of recolonization provide insights into natural processes structuring seafloor assemblages, and the response of such communities to anthropogenic disturbance (e.g., bottom trawling, seafloor mining, waste disposal). Three types of manipulations have been used in studies of recolonization on the California slope: (1) trays of azoic sediment; (2) creation of artificial mounds; and (3) implacement of food falls (dead fish and whale carcasses). Sediment-tray experiments at a depth of 1300 m in the Santa Catalina Basin yielded very low rates of recolonization, with macrofaunal abundance attaining only ~3% of that in the background community after 4.5 months (Levin and Smith, 1984). Sediment-tray colonization rates are likely to be biased downward, however, by excluding burrowers and altering flow structure over the seafloor (Kukert and Smith, 1992). Sites of burial disturbance in the Santa Catalina Basin, resulting from the creation of artificial mounds 5 cm high, were colonized much more rapidly, with macrofaunal community abundance approaching background levels after 11 months (Kukert and Smith, 1992). Nonetheless, even after 23 months, infaunal community structure on artificial mounds differed from that in surrounding sediments, in particular having higher species richness; thus, community succession continued for at least two years following small-scale burial disturbance at this site. Recolonization following carrion enrichment and scavenger disruption of sediments in the Santa Catalina Basin, and at a depth of 1240 m in the San Diego Trough, exhibited at least two phases. Within weeks to months, there were high densities of opportunistic species, including cumaceans immigrating as adults to fish falls (C.R. Smith, 1986) and dorvilleid and chrysopetalid polychaetes recruiting to sediments within 2 m of whale falls (Smith and Baco, 1998). Colonization rates by opportunists following whale-fall enrichment are the most rapid measured below 1000 m in the ocean, with dorvilleids and chrysopetalids attaining densities of 20 000 individuals m^{-2} within four months. The re-establishment of background assemblages following intense local enrichment of California margin sediments appears to occur very slowly, however, with macrofaunal community structure remaining anomalous around a whale carcass in the 1900-m-deep San Clemente Basin 2.6 years after emplacement (Smith and Baco, unpublished data).

It is noteworthy that recolonization following meter-scale sediment disturbance and enrichment on the California slope often follows patterns similar to those in shallow water, with, for instance, initial colonization by opportunistic cumaceans and dorvilleids (Zmarzly et al., 1994; Vetter, 1996). However, rates of colonization generally are markedly slower at these bathyal depths, with complete community recovery requiring time scales of years, rather than the weeks to months typical of shallow communities (e.g., VanBlaricom, 1982; Smith and Brumsickle, 1989; Vetter, 1996).

Submarine canyons

The shelves and slopes of the Pacific basin are dissected by submarine canyons; in fact, the Pacific contains 49 of the 96 submarine canyons mapped worldwide by Shepard and Dill (1966). These features typically begin at depths of 15 to 100 m and form steep, narrow-walled channels that terminate near the floors of basins or at the base of the continental slope, often producing depositional sediment fans (Shepard and Dill, 1966). All canyons serve both as channels for energetic currents and turbidity flows, and as conduits for the transport of detritus (e.g., detrital kelp and sand) and particle-bound pollutants from the continental shelf into the deep sea (Vetter, 1994). Substratum types include rocky outcrops, sediments ranging from coarse sand to mud, and in some cases, large parcels of organic debris (Vetter, 1994; Vetter and Dayton, 1998). Consumers feeding in canyons, including commercially exploited species, potentially can experience increased food supply through at least three mechanisms. Suspension feeders may benefit from accelerated currents (Rowe, 1971), demersal planktivores can exploit dense layers of zooplankton which become concentrated in canyons during vertical migrations (Greene et al., 1988), and detritivores may benefit from elevated sedimentation rates and accumulations of macrophytic debris (Vetter, 1994; Vetter and Dayton, 1998; Harrold et al., 1998). Because of high physical energy, rocky outcrops, and enhanced food availability in canyons, faunal communities differ markedly from those on the surrounding sediment-covered slopes.

The Pacific canyons which have been best studied biologically are the Scripps and La Jolla Canyons off San Diego, California. Vetter and Dayton (1998) found evidence of organic enrichment from macrophytic detritus (kelp and seagrass) to depths of 550 m, and coarse sediments suggestive of strong currents to depths of 700 m within both canyons. Infaunal assemblages in canyons were distinct from those at similar depths on the nearby slope, with macrofaunal densities and biomasses typically 2-fold to 15-fold higher in canyons; in fact, canyon macrofaunal densities were among the highest ever measured at slope depths. The most abundant species in canyons generally were detritivores, but included the bivalve *Thyasira flexuosa*, which contains endosymbiotic, sulfur-oxidizing bacteria presumably utilizing sulfides derived from anaerobic decay of buried detritus, or from porewater seepage along the canyon axis (Vetter and Dayton, 1998). Species composition within canyons also differed from that on surrounding slopes. Canyon assemblages generally had lower diversity owing to dominance by a few species (e.g., the polychaete *Capitella* sp.); nonetheless, 168 out of a total of 435 species collected by Vetter and Dayton (1998) occurred only inside the canyons. It is clear that canyons contribute substantially to habitat diversity on the continental slope.

On the northeast Pacific slope, the enhanced secondary production of canyons may also figure significantly in the life-history of demersal fishes. Food-rich patches often are critical for the recruitment success of many fish stocks, allowing larval and juvenile stages to pass through "energetic bottlenecks". In fact, Vetter and Dayton (1999) found very high densities of juvenile hake (*Merluccius productus*) within the Scripps and La Jolla Canyons, suggesting that the canyons were acting as nursery grounds. These authors also found enhanced abundance of turbot (*Pleuronichthys* sp.) and zoarcids within canyons. Perhaps not surprisingly, submarine canyons along the California coast are regularly targeted by commercial and recreational fishermen exploiting rockfish, rattails and other bottom fishes (C.R. Smith and E.W. Vetter, personal observations).

Oxygen-minimum zones

As discussed above, the eastern margin of the Pacific Ocean is intersected by an oxygen-minimum zone (oxygen-minimum zone), where bottom-water oxygen concentrations drop below 0.5 ml ℓ^{-1} (Fig. 6.10). In the equatorial zone, the oxygen-minimum zone is particularly well developed extending from a depth of 50 m to 1300 m, with oxygen concentrations falling below 0.1 ml ℓ^{-1} over most of this range (Wishner et al., 1991). On the California slope, the oxygen-minimum zone is not as well developed, but still extends over depths roughly from 500 m to 1000 m, with minimum oxygen concentrations below 0.3 ml ℓ^{-1} (Emery, 1960; Reimers et al., 1992; Fig. 6.9). In enclosed basins (e.g., Santa Monica and Santa Barbara Basins) whose sill depths intersect the oxygen-minimum zone, low-oxygen conditions may extend to basin floors, which can be much deeper than 1000 m (Emery, 1960).

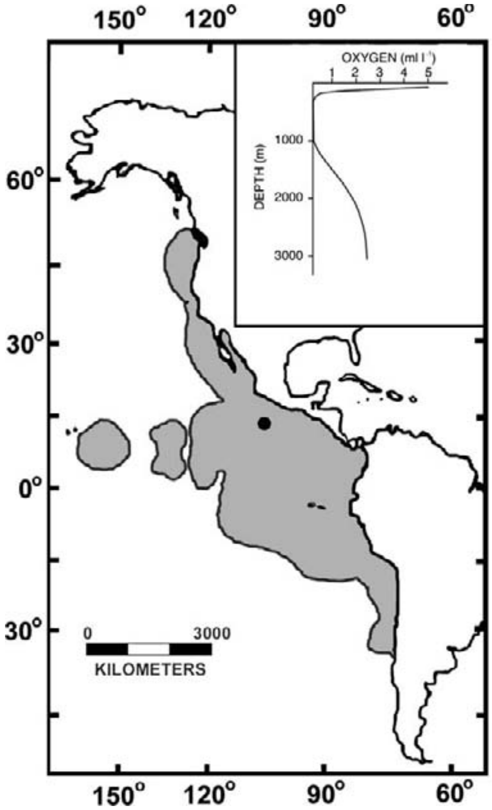

Fig. 6.10. Regions of the Pacific Ocean with a well-developed oxygen-minimum zone. In the shaded areas, dissolved oxygen concentrations fall below 0.2 ml ℓ^{-1} at some point between water depths of 100 and 1000 m. The oxgyen minimum zone is most fully developed in the eastern tropical Pacific, where it may span depths from 100 to 1000 m (see inset); the zone narrows to the north, south and west. The oxygen profile in the inset comes from Volcano 7 (black dot on map). Figure modified from Diaz and Rosenberg (1995), and Wishner et al. (1990).

Oxygen-minimum zones dramatically alter community structure and patterns of energy flow on the deep-sea floor. Alterations in community structure result from the combined effects of oxygen stress (with a threshold at roughly 0.5 ml ℓ^{-1}: Levin and Gage, 1998) and organic enrichment because sediments in the oxygen-minimum zone typically contain high concentrations of organic matter (often 3–10% organic carbon by weight) (Emery, 1960; Levin et al., 1991b, 1994). Perhaps the best studied transect in the oxygen-minimum zone lies on the slope of Volcano 7, a seamount in the equatorial Pacific (Fig. 6.1), whose summit at a depth of 730 m extends well up into the oxygen-minimum zone (Fig. 6.10; see also Wishner et al., 1990). Volcano 7 exhibits at least three biotic zones.

(1) Near the summit (depths from 730 to 770 m), oxygen concentrations fall below 0.1 ml ℓ^{-1} and the abundance and diversity of macrofauna and megafauna are very low, apparently because of hypoxic (i.e., low-oxygen) stress (Fig. 6.8; see also Levin et al., 1991b; Levin and Gage, 1998). In contrast, the standing crops of sedimentary bacteria and meiofauna within this zone are high, as is the availability of labile organic matter in the sediments (3.4% organic carbon, and 15 $\mu g\, g^{-1}$ chlorophyll *a*) (Levin et al., 1991b). In this zone, bacteria tolerant of low oxygen and certain meiofaunal taxa (e.g., nematodes) differentially exploit the unusually high flux of labile organic material to the seamount summit; organic-carbon flux is enhanced because there are very few metazoans in the hypoxic water column to consume particles sinking from the euphotic zone (Wishner et al., 1991).

(2) At depths of 770–1000 m, oxygen concentrations begin to rise, reaching levels of 0.11–0.16 ml ℓ^{-1}; here the macrofauna and megafauna become very abundant, but consist of a small number of opportunistic species (Levin et al., 1991b, 1994). Apparently, when oxygen concentrations exceed a certain threshold, a small suite of hardy macrofaunal and megafaunal detritivores are able to exploit the food-rich conditions just below the oxygen-minimum zone. The macrofauna in particular is dominated by brooding polychaetes exhibiting high levels of reproductive activity; this pattern is strikingly reminiscent of macrofaunal assemblages from organic-rich settings (e.g., sewer outfalls) in shallow water (Levin et al., 1994).

(3) At greater depths on Volcano 7 (1000–2000 m), oxygen concentration rise to 0.7–0.9 ml ℓ^{-1} and the benthic community becomes much more typical of the bathyal deep sea, being characterized by low population densities and a very high diversity, both of species and of higher-level taxa (Levin et al., 1991b; Levin and Gage, 1998).

Similar faunal zonation occurs within oxygen-minimum zones on the California margin and on the Peru–Chile slope beneath upwelling zones. For example, on the California margin off Point Sur, macrofaunal community abundance achieves maxima just above and just below the oxygen-minimum zone (i.e., at oxygen concentrations of ~0.5 ml ℓ^{-1}), and in the core of the oxygen-minimum zone (0.3ml oxygen ℓ^{-1}) the macrofauna is dominated by polychaetes (Mullins et al., 1985). Foraminifera show a similar, high-density, low-diversity assemblage of presumably opportunistic species within this oxygen-minimum zone (Sen

Gupta and Machain-Castillo, 1993). On the Peru–Chile margin, the biomass of benthic invertebrates and of demersal-fish is relatively high near the upper and lower boundaries of the oxygen-minimum zone (i.e., at oxygen concentrations $>0.6\,\mathrm{ml}\,\ell^{-1}$); at lower oxygen concentrations, the macrobenthos is dominated by polychaetes, nematodes, and bivalves (Arntz et al., 1991). In addition, dense mats of sulfur-oxidizing bacteria (e.g., *Thioploca*) may co-occur with the Peru–Chile macrobenthos at oxygen concentrations below $0.2\,\mathrm{ml}\,\ell^{-1}$ (Arntz et al., 1991). Interestingly, the macrobenthos within persistent oxygen-minimum zones on continental slopes is more resistant to oxygen stress than is the fauna of continental shelves exposed to periodic hypoxia. For example, high standing crops of macrobenthos, especially polychaetes, occur at oxygen levels as low as $0.11\,\mathrm{ml}\,\ell^{-1}$ within oxygen-minimum zones (Levin et al., 1991b), whereas on continental shelves mass faunal mortality often occurs if the oxygen concentration of the bottom water drops below $\sim 1.0\,\mathrm{ml}\,\ell^{-1}$ (Diaz and Rosenberg, 1995). The relative stability of gradients in the oxygen-minimum zone, combined with a persistent availability of labile organic material on the seafloor, apparently allows a well-adapted opportunistic community to thrive, and perhaps to have evolved, at the boundaries of oxygen-minimum zones (Levin et al., 1994; Diaz and Rosenberg, 1995).

Rates of ecologically important processes within oxygen-minimum zones in the eastern Pacific have not been well studied. Off Point Sur on the California margin, total rates of sediment-community respiration (i.e., organic-carbon mineralization) at the core of the oxygen-minimum zone do not differ markedly from those at deeper stations (Fig. 6.9). As expected, sulfate reduction is quantitatively more important in the oxygen-minimum zone than deeper on the slope, but still accounts for less than 25% of total organic-carbon mineralization (Fig. 6.9). Bioturbation rates and depths within oxygen-minimum zones have not been well quantified with radio-isotopic measurements (e.g., excess $^{210}\mathrm{Pb}$ profiles) in the eastern Pacific; however, some qualitative bioturbation patterns are evident. Below oxygen concentrations of $0.1\,\mathrm{ml}\,\ell^{-1}$ in the bottom water, the bioturbating macro- and megabenthos may be excluded, yielding laminated (i.e., unmixed) sediments (Savrda and Bottjer, 1991). At concentrations between 0.1 and $0.5\,\mathrm{ml}\,\ell^{-1}$, Savrda and Bottjer (1991) hypothesized that the rates and depths of bioturbation increase with increasing oxygen concentration, as larger-bodied, deeper-burrowing species enter the community. The only data to test this hypothesis come from the oxygen-minimum zone in the Arabian Sea, which suggest that the depth of bioturbation increases as oxygen concentrations rise from 0.1 to $0.3\,\mathrm{ml}\,\ell^{-1}$ or more, but that the intensity of mixing (as indicated by eddy-diffusion coefficients) within the bioturbated layer does not change substantially with oxygen (Smith et al., 2000). Because these hypotheses are used in reconstructions of oxygenation patterns in paleo-environments (Savrda and Bottjer, 1991), it would be very useful to test the quantitative relationships between oxygen and bioturbation depths and rates on the California and Peru–Chile margins.

Oxygen minimum zones may have played an important role in generation of the high species diversity found in bathyal deep-sea habitats (Jumars and Gallagher, 1982; Grassle and Maciolek, 1992). Intense oxygen-minimum zones, such as occur in the eastern tropical Pacific and on the Peru–Chile margin, impose barriers to gene flow between populations above and below this zone, potentially facilitating speciation in otherwise relatively homogeneous deep-sea water masses (Rogers, 2000). Over geologic time, oxygen-minimum zones have expanded and contracted, periodically isolating populations in slope and basin habitats on continental margins, and on islands and seamounts (Kennett, 1982; Rogers, 2000); this too is likely to have stimulated allopatric speciation. Finally, the steep gradients in oxygen concentrations and labile organic matter found at the lower boundaries of some oxygen-minimum zones (Levin et al., 1991b; Arntz et al., 1991) undoubtedly yield strong gradients in selective pressure for particular life histories, optimal growth rates, and types of species interactions within the benthos (Levin et al., 1991c, 1994); such selective gradients are likely to yield enhanced rates of speciation near the lower boundaries of oxygen-minimum zones (Rogers, 2000).

The abyssal equatorial Pacific

Surface waters in the equatorial Pacific sustain relatively high primary production as a result of upwelling of nutrients (in particular nitrate and iron) along the equatorial divergence (Berger, 1989; Murray et al., 1994; Landry et al., 1997). The enhanced productivity is most intense in the eastern Pacific, where equatorial upwelling and eddies combine to increase nutrient flux over a broad latitutidinal band; for example, primary production is enhanced to 15º north and south of the equator between 90 and 100ºW longitude. Further westward along the equator, nutrient upwelling gradually tapers off, yielding a narrowing tongue of productivity roughly centered on the equator. At 140ºW longitude, the equatorial "tongue" is less than 20º degrees wide and, by 160ºE longitude, the productivity tongue has disappeared (e.g., Berger, 1989).

High productivity near the equator yields an enhanced flux of particulate organic carbon to the ocean's interior (Honjo et al., 1995). Most of the equatorial zone varies little in water depth (i.e., from 4000 to 5000 m) and is far removed from lateral inputs from the ocean's margin (Fig. 6.1); thus, spatial variations in flux of particulate organic carbon to the seafloor are primarily controlled by patterns of overlying productivity. Within the equatorial zone, flux of particulate organic carbon declines gradually from east to west along any line of latitude (roughly halving from 120ºW to 180ºW; Jahnke, 1996) and steeply with distance north or south from the equator (dropping from 1.6 to 0.35 g C m^{-2} y^{-1} if one moves from 0º to 9ºN along the 140ºW meridian: Fig. 6.11). Because the deep-sea floor typically is poor in organic carbon (or "food limited"), these gradients in flux of particulate organic carbon profoundly affect the ecology of the abyssal benthos. In fact, longitudinal sampling across the equatorial Pacific provides an excellent opportunity to evaluate the effects of the flux of particulate organic carbon on deep-sea benthic ecosystems, because most other ecologically important parameters, such as temperature, depth, bottom-water oxygen concentration, and seafloor current regimes vary little.

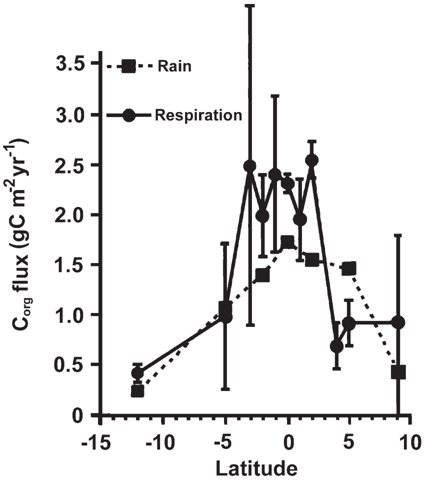

Fig. 6.11. Patterns of flux of particulate organic carbon at the seafloor along approximately the 140ºW meridian in the abyssal equatorial Pacific. Squares indicate fluxes estimated from the rain of particulate organic carbon into deep sediment traps and circles indicate fluxes estimated from sediment oxygen consumption (i.e., seafloor respiration). Modified from C.R. Smith et al. (1997).

Habitat and community description

Considering its vast size (roughly 2000 km by 11 000 km), the abyssal equatorial Pacific has received surprisingly little ecological study. Most published biological data come from three relatively small areas: (1) the eastern north Pacific enclosed by the box 10º to 15ºN, 120º to 130ºW, within the Clipperton–Clarion Fracture Zone (Mullineaux, 1987; Paterson et al., 1998); (2) the site of the German **Dis**turbance and **Col**onization Experiment (the DISCOL area, Fig. 6.1) southeast of the Galapagos Islands at ~7ºS, 88ºW (Borowski and Thiel, 1998), and (3) the EqPac Transect (Fig. 6.1) crossing the equator from 12ºS to 9ºN along approximately 140ºW (Smith et al., 1997). Data from the first two areas were collected as components of manganese-nodule mining impact studies, and from the third during the **U**nited **S**tates **J**oint **G**lobal **O**cean **F**lux **S**tudy (US JGOFS) in the Equatorial Pacific (known as EqPac). We will focus on data from the EqPac transect because of the broad suite of parameters measured, and because these data most clearly illustrate the effects of spatially varying flux of particulate organic carbon on the structure of deep-sea ecosystems.

Equatorial Pacific habitats may be divided into two types based on the flux of particulate organic carbon: (1) for instance, the "eutrophic" abyss (within 5 degrees of the equator along the 140ºW meridian, where particulate organic carbon flux is roughly 1 to 2 g C m^{-2} y^{-1}); and (2) the "mesotrophic" abyss beginning roughly at 7 to 9º from the equator, where the flux of particulate organic carbon is substantially lower (~0.4 g C m^{-2} y^{-1}) owing to distance from the equatorial upwelling. Within the eutrophic equatorial abyss, sediments typically are white, rich in calcium carbonate (50–90% CaCO$_3$ by weight), and poor in organic carbon (<0.3% by weight) (Jahnke, 1996); most of the sediment mass consists of sand-sized tests of pelagic Foraminifera. At greater distances from the equator, organic-carbon content increases slightly, and calcium carbonate content decreases to low percentages, yielding the more familiar brown, deep-sea muds at 9º to 10ºN. In the mesotrophic abyss, manganese nodules may also be abundant, providing substantial areas of hard substratum along with soft sediments (Fig. 6.6). In fact, the areas of maximum commercial interest for nodule mining fall in the mesotrophic abyss at roughly 10º to 20º north or south of the equator (Fig. 6.1). As on continental margins, the sedimented seafloor in the equatorial abyss is heavily modified by the activities of animals. Between 5ºS and 5ºN, the predominant visible structures are the decimeter-wide tracks of burrowing sea urchins that cover 10 to 18% of the seafloor, fecal mounds 5 cm in diameter or more which cover ~0.5% of the seafloor, the tests of xenophyophores (giant, agglutinating protozoans ranging 3 to 10 cm in width), and spoke-like feeding traces of echiurans and other burrow-dwelling surface-deposit feeders (Fig. 6.6; Table 6.3; C.R. Smith, unpublished data). These biogenic structures are less dynamic than those at bathyal depths on the continental margin; in the equatorial abyss, centimeter-scale biogenic features persist for somewhat more than four months prior to erasure as a result of bioturbation (Table 6.1). In the mesotrophic abyss (e.g., at 9ºN, 140ºW) xenophyophores continue to be abundant, but urchin furrows and spoke traces become much less common, covering less than 1% of the seafloor (Fig. 6.6; Table 6.3; C.R. Smith, unpublished data). Here, traces on the scale of millimeters to centimeters are substantially less dynamic than in the eutrophic abyss, requiring much more than 12 months to be erased by bioturbation (Gardner et al., 1984).

Table 6.3
Percentage of seafloor area covered by decimeter-scale bioturbation features in the abyssal equatorial Pacific [1]

Latitude	Urchin furrows	Mounds	Rosettes	Total
0º	10.6±1.5%	0.3±0.1%	0.0±0.0%	11.0±1.5%
2ºN	17.9±1.2%	0.4±0.2%	0.3±0.2%	18.5±1.2%
5ºN	10.5±1.8%	0.6±0.3%	0.0±0.0%	11.1±1.9%
9ºN	0.9±0.7%	0.5±0.3%	0.0±0.0%	1.4±0.9%

[1] From ten survey photographs at each latitude along the 140ºW meridian (Hoover and Smith, unpublished data). An area of 3.78 m^2 was analysed from each photograph. For methods, see Hoover (1995). Means ± standard errors are given.

The megafauna in the eutrophic abyss along the EqPac transect attains abundance comparable to more productive depths on the California slope (i.e., roughly 2–6 individuals per m^{-2}), but is dominated by different taxa from those on the slope. Xenophyophores in the genera *Reticulammina* and *Stannophyllum* account for 90–95% of the megafaunal abundance along the EqPac transect (C.R. Smith, unpublished data). Because these large agglutinating protozoans are less than 2% protoplasm by volume (Levin and Gooday, 1992), they undoubtedly account for much less than 90% of the megafaunal biomass, and have relatively low metabolic activity (cf. Levin and Gooday, 1992). As might be expected owing to the lower organic-carbon flux (Table 6.1), *metazoan* megafauna are roughly an order of magnitude less abundant in the equatorial Pacific than at slope depths, occurring at densities of 0.17 to 0.25 individuals per square meter. The metazoans are dominated by large burrowing urchins (up to 0.085 m^{-2}), small hexactinellid sponges, and a variety of epibenthic holothurians. Based on the frequency of fresh, spoke-shaped feeding traces on the sediment surface (0.07–0.22 m^{-2}), large, infaunal echiurans are also relatively common. However, the bulk of the burrowing megafauna remains unsampled here, as in most other parts of the deep sea, although its presence is manifested by abundant fecal mounds, pits and feeding traces at the sediment–water interface (Fig. 6.6). In the mesotrophic abyss (e.g., 10ºN, 140ºW) xenophyophores remain common (~2.3 m^{-2}), but the metazoan megafauna are only half as abundant as in eutrophic areas. In particular, burrowing urchins essentially disappear, leaving sponges and holothurians as the dominant large animals (Hoover, 1995).

As on the continental slope, the abyssal macrofauna in the equatorial zone contains a broad diversity of taxa including, in decreasing order of importance, polychaetes, tanaids, isopods and bivalves (Borowski and Thiel, 1998; Smith and Miller, unpublished data). The polychaetes dominate macrofaunal standing crop, accounting for about 62% of both abundance and biomass along the EqPac transect (Smith and Miller, unpublished), and about 52% in the DISCOL area (Borowski and Thiel, 1998). Macrofaunal community abundance in eutrophic equatorial sediments, at 1200 to 2000 m^{-2}, is roughly 25% of that on the California slope, while macrofaunal biomass (0.4 to 0.6 g m^{-2}) is an order of magnitude lower (Table 6.1). The median size of individual macrobenthos (i.e., the macrofaunal biomass divided by the number of individuals) within 5 degrees of the equator along the 140ºW meridian is about 0.3 mg, compared to roughly 0.8 mg at slope depths (Table 6.1), indicating that body size decreases concomitantly with abundance, biomass and flux of particulate organic carbon as one moves from the slope habitats to the eutrophic abyss. At least 95% of macrofaunal abundance in eutrophic equatorial sediments is concentrated in the top 5 cm of sediment, where there is access to labile organic matter depositing on the sediment–water interface. Macrofaunal species diversity has not been fully evaluated in equatorial Pacific sediments, but the local diversity of the dominant taxon, the polychaetes, appears to be high. At three equatorial sites in the northeastern Pacific, Paterson et al. (1998) found between 11 and 14 species among 20 individuals, and, for pooled box cores, about 40 species among 100 individuals. This rivals or exceeds the extremely high diversity previously described for continental-slope habitats (Fig. 6.8).

In the mesotrophic abyss, for instance, at 9ºN along the EqPac transect, macrofaunal abundance (290 m^{-2}) and biomass (0.12 mg m^{-2}) are roughly 25% of those in eutrophic abyssal sediments (Table 6.1). However, mean macrofaunal body size (~0.4 mg) remains similar to that between 0º and 5ºN (Table 6.1).

The dominant meiofaunal taxon in the equatorial Pacific, the Nematoda, has received substantial study along the EqPac transect (Brown, 1998; Brown et al., 2002). In eutrophic sediments (e.g., from 0º–5ºN), the nematodes attain mean densities of 130 000 to 140 000 individuals m^{-2}, and biomasses of 0.03 to 0.06 g wet weight m^{-2} in the top 5 cm of sediment (Brown, 1998; Brown et al., 2002). These nematode assemblages attain very high local diversity, with over 32 species among 50 individuals collected in a single 80 cm^2 sample (Lambshead et al., 2002). In mesotrophic sediments at 9ºN, the abundance and biomass of nematodes has dropped somewhat to 90 000 individuals and 0.02 g cm^{-2}, respectively, while local species diversity changes only slightly (Lambshead et al., 2002). The abundance and biomass of nematodes in the equatorial Pacific abyss falls at the low end of the ranges of nematode abundance and biomass in the abyssal northeast Atlantic near the continental margin (e.g., the Porcupine Abyssal Plain) (Brown, 1998), whereas the local species diversity of equatorial nematode fauna is relatively high (Lambshead et al., 2002).

Microbial biomass in eutrophic sediments along the EqPac transect is surprisingly high, ranging from 0.2 to 0.3 g C m^{-2} in the top 0.5 cm of sediment (Smith et al., 1997). Assuming that wet-weight biomass is 10% organic carbon, this yields a microbial wet weight between 2 and 3 g m^{-2} – roughly five-fold greater than that of the macrofauna (Table 6.1) and 100-fold higher than that of the nematodes. In mesotrophic equatorial sediments, microbial biomass declines somewhat in absolute terms (to 1.4 g C m^{-2}: Smith et al., 1997), but the ratio to other size classes increases, microbial biomass being about ten-fold larger than that of the macrofauna. Although much of the bacterial biomass in sediments may consist of cells sinking out of the water column (Novitsky, 1987), the high microbial biomass relative to other size classes suggests that the microbes may account for a large proportion of the respiration of the sediment community in eutrophic and mesotrophic sediments of the equatorial abyss.

Manganese nodules occur in the mesotrophic abyss, and occasionally in the eutrophic abyss (Fig. 6.6), and provide solid substrata for communities fundamentally different from those in surrounding soft sediments. These polymetallic accretions often attain densities between 100 and 300 m^{-2}, covering 20 to 50% of the plan area of the seafloor (e.g., Heezen and Hollister, 1971; Mullineaux, 1987). At 5ºN, 125ºW, roughly 10% of exposed nodule surfaces are covered by sessile, eukaryotic organisms, with Foraminifera accounting for over 98% of community abundance and areal cover (Mullineaux, 1987). Metazoans found attached to nodules include small sponges, molluscs, polychaetes and bryozoans; according to Mullineaux, the vast majority of the nodule species are not found in surrounding sediments. Mullineaux found that the areal density of animals >63 μm in diameter attached to nodules was roughly 10% of that of the sediment-dwelling meiofauna. Local species diversity on nodules is roughly comparable to that of the sediment-dwelling nematodes, with ~25 species among 50 individuals (Mullineaux, 1987).

In addition to manganese nodules, xenophyophores are likely to provide substantial habitat heterogeneity on the seafloor in the equatorial abyss. Although the ecology of xenophyophores in the equatorial abyss has not been explicitly studied, in other areas (e.g., seamounts) the tests of these organisms provide shelter and/or food resources for a specialized community of macrofaunal invertebrates (Levin and Gooday, 1992). Because of their abundance (2 to 6 m^{-2}), xenophyophores are very likely to contribute fundamentally to macrofaunal community structure in the equatorial abyss.

Nowhere in the equatorial Pacific have the biomasses for all size classes of benthos (i.e., the megafauna, macrofauna, meiofauna and microbiota) been tabulated. The best biomass data come from the EqPac transect, where macrofauna and microbiota occur in biomass ratios of roughly 1:5 in eutrophic sediments, as against 1:10 in mesotrophic settings. This contrasts with a macrofauna:microbiota biomass ratio of 6:1 in the bathyal Santa Catalina Basin on the California margin, suggesting that microbes may be relatively much more important in the energetics of abyssal equatorial communities.

Carbon sources and trophic types

The most important sources of organic matter in both eutrophic and mesotrophic equatorial Pacific habitats are likely to be: (1) small sinking particles, whose flux has been evaluated with moored sediment traps; (2) phytodetrital aggregates, which may be too large and rare to be reliably captured in traps; and (3) the sinking carcasses of nekton (crustaceans, fish, whales, etc.). In the eutrophic equatorial abyss, the flux of particulate organic carbon at greater depths shows substantial short-term variability, fluxes into deep sediment traps varying as much as two-fold between 17-day sampling periods (Honjo et al., 1995). Substantial interannual variability in the flux of particulate organic carbon also occurs in eutrophic and mesotrophic equatorial settings; for example, Dymond and Collier (1988) found that during the 1982–83 El Niño, the flux of particulate organic carbon at a eutrophic equatorial station (1ºN, 139ºW) was roughly half that in a non-El Niño year, whereas flux of particulate organic carbon at a mesotrophic station (11ºN, 140ºW) roughly doubled. Despite this variability, in both eutrophic and mesotrophic sites the remineralization rates of organic carbon, as evaluated by oxygen uptake in *in situ* respirometers, roughly matched the rate of rain of particulate organic carbon into deep-moored sediment traps (Hammond et al., 1996; Berelson et al., 1997; Smith et al., 1997). Thus, the prime source of organic carbon to infaunal benthos in equatorial sediments appears to be the flux of small sinking particles. However, these respirometry measurements are relatively few in number and cover only small areas (<0.2 m^2 each); they thus do not include the deposit-feeding and scavenging megafauna, and may miss important seafloor hot-spots of metabolic activity. Xenophyophore tests and echiuran feeding pits in particular may serve as important traps of food-rich sedimenting particles, adding heterogeneity to seafloor mineralization processes (Levin and Gooday, 1992; Smith et al., 1996). Thus, it is quite possible that other sources of organic matter, such as phytodetrital aggregates or large sinking carcasses, contribute significant food energy to equatorial abyssal sediments.

There is some evidence that freshly settled phytodetritus may be an important source of labile organic matter to eutrophic equatorial sediments. Recently, Smith et al. (1996) found concentrations of fresh, greenish, phytoplankton detritus on the seafloor from 5ºS to 5ºN along the 140ºW meridian in Nov.–Dec. 1992. Gardner et al. (1984) also observed phytodetrital aggregates in this region in 1977. Phytodetritus collected by Smith et al. (1996) sustained high rates of microbial activity and was rich in excess ^{234}Th activity, suggesting it had settled from the water column in the previous 100 days. This material appeared to be selectively grazed by holothurians and echiurans, and was cached in burrows as deep as 27 cm in the sediment. Smith et al. estimated that the standing stock of phytodetritus in November and December 1992 constituted about 3% of the annual flux of particulate organic carbon to the eutrophic equatorial seafloor. In addition, modeling of organic-matter reactions indicated that, during November and December 1992, organic-carbon degradation in eutrophic sediments along the EqPac transect was dominated by a very labile component with a mean degradation half-life of ~20 days; this labile organic carbon appeared to be derived from the phytodetritus (Hammond et al., 1996) and was similar in lability to the dominant material degrading in sediments from depths of 4000 m on the California margin (Sayles et al., 1994). Phytodetrital flux in the equatorial Pacific seems to be related to the formation of intense convergence zones in the euphotic zone during the passage of tropical instability waves, which are most common between August and December (Smith et al., 1996). Thus, phytodetritus may frequently settle to the eutrophic equatorial seafloor during the boreal autumn, and could supply a significant fraction of the energy requirements of the abyssal benthos. In the mesotrophic equatorial abyss phytodetritus has not been observed, suggesting that the flux of particulate organic carbon may be lower in quality, as well as quantity, in the mesotrophic regions than in eutrophic equatorial settings.

As on the California slope, there are faunal components adapted to utilize all the prominent sources of organic carbon to equatorial Pacific sediments. Although poorly studied, the megafauna include a well adapted suite of very mobile, swimming scavengers, including lyssianisid amphipods, macrourid fish, and natantian decapods, which rapidly consume fish and cephalopod bait placed on the seafloor (R. Hessler, personal communication). Unlike that of the California slope, the scavenger community of equatorial Pacific sediments does not include epibenthic species (e.g., ophiuroids, onuphid polychaetes) which walk to bait-falls.

The xenophyophores, which constitute 90–95% of the megafaunal abundance at both eutrophic and mesotrophic EqPac sites, can be considered as deposit feeders that primarily digest organic material from detrital particles (Levin and Gooday, 1992; Gooday et al., 1993). It is also quite possible that these giant protozoans take up dissolved organic matter, prey on small metazoans, and cultivate bacteria (Levin and Gooday, 1992); they thus may simultaneously occupy a number of trophic levels. Because of their low biomass, the flux of energy through xenophyophores is likely to be small compared to the remainder of the benthos, even when xenophyophores are abundant (Levin and Gooday, 1992).

Suspension-feeding glass sponges in the genus *Hyalonema* dominate the metazoan, epibenthic megafauna at eutrophic and mesotrophic stations along the EqPac transect, constituting 55% to 87% of the metazoan megafaunal abundance (Hoover et al., 1994); this contrasts sharply with California slope habitats where mobile deposit feeders or omnivores dominate the megafauna. The remainder of the megafaunal epibenthos (13% to 45%) at eutrophic stations is composed of surface/subsurface deposit feeders including irregular urchins that plow through surface sediments, and presumably holothurians feeding selectively on the surface deposits (Hoover et al., 1994; Smith and Hoover, unpublished data). Fresh spoke traces (or rosettes) formed by echiurans and large polychaetes are quite common in both eutrophic and mesotrophic settings, attaining densities (0.06 to 0.2 m^{-2}) comparable to that of the megafaunal epibenthos. These traces indicate that the burrowing megafauna is also likely to contain a relatively high abundance of selective surface-deposit feeders.

Thus far, trophic analyses of macrofauna in the equatorial abyss have been restricted to the polychaetes, which constitute more than 60% of community abundance and biomass (see above). Studies in the Clipperton–Clarion Fracture Zone (Paterson et al., 1998) and at the DISCOL site (Borowski and Thiel, 1998) indicate that more than 58% of the total polychaete abundance falls into families considered to be deposit feeders in the deep sea (e.g., Kukert and Smith, 1992), with the cirratulids, paraonids, sabellids and spionids accounting for most of the abundance. In both areas, surface-deposit feeders predominate, comprising at least 37 to 56% of polychaete abundance. Subsurface deposit feeders, consisting primarily of paranoids, make up only 8.5 to 22% of the polychaetes. In the Clipperton–Clarion Fracture Zone, predators and omnivores constitute a surprisingly high percentage of the polychaete community, accounting for 18 to 28% of polychaete abundance. Based on the limited data thus far available, there do not appear to be any marked differences in polychaete trophic composition between eutrophic and mesotrophic equatorial sediments (Paterson et al., 1998). It should be noted that the trophic structure of polychaetes in the equatorial abyss differs substantially from that on the oxygenated California margin, where subsurface deposit feeders typically constitute at least 50% of community abundance (see above).

The Nematoda are also strongly dominated by deposit feeders. Brown (1998) found that 59 to 76% of individuals, and 53 to 68% of species, of nematodes from the top centimeter of sediment along the EqPac transect (0º, 2º, 5º, and 9ºN along the 140ºW meridian) were deposit feeders. Selective deposit feeders predominated (57 to 68% of total numbers), and their absolute abundance was strongly correlated with microbial abundance in the sediments along the transect. Predatory and/or scavenging nematodes were very rare in the equatorial Pacific, accounting for less than 10% of the total number of individuals at each station (Brown, 1998). Very low predator/scavenger abundance is a typical feature of abyssal nematode communities when compared to shallow-water sediment assemblages, and is thought to reflect a lower relative availability of prey items and carrion in the abyss (Brown, 1998).

Rates of key ecological processes

A number of key ecological rates have been evaluated in the equatorial Pacific, including sediment community respiration, bioturbation, and, to some extent, recolonization following disturbance. These rate data come primarily from the EqPac study and the DISCOL experiment.

Studies with benthic incubation chambers and sediment porewaters indicate that, in January 1992, seafloor oxygen consumption was fairly constant along the equator from 103ºW to 140ºW, with rates of 0.6 to 0.8 $mmol\,m^{-2}\,d^{-1}$ (equivalent to roughly $2\,g\,C\,m^{-2}\,y^{-1}$) (Hammond et al., 1996). Seafloor respiration rate declined roughly symmetrically with distance from the equator along the 140ºW meridian during November and December 1992, falling from roughly 2.3 g C m^{-2} y^{-1} between 2ºS and 2ºN to roughly 0.3 g C m^{-2} y^{-1} at 12ºS and 9ºN (Fig. 6.11). At all these stations, at least 70–90% of the organic carbon degradation occurs in the oxygenated, top 5 cm of sediment, indicating that oxygen is the primary electron acceptor during organic-matter mineralization (Hammond et al., 1996). This contrasts sharply with California slope habitats where anaerobic metabolism (e.g., denitrification and sulfate reduction) may control up to 54% of organic matter degradation (Fig. 6.9). Between 2ºS and 2ºN, seafloor respiration rates showed substantial variability on time scales of months, apparently in response to changes in the flux of particulate organic carbon induced by El Niño events (Hammond et al., 1996; Berelson et al., 1997). This variability in seafloor respiration rates (i.e., in organic-carbon mineralization rates) is highly consistent with the results from modeling of organic-matter reactions, suggesting that most (70 to 90%) of the degrading organic carbon in eutrophic equatorial sediments is very labile, with a degradation half-life of ~20 days (Hammond et al., 1996).

Bioturbation has been well studied along the EqPac transect and, at any point, appears to result from the summation of three processes: (1) eddy-diffusive mixing of the top 2 to 8 cm of sediment by small macrofauna and meiofauna; (2) pulsed homogenization of the top 2 to 3 cm of sediment by plowing urchins (Fig. 6.6); and (3) episodic transport of surface sediments to depths between 3 and 27 cm by echiurans and other animals that feed on surface sediments from a central burrow and then defecate within their burrows (Smith et al., 1997). Eddy diffusive mixing along the EpPac transect exhibited both a rough correlation with the flux of particulate organic carbon and substantial dependence on the tracer used and the time scale. At eutrophic stations (2ºS to 5ºN), eddy-diffusion coefficients (D_b) for both ^{234}Th and ^{210}Pb were at least 10-fold higher than for the same isotopes at the mesotrophic site (9ºN), and correlation coefficients between D_b and the flux of particulate organic carbon along the whole transect were >0.88 for each isotope ($p < 0.05$). The depth to which ^{210}Pb was mixed also decreased from ~8 cm at eutrophic stations to ~2 cm at 9ºN (Smith and Rabouille, 2002). In addition, D_b values for the short-lived isotope ^{234}Th (half life = 24 d) were 5 to 70 times greater than those for ^{210}Pb (half life = 22 yr) in the same cores and over the same depth intervals (Smith et al., 1997). This tracer-dependent mixing provides strong support for the "age-dependent mixing" hypothesis, which predicts that recently deposited, relatively organic-rich particles are ingested and mixed at higher rates than are food-poor particles (see detailed discussion of age-dependent mixing above (p. 195). Phytodetritus, which is rich in ^{234}Th and labile organic compounds (Smith et al., 1996; Stephens et al., 1997), is likely the target of this age-dependent ingestion and mixing.

The second major form of mixing along the eutrophic portions of the EqPac transect results from urchins plowing through near-surface sediments (see Fig. 6.6). X-radiographs of box-core sediments indicate that urchin plowing homogenizes a swathe roughly 10 cm wide and 2–3 cm deep (Smith et al., 1997). This mixing produces a vertical "shoulder" in the profiles of excess ^{210}Pb, which then disappears over time owing to the diffusive mixing of smaller macrofauna and meiofauna described above. By modeling the disappearance of urchin shoulders in ^{210}Pb profiles, Hoover (1995) estimated that urchins rework approximately 10 to 15% of the seafloor per year, and a random spot on the seafloor is stirred by a passing urchin every 5 to 7 years. Thus, urchin mixing may have profound effects on sediment processes with recovery times longer than a few years, such as degradation of moderately labile particulate organic carbon and, perhaps, macrofaunal succession. Urchin burrowing has been shown to affect the diversity and community structure of shallow-water communities (Thayer, 1983; Austen et al., 1998) suggesting that urchin disturbance in the abyssal equatorial Pacific also influences the structure of infaunal assemblages.

The final form of mixing in equatorial Pacific sediments is the transport of superficial sediments to depths of 3 to 27 cm within the sediment column by echiuran worms and other burrow dwellers (Smith et al., 1997). At the eutrophic EqPac stations, roughly 15 to 30% of the excess inventory of ^{234}Th was found at depths of 2 to 4 cm, indicating that many particles are subducted centimeters into the sediment column within 100 days of arrival on the seafloor (Pope et al., 1996). Some of this subduction apparently results from the caching of food-rich phytodetritus in the burrows of infaunal megabenthos, such as echiuran worms (Smith et al., 1996, 1997).

Recolonization rates following anthropogenic disturbance of sediments have been evaluated on the abyssal equatorial seafloor as part of the DISCOL experiment (Fig. 6.1). In order to explore the potential effects of manganese-nodule mining on abyssal Pacific communities, a sled 8-m wide with plowshares (the "plow-harrow") was towed 78 times through a circular study area 3.6 km in diameter in 4160 m of water in the eastern tropical Pacific (~7ºS, 88ºW: Borowski and Thiel, 1998). The plow-harrow disturbed roughly 20% of the seafloor within the study area, digging furrows to roughly 10–15 cm into the sediment. Samples were collected from disturbed and undisturbed areas of the seafloor using a box corer within days of plowing, and then approximately six months and three years later. Within plowed tracks, macrofaunal abundance was initially reduced by 39%, the polychaetes being most heavily disturbed (Borowski and Thiel, 1998). After three years, the abundance of most higher-level taxa had returned to the levels in the background community, but species diversity remained significantly depressed, indicating a sustained disturbance effect (Borowski and Thiel, 1998). The vertical distribution of macrofauna within the sediment also remained anomalous, apparently because physical and chemical characteristics had not returned to normal. The unexpectedly rapid recolonization of plow tracks apparently occurred by lateral migration of benthic individuals from adjacent unplowed sediments, rather than by larval settlement. Lateral migration was facilitated by the relatively small width of individual plow furrows (~1 m: Borowski and Thiel, 1998). These results indicate that recovery of the infaunal community from moderate, relatively small-scale, physical disturbance in the equatorial abyss requires more than three years (Borowski and Thiel, 1998). Recovery of the sediment community from actual nodule mining, which would disturb much greater areas at higher intensities, is virtually certain to require much longer time periods – decades (Borowski and Thiel, 1998).

The oligotrophic abyss

More than 40% of the abyssal seafloor in the Pacific underlies oligotrophic central gyres, which are the vast nutrient-poor deserts of the ocean. In the North Pacific, the central gyre stretches from roughly 15ºN to 35ºN, and from 135ºE to 135ºW, covering an area of approximately 2×10^7 km^{-2} (Karl, 1999); a similar gyre is present in the South Pacific. Because of deep nutriclines and great distances from continental sources of nutrients (e.g., river outflow and dust), the central gyres sustain lower rates of primary production than any other ice-free areas of the ocean (e.g., Berger, 1989). This low productivity, combined with great water depths (typically 5000 to 6000 m), results in extremely low flux rates of particulate organic carbon to the underlying seafloor (typically ~0.3 g C m^{-2} y^{-1}: K.L. Smith, 1992). Ecosystem characteristics in these extraordinarily food-poor habitats differ markedly from those in the eutrophic deep sea.

Habitat and community description

The benthic ecology of two abyssal sites in the North Pacific Gyre have been investigated in some detail. The first is the CLIMAX II region (named after the CLIMAX II research expedition), which is ~50 km in diameter and centered on 28º28′N, 155º20′W (Hessler and Jumars, 1974). The second area, MPG-I (Fig. 6.1), falls roughly within the box 30º to 32ºN, 157º to 159ºW (K.L. Smith, 1992). Both areas have water depths ranging from 5500 to 6100 m, and very sluggish bottom currents with no evidence of sediment resuspension (K.L. Smith, 1992) and appear to be representative of the oligotrophic abyss. These sites were studied, in part, to explore the feasibility of burying high-level nuclear wastes within the clay sediments of the North Pacific central gyre during the SubSeabed Disposal Program of the United States in the late 1970s and early 1980s.

Sediments at these oligotrophic sites are red clays (85% of mass consisting of particles <6 μm in diameter) of very low organic-carbon content (typically ~0.25% by weight) studded with manganese nodules (Fig. 6.6). Net sedimentation rates are extremely low, with sediments accumulating at ~1 μm yr^{-1}. Bottom waters are well oxygenated (3.7 ml O_2 ℓ^{-1}) and sediment pore-waters typically contain oxygen to tens of centimeters below the sediment–water interface (Hessler and Jumars, 1974; personal observations). Biogenic structures are much rarer at the sediment surface than in more eutrophic settings, and include occasional holothurian trails and decimeter-scale mounds formed by echiurans and other unidentified infaunal megabenthos. The dynamics of these biogenic structures have not been evaluated in the oligotrophic Pacific, but by extrapolation from eutrophic and mesotrophic habitats one may suppose that such structures likely persist for years.

The known oligotrophic megafauna is characterized by two components: (1) a very sparse epibenthos composed mainly of holothurians, cnidarians and xenophyophores, and (2) highly mobile scavengers. At the station MPG-I, the epibenthic megafauna is dominated by the holothurian *Amperima* sp. feeding on surface deposits, and an unidentified, suspension-feeding cnidarian (K.L. Smith, 1992). The combined densities of these metazoans is ~0.15 m^{-2}, which is comparable to the abundance of metazoan megafauna in the mesotrophic abyss (Table 6.1). Xenophyophores appear to be common relative to metazoan megabenthos (K.L. Smith, 1992), but their identification and abundance remain unknown.

The scavenging megafauna have been well studied in the oligotrophic abyss, in part because of their potential to disperse radioactive wastes spilled on the seafloor. In the absence of food falls, scavenging megafauna rarely appear in photographs and are likely to be very sparsely distributed. Nonetheless, baited-trap and camera deployments rapidly attract a voracious assemblage of highly mobile necrophages (Dayton and Hessler, 1972; Hessler, 1974; Ingram and Hessler, 1983). Scavengers include two species of giant lysianassid amphipods reaching lengths greater than 10 cm (*Alicella gigantea* and *Eurythenes gryllus*), a suite of smaller lysiannassids a few centimeters in length (*Orchomene gerulicorbis, Paralicella caperesca* and *P. tenuipes*), rattail fish (*Coryphaenoides armatus*) and natantian decapods (Hessler et al., 1972; Hessler, 1974; Ingram and Hessler, 1983, 1987; Barnard and Ingram, 1986; Priede et al., 1991). All these scavengers are very good swimmers, typically arriving at bait-falls within minutes to hours and achieving concentrations of tens to hundreds of individuals at single bait-falls (Dayton and Hessler, 1972; Priede et al., 1994). Bait parcels are consumed very rapidly, tens of kilograms of fish flesh being eaten within 12 to 24 hr (Dayton and Hessler, 1972; Hessler, 1974). The abundance and biomass of mobile scavengers is very difficult to evaluate, but Priede et al. (1990, 1994) and K.L. Smith (1992) have used arrival times at baits to estimate roughly the abundance and biomass of *Eurythenes gryllus* (3.5 to 47.2 individuals km^{-2} and 0.5 to 6.2 g wet weight km^{-2}) and *Coryphaenoides armatus* (330 individuals km^{-2} and ~150 kg wet weight km^{-2}) in the oligotrophic abyss.

The macrofauna of the oligotrophic abyss is very sparse, diminutive in body size, and yet highly diverse. Densities of infaunal metazoan macrobenthos at the CLIMAX II site range from 64 to 160 individuals m^{-2}, that is, they are roughly one-hundredth as numerous as those in oxygenated slope habitats. Macrofaunal abundance is dominated by polychaetes (55%), tanaids (18%), bivalves (7%) and isopods (6%) (Hessler and Jumars, 1974); thus, the polychaetes are somewhat less important, and the tanaids substantially more important, than on the slope (Hessler, 1974). At the familial level, the macrofauna has substantial proportions of cirratulid (25%), capitellid (14%), fauveliopsid (11%), and paraonid (>6%) polychaetes (Hessler and Jumars, 1974); these families are also prominent in equatorial and California-slope sediments (Kukert and Smith, 1992; Borowski and Thiel, 1998). Mean macrofaunal body size is very small at ~0.07 mg (Table 6.1) – that is, nearly an order of magnitude lower than in the equatorial abyss. Total macrofaunal biomass (0.02–0.12 mg m^{-2}: K.L. Smith, 1992) is roughly two orders of magnitude lower than in slope settings, and somewhat lower than in the mesotrophic abyss (Table 6.1). Species diversity in the oligotrophic macrofauna is very high, even by deep-sea standards, with more than 45 species found among 100 polychaete individuals from pooled box-core samples (Fig. 6.7; Hessler and Jumars, 1974). Because of the low standing crop of macrobenthos, however, the number of macrofaunal species in any unit area of seafloor is relatively low.

The macrofaunal size class in the oligotrophic abyss also includes the relatively abundant Komokiacea, a group of agglutinating protozoans (Foraminifera) in which the test consists of systems of fine tubules (Tendal and Hessler, 1977). The tests of these protists frequently reach several centimeters in diameter, but their standing crop is difficult to evaluate because they usually fragment, and because their diffuse protoplasm occupies only a small proportion of their test volume (Tendal and Hessler, 1977).

The meiobenthos have been studied at one oligotrophic abyssal site (MPG-I) and appear to constitute a major component of the infaunal benthos. Snider et al. (1984) found 202 000 meiofaunal individuals m^{-2}, with 90% of them concentrated in the top 3 cm of sediment. Foraminifera and nematodes accounted for the bulk of meiofaunal abundance (50% and 45%, respectively), with harpacticoids (5%) also occurring frequently. Tardigrades, ostracods, kinorhynchs and gastrotrichs constituted less than 1% of the meiofauna (Snider et al., 1984). Meiofaunal biomass (0.24 mg wet weight m^{-2}) was dominated by the Foraminifera (87%) nematodes (7%) and harpacticoids (6%).

The sediment microbes (or nanobenthos) larger than 10 μm in diameter were also studied at MPG-I by Snider et al. (1984). In decreasing order of numerical importance, these consisted of prokaryotes (e.g., large bacteria), "yeast-like" cells, flagellates, and amoebae.

For this sediment nanobiota, Snider et al. estimated numerical density of $6.6 \times 10^7\,m^{-2}$ and biomass of 0.13 g wet weight m^{-2}.

Manganese nodules are common in the oligotrophic abyss, typically covering roughly 30% of the seafloor (Mullineaux, 1987). As in the mesotrophic equatorial Pacific, Mullineaux (1987) found the eukaryotic nodule fauna of the MPG-I site to be dominated (>99%) in numbers and biomass by Foraminifera and related rhizopod protozoans, which covered approximately 10% of exposed nodule surfaces. Interestingly, 92% of the nodule taxa found at MPG-I were also found on nodules 4000 kilometers away in the equatorial Pacific, whereas virtually none were found in surrounding sediments (Mullineaux, 1987). With densities of very roughly 4000 m^{-2} of total seafloor, these hard-substratum "meiobenthos" were roughly two orders of magnitude less abundant than their meiofaunal counterparts dwelling in surrounding MPG-I sediments (Mullineaux, 1987). The abundance and species diversity of the MPG-I nodule fauna was approximately half that on nodules in the mesotrophic equatorial Pacific, presumably reflecting lower inputs of particulate organic carbon (Mullineaux, 1987).

The biomass distribution of the total benthic community has perhaps been better studied at MPG-I than at any other site in the deep Pacific Ocean. K.L. Smith (1992) compiled biomass data from the vicinity of MPG-I to examine carbon cycling through the oligotrophic abyssal benthos. The ratios of biomass between megafauna, macrofauna, meiofauna and microbiota at this 5800-m site were roughly as 0.5:0.03:0.6:1.0 (K.L. Smith, 1992). Thus, the microbes (which here includes bacteria >10 μm in diameter) dominate community biomass, with megafauna and meiofauna also being relatively important. In the oligotrophic abyss, relatively little metabolically active biomass appears to be concentrated in the macrofauna, suggesting that other size classes, especially the microbes and meiofauna, dominate metabolism (K.L. Smith, 1992). This situation contrasts with biomass distributions on the California slope and in shallow water, where megafauna and macrofauna typically dominate the biomass distribution (Gray, 1981; Snider et al., 1984; Gerlach et al., 1985). Thus, under extremely oligotrophic conditions, the smallest size classes of benthos appear to assume much greater importance in the recycling of organic matter on the deep-sea floor.

Carbon sources and trophic types

The primary sources of organic matter for the oligotrophic Pacific abyss are likely to be (1) the flux of small sinking particles measured in sediment traps and (2) the sinking carcasses of nekton (particularly crustaceans, fishes and whales). Other sources of organic matter found in more eutrophic settings (e.g., phytodetrital aggregates, macroalgal debris) have not been observed in the oligotrophic abyssal Pacific.

The flux of fine particulate organic carbon to the oligotrophic seafloor, as measured in sediment traps in the MPG-I area, is roughly 0.3 g C $m^{-2}\,y^{-1}$ (K.L. Smith, 1992); this is equivalent to one-sixth to one-third of the flux measured in the eutrophic equatorial abyss, and only about one-thirtieth of the flux measured on the California slope (Table 6.1). When compared to the organic-carbon demand of the sediment community measured by seafloor respirometry, this sinking flux of particulate organic carbon appears inadequate by up to 50% in meeting the metabolic requirements of the oligotrophic benthos (K.L. Smith, 1992). This may imply that other sources of organic matter, such as large food falls, provide substantial carbon flux to the oligotrophic seafloor. Given the normal sparseness of scavengers and the low biomass of scavenging rattails and amphipods (Priede et al., 1990, 1994; K.L. Smith, 1992), it seems unlikely that nekton falls constitute a large proportion of the organic-carbon flux. A more likely explanation for the inadequacy of the flux of small particulate organic carbon is that all deployments of sediment traps in the MPG-I region have been for very short periods of time (7 to 14 days); thus, as on the continental margin (K.L. Smith et al., 1992), they are likely to have missed important pulses of particulate organic carbon flux. Karl et al. (1996) showed that, even in oligotrophic waters, a substantial proportion of the flux of particulate organic carbon may occur as brief pulses following occasional, intense bursts of primary production. Clearly, sediment-trap deployments for longer time scales (a year or more) must be combined with synchronous measurements of seafloor respiration to determine whether the flux of small particulate organic carbon is sufficient to feed the oligotrophic benthos.

The flux of large organic falls to the oligotrophic seafloor has not been evaluated, but the consumption of large carrion parcels within hours (Dayton and Hessler, 1972; Hessler, 1974) and the extreme adaptations of scavengers (Dahl, 1979; Barnard and Ingram, 1986) indicate that this flux is evolutionarily and ecologically important. Oligotrophic scavenger aggregations differ markedly from those from eutrophic slope habitats in a number of intriguing ways. Oligotrophic aggregations are comprised of relatively few species of fast swimmers (mostly amphipods and rattails), and do not include the epibenthic ophiuroids, crabs and polychaetes that are attracted to bait-falls on the Californian slope (Hessler, 1974; Smith, 1985). The body sizes of oligotrophic scavengers also tend to be larger, the amphipod *Eurythenes gryllus* attaining a length of 14 cm (Ingram and Hessler, 1983) and *Alicella gigantea* reaching the "supergiant" size of 34 cm (Barnard and Ingram, 1986), whereas scavenging amphipods from depths of 1000–1700 m on the Californian slope are less than 1 cm in length (Smith, 1985; C.R. Smith, unpublished data). The abyssal lysianassids also exhibit dramatic adaptations for scavenging, including mouthparts capable of tearing off and ingesting large chunks of flesh, and capacious guts designed to store enormous quantities of food (Dahl, 1979; Barnard and Ingram, 1986; Hargrave et al., 1994). Adult *E. gryllus,* for example, can fill their guts in less than thirty minutes, and apparently can survive on one such meal for some 300 days (Hargrave et al., 1994). The exploitation of carrion by fewer species of more specialized necrophages in the oligotrophic abyss suggests that large food falls provide a higher proportion of the energy requirements for the scavengers than on the California slope.

The epibenthic megafauna of the oligotrophic abyss is dominated by deposit feeders in the form of xenophyophores and the holothurian *Amperima* sp., although apparently suspension-feeding cnidarians are also important (K.L. Smith, 1992). It should be noted, however, that the xenophyophores could conceivably occupy a number of trophic levels, because they may have the potential to take up dissolved organic matter, to prey on small metazoans, and to garden bacteria (Levin and Gooday, 1992). Overall, megafaunal trophic structure in the oligotrophic abyss appears to be fairly similar to that in the eutrophic equatorial Pacific (see discussion above), although the oligotrophic data base is very slim. The infaunal macrobenthos is overwhelmingly dominated (93%) by deposit feeders, with potential suspension feeders and carnivores/omnivores constituting just 7% of abundance (Hessler and Jumars, 1974). Among the polychaetes, the deposit feeders are divided roughly equally between surface- and subsurface-deposit feeders, and nearly all are motile (Hessler and Jumars, 1974; Jumars and Gallagher, 1982). Based on analogies with other deep-sea settings, the infaunal meiobenthos of the oligotrophic abyss is dominated (95%) by taxa (the Foraminiferida and Nematoda) thought to indulge primarily in detritivory, which may include scavenging, deposit-feeding, and uptake of dissolved organic matter (Gooday et al., 1992; Brown, 1998). Because of the extreme nature of oligotrophic habitats, the feeding biology of the oligotrophic meiobenthos merits greater direct study before drawing strong conclusions about trophic composition.

In contrast to the infaunal macrofauna and meiofauna, a large proportion (>44%) of the nodule-encrusting fauna in the oligotrophic abyss appear to be suspension-feeders (Mullineaux, 1987). The trophic (as well as taxonomic) composition of the oligotrophic nodule fauna closely resembles that on nodules in mesotrophic equatorial habitats (Mullineaux, 1987).

Rates of key ecological processes

The rates of very few key ecological processes have been measured in the oligotrophic abyssal benthos. Reliable data exist for sediment community respiration, and respiration rates of the epibenthic megafauna and benthopelagic fauna (specifically, rattails and *E. gryllus*) also have been roughly estimated (e.g., K.L. Smith, 1992). Sediment-community respiration rates, as estimated by seafloor respirometers, range from 0.25 to 1.02 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ in the MPG-I area (K.L. Smith, 1992). Because the microbiota and meiofauna dominate the sediment community biomass (see above, pp. 207–208), these size classes are likely to control sediment-community respiration in the oligotrophic abyss. These rates overlap the lower half of the range for the mesotrophic equatorial Pacific, and are roughly one-third to one-tenth of those for California-slope habitats (Table 6.1). Respiration rates estimated for the epibenthic metazoan megafauna (*Amperima* sp. and cnidarians) and the benthopelagic fauna (scavenging amphipods and rattails) are ~0.05 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ and ~0.001 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$, respectively (K.L. Smith, 1992). Thus, the seemingly sparse epibenthic megafauna appear to account for roughly 5–15% of total benthic community respiration, while benthopelagic amphipods and rattails account for no more than about 0.3%.

It should also be noted that sediment-community respiration in the MPG–I area shows significant temporal variability, which could be related to seasonal or aperiodic pulses in the flux of particulate organic carbon resulting from phytoplankton blooms (Smith and Baldwin, 1984; K.L. Smith, 1989). However, because of insufficient temporal coverage from sediment traps and seafloor respirometers, the strength of coupling between surface-ocean processes and seafloor respiration in the oligotrophic abyss remains unclear.

Seamounts

There are tens of thousands of seamounts protruding more than one thousand meters above the abyssal seafloor of the Pacific; these create a complex mosaic of deep-sea benthic habitats.

Habitat and community description

Many Pacific seamounts are steep-sided and current-swept because of intensification of topographic flow; these contain large areas of rocky substratum. Many seamounts also contain soft sediments (frequently foraminiferal or basaltic sands) inside craters and on level benches and shelves where slopes and currents are moderate enough to allow sediment accumulation [see Levin et al. (1991c) for a schematic diagram of a typical seamount]. Seamounts interact with ocean currents on a variety of scales, potentially yielding internal waves, eddy formation, local upwelling and trapped circulation cells called Taylor columns (Boehlert and Genin, 1987). Because of the complex nature of seamount topography, current regimes and sediment composition, benthic habitats on seamounts typically are highly heterogeneous on scales of 1–10 km (Boehlert and Genin, 1987; Levin et al., 1991c, 1994), making broad ecological generalizations difficult.

The benthic ecology of Pacific seamounts has received significant study because these features may support productive (albeit small-scale) fisheries (Boehlert and Genin, 1987; Rogers, 1994), they may be of strategic significance for submarine warfare, and they may provide sites for allopatric speciation in populations with restricted bathymetric distributions (Wilson and Kaufmann, 1987).

The hard, rocky substratum of deep seamounts is characterized by suspension-feeding megabenthos such as antipatharians, gorgonians and other cnidarians, as well as occasional crinoids, ophiuroids, cirripeds and a variety of other taxa (Genin et al., 1986; Wilson and Kaufmann, 1987; Grigg et al., 1987; Rogers, 1994). Suspension-feeding antipatharians and gorgonians typically are more abundant near seamount peaks, where flow acceleration may enhance the flux of suspended food particles (Genin et al., 1986); these same taxa are much less abundant where currents are reduced, or where manganese crusts may inhibit recruitment (Grigg et al., 1987). A number of precious corals are found on Pacific seamounts and some are commercially harvested. These include red and pink corals (*Corallium* spp.) and black corals (*Antipathes* spp.) (Rogers, 1994). A surprisingly large proportion of the world's catch of red coral historically has come from Pacific seamounts; for example, in 1983, roughly 140 000 kg (70% of the world catch) of red coral was harvested from the Emperor–Hawaiian seamounts (Rogers, 1994). These deep corals are characterized by very low rates of recruitment and growth, and may easily be overexploited (Grigg, 1984).

Large xenophyophores dominate the megafauna on soft substrata of many bathyal seamounts in the eastern Pacific, reaching densities as high as 18 m^{-2} (Levin and Thomas, 1988). The decimeter-sized tests of xenophyophores provide habitat for a broad range of macrofaunal and meiofaunal taxa, including isopods, tanaids, ophiuroids and nematodes, contributing to small-scale spatial heterogeneity of seamount sediment communities. Xenophyophores are thus likely to contribute to the maintenance of species diversity in seamount sediments (Levin and Thomas, 1988).

The infauna of a variety of deep Pacific seamounts has been studied to explore the effects of hydrodynamic regime, sediment type and mobility, water depth and latitude on macrobenthic community structure and recolonization rates. In a study of 18 seamounts ranging in depth from 788 to 3533 m, Levin et al. (1991c) found little relationship between the abundance of polychaetes and either water depth or sediment sand content. In addition, the representation of polychaete families on the seamounts was similar to that in other deep-sea soft-substratum communities, and levels of species diversity were comparable. However, filter feeders, especially sabellids, were more abundant in rippled foraminiferal sands that in other sediment types (Levin et al., 1991c). At water depths of 1480 to 3150 m on Horizon Guyot and Magellan Rise in the central Pacific, Levin and Thomas (1989) found substantial differences between macrobenthos in coarse, rippled sands (subjected to strong bottom corrents) and assemblages in unrippled, finer-grained sediments. Macrobenthos were less abundant in the high energy sites (255 m^{-2} versus 388 to 829 m^{-2}), and were dominated by sessile, surface-feeding forms. In contrast, the quieter, finer-grained sediments were dominated by motile, subsurface-feeding forms living closer to the sediment–water interface (Levin and Thomas, 1989). In another set of studies of contrasting sediment-mobility regimes, Levin et al. (1994) found that, on Fieberling Guyot in the eastern Pacific at depths of 585 to 635 m, sediment mobility was associated with higher macrofaunal densities (1870 m^{-2} versus 1489 m^{-2}) and lower species diversity than in a quiescent setting. Tube building, surface-deposit feeding, and filter feeding were more common in the stable substrata, whereas subsurface burrowers were more common in shifting sands. Colonization rates were also faster in the shifting-sand habitat on Fieberling Guyot, apparently because bedload transport of juveniles and adults was the dominant recolonization mode over small spatial scales at this site (Levin and DiBacco, 1995). In fact, the macrofaunal community in the shifting-sand site retained features of early successional stages, suggesting that ripple migration constituted a significant macrofaunal disturbance (Levin and DiBacco, 1995). All of these studies suggest that substrate mobility may exert substantial control over community structure and colonization rates on Pacific seamounts, and that the structure of the benthic community on seamounts is controlled by a complex suite of variables (e.g., hydrodynamic regime, sediment mobility, grain size, presence/absence of xenophyophores) which vary dramatically over space and time within and among seamounts.

Other features of the ecology of deep seamounts, such as rates of organic carbon flux and mineralization, broad-scale patterns of species diversity and size-class structure of benthos, are either too poorly studied or are too heterogeneous to allow useful generalizations to be drawn. In general, we expect that the specific conditions in seamount habitats (in terms of hydrodynamic regime, sediment type and mobility, horizontal and vertical fluxes of particulate organic carbon) overwhelm the broader regional and depth patterns discussed above for the level, sediment-covered deep-sea floor. Nonetheless, a number of insights into deep-sea biology can be gained from the study of seamounts, and Rogers (1994) has provided a detailed overview of current knowledge of the biology of seamounts, including their potential importance as sites of speciation and for commercial fisheries.

Deep ocean trenches

The hadal zone – that is, deep-ocean trenches with depths ranging from 6000 to 11 000 m – covers about 2% of the Pacific Ocean floor. The most dramatic environmental characteristic of the hadal zone is extremely high hydrostatic pressure which exceeds that in any known metazoan habitat. In the deepest portions of the hadal zone (9000 to 11 000 m), the pressures of 900 to 1100 bar have profoundly affected the composition and zoogeography of the benthos.

Habitat and community description

The bottom waters of Pacific trenches range in temperature from 1.1 to 3.3ºC. Despite their great depth, trench floors receive relatively high fluxes of particulate organic carbon and sediments, as a result of their proximity to coastal productivity and/or the focusing effects of their steep, narrow walls (Belyaev, 1972). In addition, the high supplies of sediments from coastal waters, combined with steep slopes, topographic enhancement of bottom currents, and frequent seismic activity, are likely to make turbidity flows and sediment slumps common at the bottom of trenches (Jumars and Hessler, 1976). As a consequence, trench-floor sediments often are poorly consolidated (or "soupy") clayey sediments rich in organic carbon compared to surrounding abyssal areas (Belyaev, 1972; Jumars and Hessler, 1976; Hessler et al., 1978). In addition, trench walls often contain substantial areas of rocky substratum exposed by erosive currents and/or sediment slumping (Hessler et al., 1978). In general, trench habitats are thought to be food-rich but physically unstable compared to the most of the abyssal seafloor.

The benthic ecology of Pacific trenches has not been well studied in recent decades, so little specific can be said about carbon sources and ecological rates. Most trench data are derived from older, semiquantitave studies with trawls and grab samples. These studies reveal a "hadal" (or trench) fauna distinct from that of shallower depths in the deep sea (Vinogradova, 1979). Based on trawl samples from 27 trenches in the Pacific Ocean, Belyaev (1972) reported that the hadal fauna from depths exceeding 6000 m contains broad taxonomic diversity, and is missing only a few higher-level marine taxa (for example, decapods and brachiopods). However, species diversity declines dramatically from 6000 m to depths exceeding 8500 m. Holothurians dominate megafaunal abundance and biomass in trenches, especially at depths greater than 7000 m. Bivalves and polychaetes also are important components, with ophiuroids, sipunculans, asteroids, and non-decapod crustaceans occurring frequently as well. Megafaunal densities and biomasses appear to be relatively high compared to adjacent abyssal plains, almost certainly because of enhanced fluxes of particulate organic carbon in trenches (Belyaev, 1972). A notable characteristic of trench megafaunal assemblages is pronounced numerical dominance by one to three very common species (Belyaev, 1972). The pattern of numerical dominance intensifies with increasing depth in trenches (Belyaev, 1972) and is reminiscent of oxygen-stressed communities in oxygen-minimum zones (Levin et al., 2000). This numerical dominance, combined with a high proportion of endemic megafaunal species in trenches (on average 58% of the total species in each trench), and reduced diversity below depths of 8500 m, suggest that the high hydrostatic pressure of trenches serves as a physiological barrier to many megafaunal species found in abyssal habitats (Belyaev, 1972).

More recently, a few trench sites have been studied with more modern techniques, in particular, quantitative box-core sampling for macrofauna in the Aleutian Trench, and baited camera and trap studies of scavengers in the Mariana, Philippine and Peru–Chile Trenches (Fig. 6.1). Based on a single 0.25 m^2 box-core sample, Jumars and Hessler (1976) found a dense, low-diversity macrofaunal assemblage at a depth of 7298 m on the central axis of the Aleutian Trench. Macrofaunal abundance (1272 individuals m^{-2}) was comparable to that in the eutrophic equatorial abyss and approached the lower limits of macrofaunal abundance on the continental slope (Table 6.1). As in most deep-sea settings, polychaetes dominated the macrofaunal assemblage (49%), with tanaids and bivalves also relatively abundant (Jumars and Hessler, 1976). Unlike most deep-sea sites, however, aplacophorans (10%), enteropneusts (8%) and echiurids (3%) were also quite common, suggesting that trench macrofaunal communities differ at high taxonomic levels from deep-ocean assemblages in general (c.f., Belyaev, 1972). The factors causing unusual taxonomic structure in trenches are not clear, but could include unusually high food availability, relatively frequent physical disturbance, and extreme hydrostatic pressure.

The Aleutian Trench macrofauna sampled by Jumars and Hessler (1976) appeared to be remarkable by deep-sea standards in two other ways. (1) The polychaetes were unusually dominated by mobile surface-deposit feeders, and (2) species diversity, as measured by rarefaction, was remarkably low (Jumars and Hessler, 1976). Both characteristics are likely to be responses to environmental instability – that is, frequent physical disturbance (Jumars and Hessler, 1976).

Baited camera and trap studies suggest that the scavenging fauna of the Mariana, Philippine and Peru–Chile trenches below 6700 m consists exclusively of crustacea, and overwhelmingly of large lysianassid amphipods (Hessler et al., 1978). In contrast, at nearby abyssal sites below the depth of 6000 m, an abundance of scavenging fishes of several species are attracted to bait-falls. One large scavenging amphipod, *Hirondellea gigas,* appears to be endemic to the Pacific hadal zone, occurring in the Mariana, Philippine and Kuril–Kamchatka trenches below 6000 m (Hessler et al., 1978). The amphipods of Pacific trenches form large aggregations at bait parcels very rapidly (within hours) and are particularly voracious; they often consume tens of kilograms of dead fish within 1–2 days (Hessler et al., 1978). It has been suggested that a greater proportion of the food reaching the trench benthos arrives in the form of larger, more widely scattered particles than at shallower depths in the ocean; if so, scavengers are likely to be especially important in the energy flow to the seafloor of the hadal zone (Hessler et al., 1978).

CONCLUSIONS AND OUTSTANDING PROBLEMS

Comparisons among deep benthic ecosystems in the Pacific indicate the overriding importance of several key environmental parameters. Perhaps the most important parameter is the flux of particulate organic carbon to the seafloor. Regional variations in many aspects of community structure, and in numerous ecological rates, can be directly related to the amount of organic material sinking to deep-sea sediments from the surface ocean (Tables 6.1 and 6.3). These include variations in the abundance, biomass, and community structure (in terms of taxonomic composition, relative importance of size classes, and feeding types) of both the infauna and scavengers, and the rates of key processes such as sediment-community oxygen consumption, bioturbation, rates of trace erasure, and rates of recolonization. Thus, in the deep Pacific Ocean (and in the deep-sea generally), flux of particulate organic carbon appears to play a dominant role in controlling regional variations in biotic structure, much as temperature and rainfall control ecosystem structure in terrestrial habitats. In many ways, ecosystems of the deep Pacific (and of the deep ocean generally) can be considered to be food-limited.

A variety of other factors may also be important in dictating ecosystem structure in the deep Pacific Ocean. These include hydrodynamic regime (especially in canyons, on seamounts and beneath western boundary currents), bottom-water oxygen concentration (in oxygen-minimum zones), availability of hard substrata (in canyons, on seamounts), and hydrostatic pressure (in trenches below roughly 6000 m depths). In extreme cases, these factors may overwhelm the influence of the flux of particulate organic carbon. For example, one expects the structure of communities in the oxygen-minimum zone to remain relatively constant as one moves between sites characterized by different absolute fluxes of particulate organic carbon, and the fauna of manganese nodules exhibits great similarities across the mesotrophic and oligotrophic abyss. Nonetheless, within the low-energy, soft-sediment habitats that really dominate the deep Pacific seafloor, the flux of particulate organic carbon must be considered the master variable influencing ecosystem structure.

Deep-sea benthic habitats of the Pacific have perhaps been better studied than those in any other ocean; nonetheless, there remain major gaps in the understanding of these ecosystems. Some of these gaps are highlighted below.

(1) Complete energy budgets (including all major outputs), as well as detailed biomass distributions for all size classes (i.e., the microbes to megafauna), are not available for any single benthic habitat in the deep Pacific. Estimates of biomass production for individual populations are almost wholly lacking. Thus, there is still only very limited understanding of biomass distributions and the roles of various biotic size classes in the energetics of deep Pacific ecosystems.

(2) The nature, rates and variability of the flux of particulate organic carbon to the deep-sea floor are still very poorly quantified. In particular, the flux of nekton falls has been measured in only one site (the Santa Catalina Basin), where it appeared to be quantitatively important. Deep-sea ecosystems appear to be largely food-limited; until the nature of food flux to the deep-sea floor is understood, the key ecological and evolutionary forces shaping these ecosystems cannot be elucidated.

(3) Knowledge of most ecological rates on the deep-sea floor is extremely fragmentary. For example, the rates of a variety of processes including bioturbation, natural disturbance and succession, and patterns of community recovery following anthropogenic disturbance (e.g., the dumping of sewage sludge and other waste disposal, nodule mining) have been measured at only a handful of locations (Tables 6.1 and 6.3). Such information about rates is essential if one wishes to predict the response of deep-sea ecosystems to natural and anthropogenic change. Ecological intuition suggests that the resistance and resilience of food-poor, physically stable, deep-sea communities may be lower than those of any other ecosystems on earth, although even that is uncertain (for example, slope habitats exhibit remarkable resilience in absorbing the massive organic enrichment associated with whale falls). Current ignorance of the rates of important processes in some of the most extensive deep-sea habitats is sobering. For example, to our knowledge, rates of bioturbation, or of recolonization following any type of disturbance, have *never* been measured in oligotrophic abyssal habitats. This lack of rate data from the oligotrophic abyss is particularly frustrating because this region is enormous in size (it covers more than 40% of the Pacific seafloor), and because it should provide fascinating insights into ecosystem responses to extraordinarily food-poor conditions (it is close to being the most oligotrophic system in the biosphere).

Until these gaps are closed, one can only claim a very incomplete understanding of the structure and function of those ecosystems covering most of the Earth's solid surface.

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Chapter 7

THE DEEP INDIAN OCEAN FLOOR

Amanda W.J. DEMOPOULOS, Craig R. SMITH and Paul A. TYLER

INTRODUCTION

The Indian Ocean is the world's third largest, stretching 9600 km from Antarctica to the Bay of Bengal and 7600 km from Africa to Australia. Compared to the Atlantic and Pacific, the Indian Ocean remained poorly explored scientifically until the International Indian Ocean Expedition (IIOE) in 1962–1965, the results of which were published in the *Atlas of the Indian Ocean* (Wyrtki, 1971). Prior to the IIOE, the voyages of the 'heroic age' of deep-sea exploration had sampled relatively little in the Indian Ocean. During the circumnavigation of the world's oceans by HMS *Challenger* (1872–1876), study of the Indian Ocean was confined to circumpolar waters south of the Polar Front. The *Valdivia* expedition (Chun, 1900) sampled the free-swimming larvae of the deep-water brachiopod *Pelagodiscus* in surface waters of the Indian Ocean, benthic adults being collected from depths as great as 2490 m (Helmcke, 1940). In the 1930s, the John Murray Expedition to the Indian Ocean worked mainly in shallow water, but some deep-water sampling provided material for monographs (e.g., Knudsen, 1967). The Swedish Deep Sea Expedition of 1947–1948 on the *Albatross* sampled extensively in all the oceans (Pettersson, 1957), taking bottom-living specimens and cores from the deep sea (for a list of publications see Menzies et al., 1973). The last of the 'heroic age' cruises, on the *Galathea* (1950–1952), sampled deep-water fauna between Sri Lanka (formerly Ceylon) and the Kenyan coast, as well as along the Mozambique Channel to South Africa (for a list of publications see Menzies et al., 1973). The taxonomic studies of these major expeditions were supplemented by Soviet cruises to the Indian Ocean, particularly on the *Vityaz*, again resulting in monographic treatments (e.g., Pasternak, 1964, 1976). The IIOE also gave the opportunity for quantification of the bottom fauna of the Indian Ocean (Neyman et al., 1973). A historical perspective of the major early cruises, including those to the Indian Ocean, has been given by Mills (1983).

Since the IIOE, deep-sea research in the Indian Ocean has focused on the Arabian Sea. Because few systematic surveys or conceptually integrated studies exist, deep-sea ecosystems in the Indian Ocean remain poorly known (Banse, 1994).

The Indian Ocean is characterized by a number of unusual oceanographic features. Patterns of circulation are unlike those in any other oceans, owing to large-scale monsoonal shifts in wind stress and current directions north of 5ºS. In addition, the Indian Ocean is landlocked to the north and lacks temperate and polar regions north of the equator, further modifying oceanic circulation and hydrology. The basin also harbors one of the largest and most intense intermediate-depth oxygen minimum zones in the world ocean (Kamykowski and Zentara, 1990; Rogers, 2000). These unusual features of the Indian Ocean substantially affect the spatial and temporal variability of primary production, the deep flux of particulate organic carbon (POC) and the oxygen concentration, profoundly influencing the nature of the deep seafloor habitats.

Deep-sea habitats studied with modern techniques in the deep Indian Ocean include the Kenya slope, the oxygen minimum zone of the Oman Margin, and the abyssal Owen Basin in the Arabian Sea. In addition, limited deep-sea data exist for continental-rise and abyssal habitats in the central Indian Ocean and in the Bay of Bengal. In this chapter, we first describe physical characteristics and key habitat variables of the deep Indian Ocean; we then summarize the limited deep-sea benthic data available from this ocean, and highlight topics of interest for future research.

PHYSICAL CHARACTERISTICS OF THE DEEP INDIAN OCEAN

The Indian Ocean, including adjacent seas (e.g., the Arabian Sea, the Bay of Bengal, and the Southern Ocean), covers 73 426 000 km^2, roughly one-fifth of the total world oceanic area. It has an average depth of 3890 m, which is approximately equivalent to the average world-ocean depth.

Morphology

The morphological features of the Indian Ocean are similar to those of the Atlantic Ocean (see Chapter 6), and include mid-ocean ridges, abyssal plains, and few deep-sea trenches. The Indian Ocean has very few seamounts and islands (see Rogers, 1994), but contains numerous submarine plateaus and rises (Fig. 7.1). Two types of continental margins are present in this basin: divergent and convergent. Divergent margins are the most common, and are characterized by wide continental shelves, broad continental rises, and little seismic activity. Such margins are found along East Africa, the Arabian Peninsula, much of the Indian subcontinent, and Western Australia. The Indian Ocean contains only one convergent margin in its northeast corner, the Java (Sunda) Trench, where oceanic crust is subducted beneath a continental plate (Fig. 7.1). The 7500 m deep Java Trench is part of the Indonesian Arc, which contains 14% of the world's active volcanoes.

Because of large riverine inputs of terrigenous sediment, particularly from the Indus and Ganges Rivers, onto gradually sloping divergent margins, the Indian Ocean has vast continental rises and abyssal plains (Kennett, 1982). The rises are gradually sloping plains of terrigenous sediment several kilometers thick. Beyond the continental rises lie level abyssal plains; the abyssal plain south of the Bay of Bengal is the flattest large area of the earth's surface (Tomczak and Godfrey, 1994). Much of this plain has arisen from a turbidity flow down the northern slopes of the Bay of Bengal, extending 3000 km southwards into the deep sea of the Bay.

Like the Atlantic Ocean, the Indian Ocean is subdivided into a number of major basins by long sections of mid-ocean ridge (Fig. 7.1). In the Indian Ocean, some of these ridges (e.g., the Ninety-East Ridge, the Mascarene Ridge and the Chagos-Laccadive Ridge) are aseismic; they do not appear to be sites of active seafloor spreading. Active ridges include the Carlsberg Ridge and the Mid-, Southwest and Southeast Indian Ridges, the last two of which extend beyond the limits of the Indian Ocean, connecting with the world Mid-Ocean Ridge system. The abyssal Indian Ocean is divided into several smaller basins by meridional ridges. The West Australian Basin and the Mid-Indian Basin are separated by the Ninety-East Ridge whilst to the west of the Mid-Indian Ridge are a series of basins including the Somali, Mascarene, Madagascar and Natal Basins. The Carlsberg Ridge lies north of the Arabian Basin (Fig. 7.1).

Surface circulation

Three important factors make the circulation and hydrology of the Indian Ocean different from those of any other ocean: the closure of the Indian Ocean in the northern subtropics; the seasonally-reversing Monsoon Gyre; and the blocking effects of the equatorial currents to the spread of water masses along the thermocline (Fig. 7.2). Owing to seasonal heating and cooling of the vast Asian landmass, winds vary seasonally north of the equator, resulting in the Indian Ocean monsoons. From November to March the Northeast Monsoon is accompanied by the northeast trades, which are reinforced by the rapid winter cooling of air over Asia. As a result, the westward-flowing North Equatorial Current from 8ºN to the equator is prominent in January through March, generating a small anticyclonic gyre north of the equator (Fig. 7.2). Very little upwelling occurs during the Northeast Monsoon, and hydrological effects are generally superficial (Wyrtki, 1973). From April to September, the Asian landmass warms faster than the ocean, drawing moist air ashore from over the ocean, and creating the Southwest Monsoon. During this period, eastward surface currents north of the equator combine with the Equatorial Countercurrent, establishing the Southwest Monsoon Current between 15ºN and 7ºS (Fig. 7.2) and a strong westward-flowing South Equatorial Current around 5ºS. This reversal of surface currents gives rise to the greatest seasonal variation in hydrography of any ocean basin (Burkill et al., 1993). Strong upwelling occurs off the Somali and Oman coasts, resulting in substantial increases in surface production.

The South Equatorial Current forms a marked hydrographic boundary between the monsoon-driven circulation in the north and the Southern Hemispheric Sub-tropical Anticyclonic Gyre to the south. The circulation pattern to the south of 5ºS is analogous to

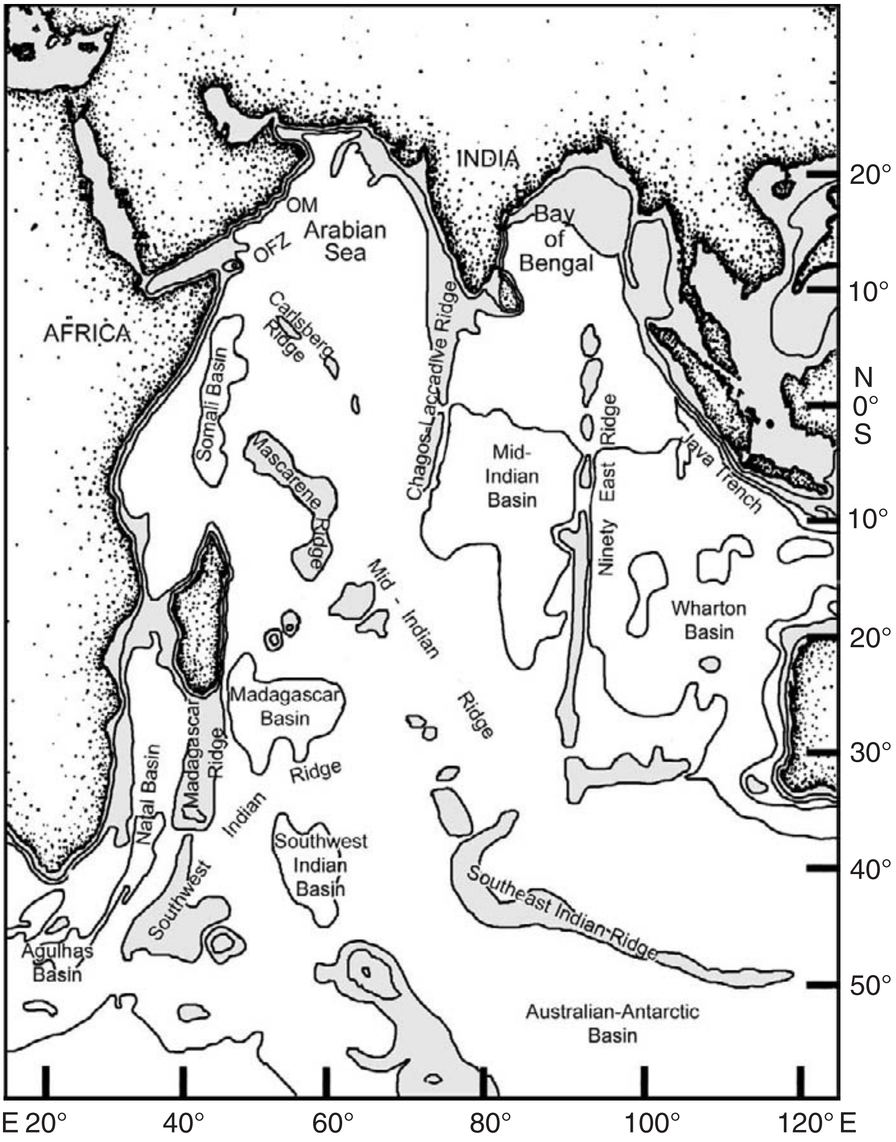

Fig. 7.1. Topography of the Indian Ocean including major ridges and basins. OM, Oman Margin. Modified from Tomczak and Godfrey (1994). The 1000, 3000, and 5000-m isobaths are shown, and regions less than 3000 m deep are shaded.

the gyres of the South Atlantic and South Pacific. In the southern Indian Ocean, western boundary currents include the East Madagascar, Mozambique, Agulhas, and Zanzibar Currents (Fig. 7.2). All of these currents extend to great depths, disturbing sediments with their high velocity flow to depths as great as 2500 m (Tomczak and Godfrey, 1994). Off South Africa, the Agulhas Current forms a cyclonic loop, and, although some water is lost to the Atlantic, most flows eastward forming the northern boundary of the Circumpolar Current.

Upwelling

A significant consequence of the seasonally changing circulation pattern in the north Indian Ocean is pronounced upwelling along the western coastline when the Southwest Monsoon produces strong Ekman transport away from the coasts of Somalia and Arabia (Swallow, 1984). During the Southwest Monsoon, the strong winds from the northwest force intense upwelling and deep mixing, which reduce coastal sea-surface temperatures by approximately 5ºC, and

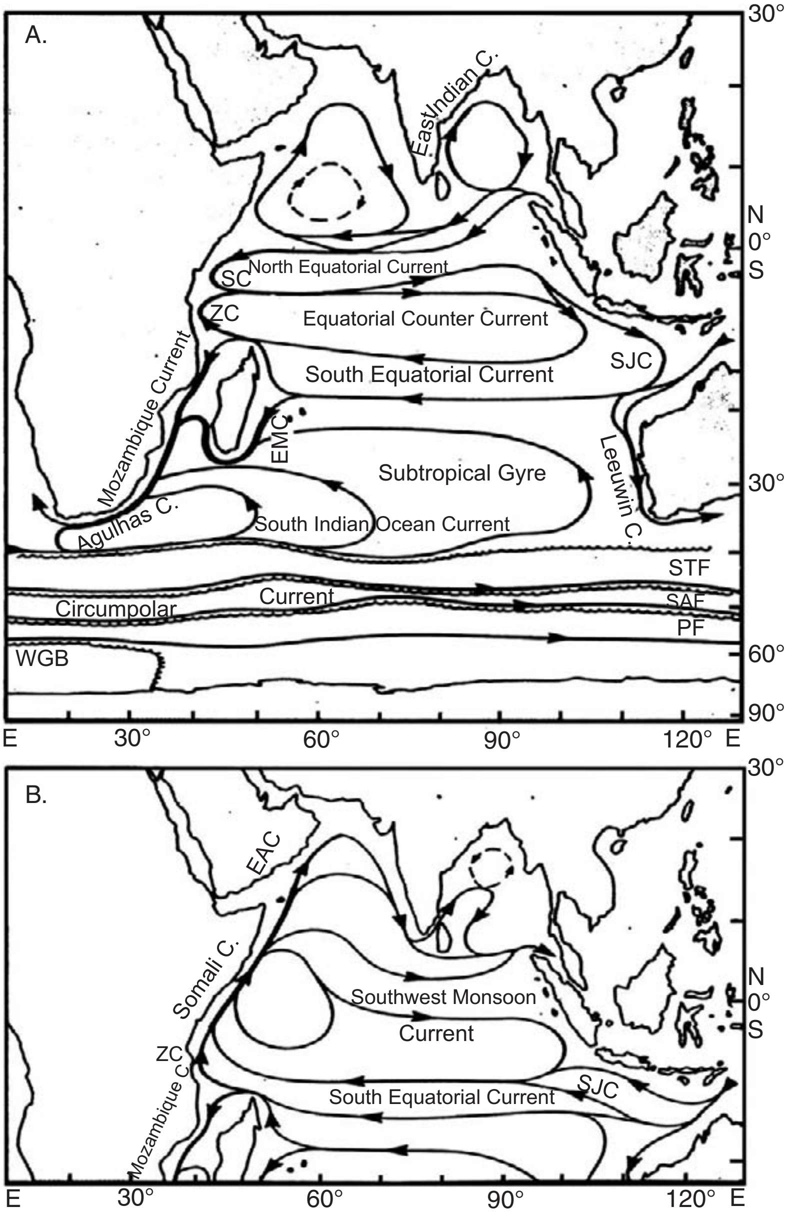

Fig. 7.2. Major surface currents of the Indian Ocean (A) during the Northeast Monsoon season (March–April), and (B) during the Southwest Monsoon season (September–October). The circulation south of 20ºS remains unchanged. Abbreviations: STF, Subtropical Front; SAF, Subantarctic Front; PF, Polar Front; SJC, South Java Current; ZC, Zanzibar Current; SC, Somali Current; EAC, East Arabian Current; EMC, East Madagascar Current; WGB, Weddell Gyre Boundary. Modified from Tomczak and Godfrey (1994).

cause high primary productivity and a substantial flux of sinking particles in this region (Cushing, 1973; Banse and McClain, 1986; Nair et al., 1989). Primary production is exceptionally high and widespread during this period, reaching levels of 547.5 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ (Krey, 1973; Nair et al., 1989). Because upwelling is embedded in the swiftly moving western boundary current, nutrient upwelling has a reduced effect on local primary production. The strong current removes much of the additional planktonic biomass from the upwelling system before it can be utilized, with a consequent enhancement of biomass and secondary production in the open Arabian Sea. As a result, zooplankton concentrations in the upwelling system of the Arabian Sea are not as high as those of coastal upwelling systems in the Pacific and the Atlantic Oceans. Upwelling also occurs off the southeast margin of Oman, associated with enhanced biological productivity (Hermelin and Shimmield, 1990). The sediments of the Oman Margin and northwest Arabian Sea vary laterally between facies rich in organic carbon, in biogenic silica, or in carbonate, deposited under this highly productive upwelling regime (Kennett, 1982; Tomczak and Godfrey, 1994).

Upwelling along the eastern boundary of the Indian Ocean is uncommon, because winds favorable for upwelling are weak during the Northeast Monsoon and absent during the Southwest Monsoon. This is in contrast to the eastern boundary of the Pacific, where there is significant upwelling in both the northern and southern hemispheres (see Chapter 6). A small amount of upwelling occurs along the coast of Java during the Southwest Monsoon and weak upwelling also occurs off southwest India (Wyrtki, 1973; Burkill et al., 1993). Unlike typical eastern boundary currents, the Leeuwin Current (Fig. 7.2) off the west coast of Australia flows poleward against the wind, and the undercurrent is equatorward, instead of moving toward the continent, as in the Peru–Chile Margin. For these reasons, upwelling does not occur on the Western Australian shelf, and thus overall biological productivity in this region is relatively low.

Deep water masses

The hydrology of the deep Indian Ocean is much less affected by the seasonal monsoon cycle than near-surface currents. Monsoonal influence is restricted to the surface mixed layer and western boundary currents. Three mediterranean-type seas influence the hydrographic properties of the Indian Ocean: the Persian Gulf, the Red Sea, and the Australasian Mediterranean Sea. In the Persian Gulf and Red Sea, evaporation exceeds precipitation and warm, dense water flows out of the Persian Gulf and Red Sea into the northern Indian Ocean forming North Indian Ocean Intermediate Water. This intermediate water does not reach the deep sea bed. In the southern Indian Ocean, south of 10ºS, between the depths of ~500 and 1000 m, the northward flow of Antarctic Intermediate Water is blocked by the equatorial current system (Tomczak and Godfrey, 1994).

Abyssal flow in the Indian Ocean is divided into three components associated with three western boundary currents. Western basins are penetrated by bottom waters derived from the Indian and Atlantic Basins (Warren, 1981). Like the Atlantic and Pacific Oceans, the water masses in the Indian Ocean below 3500 m consist mostly of cold Antarctic Bottom Water (AABW), with a potential temperature T of 0.3ºC. Antarctic Bottom Water leaves the circumpolar current to enter and fill the Indian Ocean below a depth of 3800 m at two locations: the Madagascar Basin, and gaps in the Southwest Indian Ridge. Antarctic Bottom Water then flows across the Madagascar continental slope and forms a deep western boundary current (Swallow and Pollard, 1988). Recirculation of Antarctic Bottom Water in the Madagascar Basin is fast, bottom currents flowing northward at a speed of approximately $0.2\,\mathrm{m\,s^{-1}}$. The bottom water continues along the western pathway in the Somali Basin, where it eventually enters the Arabian Basin and disappears through gradual mixing into overlying Deep Water. In the eastern Indian Ocean, Antarctic Bottom Water, also called Circumpolar Water, enters the South Australian Basin via the Australian-Antarctic Discordance. It fills the Great Australian Bight and moves west then north, forming a western boundary current along the Ninety-East Ridge. The oxygen concentration follows the flow pattern, with the concentration in the bottom water decreasing towards the north from $5\,\mathrm{ml}\,\ell^{-1}$ at 60ºS to $0.2\,\mathrm{ml}\,\ell^{-1}$ in the Arabian Sea and Bay of Bengal, as the water mass increases in age and isolation. This situation is in contrast to that in the Atlantic and Pacific, where the most notable regions of low oxygen are on the east side around the equator. From a depth of 1500 to 3800 m, the Indian Ocean is filled with Indian Deep Water formed from North Atlantic Deep Water (NADW) carried into the Indian Ocean with the upper Circumpolar Current. It spreads north in the western boundary current to the Arabian Sea and the Bay of Bengal. The water properties consist of a moderate oxygen concentration ($4.7\,\mathrm{ml}\,\ell^{-1}$), low temperature (2ºC), and high salinity (35.85), similar to the North Atlantic Deep Water. The northern Arabian Sea is closed by land mass in the north, and is semi-enclosed altogether (Fig. 7.1). The Arabian Sea is deeper than 3000 m, and the basin is closed in the south by the Central Indian Ridge, the Carlsberg Ridge, and the Chagos–Laccadive (or Maldive) Ridge (Fig. 7.1). Therefore, bottom water must enter in the west, through the Owen Fracture Zone, rather than from the south (Tomczak and Godfrey, 1994).

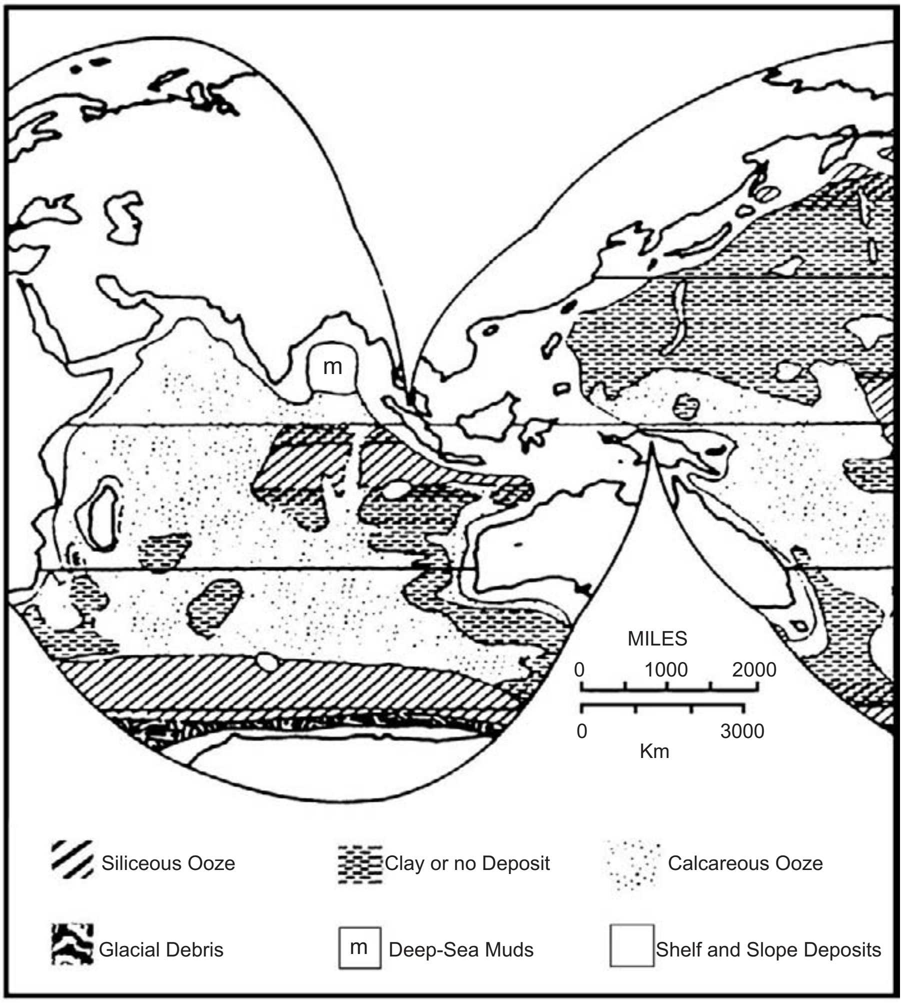

Fig. 7.3. Distribution of surface-sediment types in the deep Indian Ocean. Modified from Berger (1974).

Substratum type

Substratum types in the deep sea can influence the distribution patterns of benthic organisms. Specifically, the organic-matter content of deep-sea sediments can be correlated with the abundance, composition, and diversity of benthos (Grassle and Grassle, 1994; Rice and Lambshead, 1994; Snelgrove and Butman, 1994). In general, organic-rich sediments often are low-diversity habitats, containing mostly tube-dwelling polychaetes, whereas organic-poor sediments typically contain a diverse community of deposit feeders (Levin and Gage, 1998). Hard substrata in the deep sea provide niches for a broad variety of sessile organisms (see Chapter 2).

Most of the Indian Ocean seafloor, particularly that remote from land, is covered with calcareous ooze (Fig. 7.3) (Berger, 1974). Calcium carbonate concentrations are typically intermediate between those of the carbonate-rich Atlantic and the carbonate-poor Pacific. The carbonate critical depth, CCRD, where calcium carbonate drops to <10% of the sediment mass, is deepest in the equatorial region, and shoals to 3900 m between 50º and 60ºS. Carbonate sediments are relatively poor in organic carbon (<1%) and have coarse grain size (Berger, 1974; Kennett, 1982). Nearly all river discharge occurs in the northern part of the Indian Ocean adjacent to Asia, thick terrigenous sediment being deposited in the northern and western parts of the Indian Ocean, especially the Arabian Sea and the Bay of Bengal. These sediments have high concentrations (2–5% by weight) of organic carbon, and are composed mostly of terrestrial plant material, phytodetritus, and mineral grains transported by rivers (Kennett, 1982; Levin and Gage, 1998; Levin et al., 2000). In the Bay of Bengal, terrigenous sedimentation from the Ganges is particularly extensive, reaching depths of 5000 m. In the Arabian Sea, there is an organic carbon maximum (4.9%) at 400 m, owing apparently to preferential preservation and accumulation of organic matter under low-oxygen conditions in the bottom water (Levin et al., 2000). The particle flux to the deep Bay of Bengal is enhanced by the freshwater input from the major rivers entering at the north of the Bay (Ittekkot et al., 1991).

Sediments are at most very thin on the crests of mid-ocean ridges, and essentially absent on the ridge axes (Fig. 7.3). Thick siliceous oozes, composed primarily of radiolarian and diatom tests, occur at depths of ~5000 m south of the polar front and along a few mid-ocean ridges, where there is high biological productivity (Berger, 1974; Kennett, 1982). However, because of the oligotrophic nature of the equatorial Indian Ocean, siliceous sediments are rare in low latitudes of the Indian Ocean compared to the Pacific Ocean (Kennett, 1982). Red clay is present mostly in the eastern and southern Indian Ocean, near the equator and high latitudes. It is composed of fine-grained, organic-poor sediments resulting from volcanic activity at ridges (Berger, 1974; Pilipchuk et al., 1977; Kennett, 1982).

Hard substrata in the Indian Ocean consist of basalt rocks, rock faces, and the surfaces of ferromanganese concretions. The morphology of the central Indian Ocean Basin is composed of abyssal hills and seamounts, as well as valleys and abyssal plains. The topographic highs, which are in the proximity of three major fracture zones, are composed of hard, massive basalts occurring at the crests, along the slopes and on the foothills as talus deposits (Sharma et al., 1997). Owing to strong geostrophic currents and consequent scouring of the sediments, the Wharton Basin, the southern Mascarene Basin, and parts of the Southwest Indian and Australian–Antarctic Basins have little or no sediment (Kennett, 1982). Sediment in these areas, when present, is mostly brown clay. Along the Southwest Indian Ridge, German et al. (1998) have identified hydrothermal activity. The associated fauna inhabiting these hydrothermal regions is dominated by shrimps and anemones (T. Shank, pers. comm.). In the southeast and southwest Indian Ocean, and in the Mozambique Basin, there are extensive pavements of manganese nodules at depths of about 4000 m (Kolla et al., 1980). It has been suggested that their presence at the sediment–water interface is a result of benthic biological activity and strong bottom currents. Benthic organisms may nudge the nodules upward, maintaining them near the sediment–water interface, while strong currents may limit the deposition of sediment, allowing the nodules to grow (Berger, 1974; Paul, 1976; Kennett, 1982).

Near-bottom currents

Currents in the deep sea influence sediment deposition and the organisms that inhabit the seafloor (Nowell and Jumars, 1984). In regions where there are strong currents, sediment deposition is minimal. These currents can smother sessile and suspension-feeding organisms with sediment grains. Where currents are weak, sediment chemistry and biology may be controlled by diffusive processes. In these environments, suspension feeders may suffer owing to the inadequate supply of advected particles (e.g., Jumars and Gallagher, 1982). Thus, near-bottom currents not only may control sediment deposition, but can also manipulate sediment chemistry and the structure of the benthic communities (Nowell and Jumars, 1984).

Both bottom and deep waters of the Indian Ocean are derived from the Atlantic, and spread throughout the deep sea by active flow (Wyrtki, 1973). Antarctic Bottom Water warms as it spreads north, and fills the deep basins of the central Indian Ocean. Therefore, the abyssal Indian Ocean is an area of active deep-sea circulation. Antarctic Bottom Water supplies fine-grained sediments from the Africa–Madagascar source to the marginal areas of the Mozambique Basin and generates wavy bedforms in this region. In addition, eddies appear to penetrate to great depths in the Arabian Sea, and the circulation influences the bottom topography, causing depressions and rises (Das et al., 1980). There are strong bottom currents, with speeds approaching 10–20 cm s^{-1}, in the Wharton Basin and the southern Mascarene Basin, and in parts of the Southwest Indian Basin and Australian–Antarctic Basins, resulting in minimal sediment deposition (Kennett, 1982; Gage and Tyler, 1991). The active circulation ensures that the abyssal bottom waters of the Indian Ocean remain oxygenated.

There is no evidence for benthic storms (see Chapter 2) in the deep Indian Ocean although they are predicted to occur in the extreme southwest region of the ocean (see Gage and Tyler, 1991).

Bottom-water oxygen

Oxygen concentration in the bottom water can be a controlling factor in the preservation of organic carbon and benthic fauna assemblages. For example, at depths between ~100 and 1000 m, oxygen minimum zones may develop below productive waters and coastal upwelling zones, where the average annual flux of organic matter to the seabed is high. The resulting hypoxia can reduce abundance and biomass of many benthic animals, altering species composition and richness (Diaz and Rosenberg, 1995).

In the Northern Indian Ocean, an oxygen minimum zone occurs between depths of 100 m and 1000 m, where oxygen concentrations are $<0.5\ \mathrm{ml}\ \ell^{-1}$. This zone results from a combination of high surface productivity driven by upwelling, inflow of oxygen-poor waters from the Persian Gulf, Red Sea, and Banda Sea, and slow deep-water circulation (Wyrtki, 1973). Such a hypoxic layer at intermediate depths has significant consequences for the quantity and quality of organic matter reaching the deep sea from surface production.

Sinking flux of particulate organic carbon (POC)

Benthic organisms are fueled by sinking organic matter from surface waters. Therefore, it is important to evaluate what controls the flux of particulate organic carbon to the deep sea. In general, regional flux of particulate carbon decreases with depth and distance from continents, and is directly controlled by overlying primary production, the depth of the water column (Suess, 1980; Smith and Hinga, 1983; Jahnke, 1996), and the freshwater supply (Ittekkot et al., 1991). Therefore, along continental slopes, where primary production is high and the water column is shallow, the flux of particulate organic carbon to the seafloor is high over annual periods. Specifically, over the Oman Margin of the Arabian Sea, particle flux is strongly seasonal, with peaks during the Southwest and Northeast Monsoons (Nair et al., 1989; Honjo et al., 1999). High monsoonal primary production ($912.5\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$), resulting from wind-induced mixing and nutrient injection into the euphotic zone, is the main factor controlling the observed pattern of particle flux (Burkill et al., 1993). For example, off the Oman coast during the Southwest Monsoon, the rate of sedimentation is approximately $365\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$ at depths between 100 and 500 m (Burkill et al., 1993; Pollehne et al., 1993). At 1500 m, the total annual flux of particulate organic carbon drops to $53\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$, decreasing with depth to $23\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$ at 3500 m (Honjo et al., 1999). In general, particle fluxes during the Southwest Monsoon are greater than during the Northeast Monsoon (Honjo et al., 1999). Because of the lack of upwelling, the spring inter-monsoon period is the most oligotrophic season. Low sedimentation rates are recorded during the inter-monsoon period, corresponding to 6% of the total annual flux (Nair et al., 1989). Therefore, there is high seasonal variability in the total flux of particulate organic carbon, as a result of monsoonal forcing.

Rates of primary production in the central abyssal Indian Ocean, however, are similar to those of the south Atlantic Ocean, which is characterized by low production rates (Steeman Nielsen, 1975). For example, in the oligotrophic gyre of the Indian Ocean, net primary production is less than $109\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$. The corresponding organic carbon flux in this region is approximately $36.5\ \mathrm{g\,C\,m^{-2}\,y^{-1}}$ (Burkill et al., 1993; Pollehne et al., 1993).

REPESENTATIVE DEEP INDIAN OCEAN HABITATS

Oxygenated slopes and basins on the Kenya margin

An oxygenated slope and basin region occurs along the margin off the coast of Kenya. Preliminary investigations of the benthic fauna have been conducted here, making this the best-studied region of its type in the Indian Ocean.

Habitat and community description

Several rivers discharge terrigenous material onto the Kenya shelf, and during monsoon periods the outflow is large. The continental-shelf region of Kenya is narrow, and the ocean is very deep near the coastline. Although knowledge of the benthic communities is limited, some data exist for densities and biomass of macro- and meiofauna from sediments collected by a boxcorer-respirometer (belljar). Along the Kenyan Slope, the densities and biomass of macrofauna (animals retained on a 500 μm sieve) decrease with increasing depth to 1000 m. Macrofaunal densities decrease from 7590 individuals $\mathrm{m^{-2}}$ at 500 m to 2960 individuals $\mathrm{m^{-2}}$ at 1000 m, and the biomass decreases from $26.0\ \mathrm{g\,C\,m^{-2}}$

(500 m) to 4.9 g C m^{-2} (1000 m) (Duineveld et al., 1997). The meiofauna (animals retained on a 32 μm sieve) follow the same spatial patterns as the macrobenthos, with densities ranging from 806 individuals m^{-2} (500 m) to 223 individuals m^{-2} (1000 m). Nematodes are the dominant taxon among the meiofauna, but foraminifera are also present, especially branching forms (Duineveld et al., 1997).

Carbon sources and trophic types

The Kenya shelf lacks the pulses in primary productivity driven by upwelling (Feldman, 1989), and thus this area has a low rate of primary production, ranging from 109.5 to 182.5 g C m^{-2} y^{-1} (Kromkamp et al., 1997). The concentration of organic carbon in the sediment is 0.4 to 1.6% and concentrations of organic nitrogen range from 0.05 to 0.2% (Everaarts and Nieuwenhuize, 1995). Most of the organic matter present in the sediments originates from pelagic production (Duineveld et al., 1997; Kromkamp et al., 1997). Sediment pigment concentrations decrease downslope along the Kenyan margin (Duineveld et al., 1997), suggesting that benthic faunal distribution may be influenced by the concentration of organic matter in the sediment and/or the flux of organic matter to the seafloor.

Rates of key ecological processes

In order to understand the biological and chemical processes of benthic communities, it is important to estimate rates of key ecological processes including respiration, production, bioturbation, and recolonization following disturbance. On the Kenyan slope, cross-shelf and downslope transport of particulate organic carbon (POC) adds to the flux of sinking particles on the slope (Duineveld et al., 1997). These processes supplying organic matter to the seafloor are tightly coupled with benthic metabolism (Duineveld et al., 1997). On the Kenyan margin, oxygen consumption by the sediment community (SCOC) ranges from 1 to 14.2 mmol m^{-2} d^{-1}, decreasing with increasing water depth down to 1000 m. In addition, there appears to be little temporal variation in the rate of oxygen consumption from June to December.

Oxygen minimum zones

Oxygen minimum zones are found in the Arabian Sea and Bay of Bengal (Fig. 7.4). The most studied of these is on the Oman Margin of the Arabian Sea. The initial systematic investigation of the entire Arabian Sea was conducted within the scope of the Indian Ocean Expedition (IIOE), from 1959 to 1965 (Wooster, 1984; Banse, 1994).

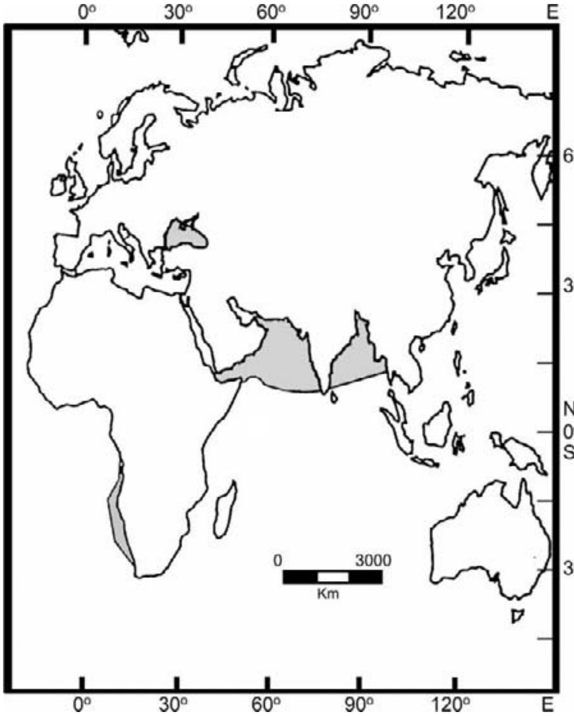

Fig. 7.4. Locations of major oxygen minimum zones in the Indian Ocean. In the shaded areas, dissolved bottom-water oxygen concentrations are less than 0.2 ml ℓ^{-1}. Modified from Diaz and Rosenberg (1995).

Habitat and community description

Upwelling of nitrate-rich water along the southern Arabian coastline during the Southwest Monsoon gives rise to high rates of primary production (304 g C m^{-2} y^{-1}) based on the newly-supplied nutrients (Burkill et al., 1993), making the basin one of the most productive oceanic regions in the world (Nair et al., 1989). High productivity during the upwelling season affects more than one-third of the Arabian Sea (Ryther et al., 1966; Wyrtki, 1971, 1973; Banse, 1973). Sediments accumulating on the Oman Margin under the oxygen minimum zone have a high content of organic matter, owing to the high settling flux of organic matter, supported by monsoon-driven upwelling and redistribution of the organic material by hydrodynamic influences after deposition (Pedersen et al., 1992). Because of the semi-enclosed nature of the northwest Arabian Sea and the resulting sluggish intermediate-depth circulation of water from the Red Sea and Persian Gulf, microbial decay of the high standing crop of organic matter promotes an intense oxygen minimum zone between the water depths of 50 and ~1000 m. Bottom-water oxygen concentrations within this zone range from 0.5 ml ℓ^{-1} near the boundaries of the zone to ~0.02 ml ℓ^{-1} within the core at depths of 400–700 m (Fig. 7.5) (Smith et al., 2000). Concentrations of organic carbon in sediments within the zone reach ~4% (Levin and Edesa, 1997; Levin et al., 2000). In the upper part of the oxygen minimum zone, the high flux of particulate organic carbon coupled with the low oxygen concentration and free hydrogen sulfide appears to modify the distribution of benthic organisms (Gage et al., 2000). Within the core of the oxygen minimum zone (i.e., at oxygen concentrations <0.3 ml ℓ^{-1}), the macrofaunal assemblages are characterized by high densities and low diversities (Levin et al., 1997). Macrofaunal species diversity is limited within the Oman oxygen minimum zone, apparently because only a relatively small number of species can tolerate oxygen concentrations below 0.2 ml ℓ^{-1} (Levin et al., 2000).

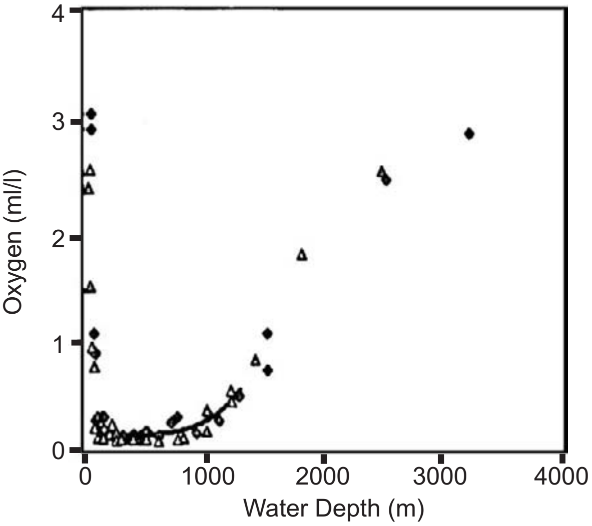

Fig. 7.5. Profile of oxygen versus water depth from the Oman Margin. Modified from Smith et al. (2000).

Between depths of 400 and 700 m within the Oman oxygen minimum zone, sediments are frequently speckled with remarkable worm tubes created by cirratulid polychaetes. These worms, in the genus *Tharyx,* produce cigar-shaped mudballs, 4.5–25 mm long, which protrude several millimeters above the sediment–water interface. Mudball densities reach ~16,000 individuals m^{-2} and they provide a habitat for a variety of benthic organisms, including cirratulids, epizoic polychaetes, and agglutinated and calcareous foraminifera. Polychaetes, nemerteans, and nematodes are also found inside the tests. Mudballs appear to inhibit colonization by certain tube-building taxa (two polychaetes and an amphipod), possibly because tube-building organisms compete for food and space. In addition, the mudballs may provide effective refuges from predation, both for the cirratulids inside, and for nearby burrowing taxa (Levin and Edesa, 1997). Distribution of mudball-building cirratulids appears to be highly restricted in terms of depth and location; they are abundant in at least two other margin settings with low oxygen concentrations (the San Diego Trough and the Santa Catalina Basin). Other biogenic features within the Oman oxygen minimum zone include sediment mounds and burrows. Burrow diameter and the diversity of burrow types are positively correlated with oxygen concentration in bottom water within the depth range of the oxygen minimum zone (Smith et al., 2000).

Carbon sources

The flux of small organic particles to the deep Arabian Sea is the best documented source of carbon to the benthos. The results of short-term and long-term measurements with sediment traps indicate a seasonal pulse of particulate organic carbon to the Arabian Sea bottom (Nair et al., 1989; Passow et al., 1993; Honjo et al., 1999). The seasonal fluctuation in particulate organic carbon is the result of intense biological productivity in the surface waters driven by the monsoon (Nair et al., 1989; Passow et al., 1993; Honjo et al., 1999). Particle flux is most intense during the Southwest Monsoon (Honjo et al., 1999). However, one study of sediment-community oxygen consumption (SCOC) revealed no significant differences between the Southwest and Northeast Monsoon periods (Duineveld et al., 1997). There are seasonal fluctuations in phaeopigment concentrations on the slope; however, high concentrations occur during the non-upwelling season (Duineveld et al., 1997). In general, the highest vertical fluxes of particulate organic carbon occur during the upwelling season, so it is interesting that the sediment phaeopigment concentration does not show a peak thereafter (Duineveld et al., 1997). It is possible that there is a delay in chloropigment degradation, thus providing a pool of labile organic matter available to the benthos over long time periods (Duineveld et al., 1997).

Aggregates of phytoplankton detritus (phytodetritus) occur within the sediments of the oxygen minimum zone. Phytodetritus accumulations are usually thickest in the fall, (up to 2 cm thick), but have also been observed as a thin layer on the sediment surface during the spring months (Prell and Murray, pers. comm.). The deep oxygen minimum layer allows great quantities of detrital material to sink to the deep sea, without being recycled by mid-water consumers; this results in an intense flux of labile organic material to the deep-sea benthos (Gage et al., 2000). Thus, metazoan densities and biomass observed in November may be a response to the abundant phytodetritus available on the surface sediments.

Faunal composition

Most of the quantitative data available for deep-water benthic metazoans in the oxygen minimum zone were collected during November, which corresponds to the onset of the Northeast Monsoon upwelling period and is five months after the onset of the Southwest Monsoon (Levin et al., 1997, 2000; Cook et al., 2000; Gooday et al., 2000). Therefore, the abundance of metazoans found during this period may result from the seasonal pulse of organic matter. Sampling needs to be conducted during other time periods to evaluate any seasonal fluctuation in metazoan abundance and biomass as a result of monsoonal forcing.

Megafauna: On the highly productive Oman margin, in the most intense oxygen-deficient layer, the megafaunal assemblage has a high-biomass but low diversity. Between 300 and 700 m, the community is dominated by the spider crab *Encephaloides armstrongi,* a cocoon-dwelling mytilid (*Amygdalum* sp.), and an ascidian (*Styela gagetyleri*) (Creasey et al., 1997; Young and Vázquez, 1997). At depths between 900 and 1000 m, oxygen levels and megafauna diversity increase, the community consisting primarily of ophiacanthid ophiuroids, spider crabs, and galatheid crabs, including an abundance of *Munidopsis* spp. (Gage, 1995; Smallwood et al., 1999; Creasey et al., 2000). The ophiacanthid *Ophiolimna antarctica* has a density of 51 individuals m^{-2} (Smallwood et al., 1999). *Encephaloides armstrongi* is abundant throughout the oxygen minimum zone on the Oman Margin and appears to tolerate low oxygen concentrations (Creasey et al., 1997; Smallwood et al., 1999). At 1000 m, the density of crabs in general is approximately ten times greater than that at 800 and 1250 m, with spider crabs averaging 47 individuals m^{-2} (Smallwood et al., 1999). It is possible that this depth is a boundary between the more significant oxygen minimum zone above and the increasingly oxic conditions below (Smallwood et al., 1999).

The high densities of spider crabs and ophiuroids in the oxygen minimum zone have implications for the burial of deposited organic material. Spider crabs and ophiuroids may be highly mobile, and may resuspend fine organic material from surface sediments; in addition, phytoplankton-derived sterols are altered by their digestive processes (Smallwood et al., 1999). These megabenthic activities may influence the quality of organic matter in organic-rich sediments on the continental slope (Smallwood et al., 1999).

Macrofauna: The macrobenthos (for the Arabian Sea, defined as animals retained on a 300 μm sieve) are represented in the oxygen minimum zone by an abundant, low-diversity soft-bodied fauna. Polychaetes are the dominant group within this zone, defined by the depth range 100–1000 m and oxygen concentrations <0.5 ml ℓ^{-1} (Herring et al., 1998). Spionids and cirratulids are most common in the upper part of the zone (400–700 m), where oxygen concentrations are low (0.13 ml ℓ^{-1}), and ampharetids and paraonids in the lower portion (850–1000 m), where oxygen concentration increases to 0.29 ml ℓ^{-1}. Between 400 and 1000 m, macrofaunal density ranges from 5818 to 19 183 individuals m^{-2}, the highest densities being found at 700 m (Fig. 7.6; Levin et al., 2000). Macrofaunal biomass at these depths ranges from 14.2 to 59.7 g m^{-2}, and again the biomass is highest at a depth of 700 m. Each taxon appears to have a threshold above which oxygen concentration and organic matter supply are high enough for the animals to survive (Levin and Gage, 1998; Levin et al., 2000).

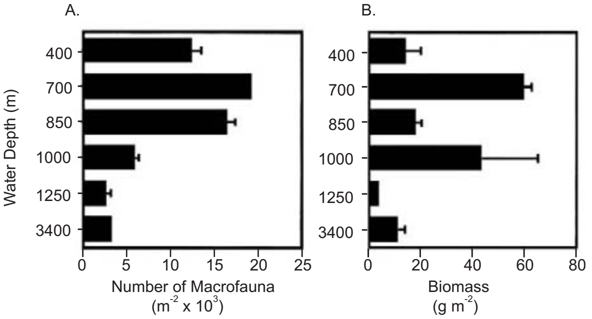

Fig. 7.6. (A) Mean density and (B) biomass for macrofauna sampled at six water depths within and beyond the oxygen minimum zone on the Oman Margin. Error bars represent standard error. Modified from Levin et al. (2000).

The families represented vary with depth as bottom-water oxygen concentration varies within the oxygen minimum zone. At 400 m, where the oxygen minimum is most intense, the dominant taxon is the tube-building spionid polychaete *Prionospio* (*Minuspio*) sp. A (63%), followed by the cirratulid polychaete *Aphelochaeta* sp. A (27%) (Levin et al., 1997). Macrofauna are most abundant in the upper 5 cm of sediment, this layer accounting for 84% of the individuals found and 77% of the biomass (Levin et al., 1997, 2000). Overall, 10 species were found at this depth. At 700 m, two species of spionid polychaetes (*Minuspio* sp. A and *Paraprionospio* sp. A) dominate, whereas at 850 m the most abundant species is a paraonid polychaete, *Aricidea* sp. A (21.3% of the total individuals in the macrofauna). The most abundant species at 1000 m is an ampharetid polychaete, *Eclyssipe* sp. B. Crustaceans between 400 and 1000 m primarily consist of amphipods (*Ampelisca* sp., and an unidentifed gammarid), together with a few tanaids (Levin et al., 2000). In total, 28 species are found at 700 m, indicating an increase in species richness with increase in oxygen concentration within this zone. The oxygen minimum zone in the Arabian Sea is characterized by significantly lower species richness than in other oxygen minimum zones such as Walvis Bay (Sanders, 1969) and that in the eastern Pacific on the summit of Volcano 7 (Levin et al., 1991) where oxygen concentrations range from 0.08 to 1.3 ml ℓ^{-1}.

Most (63%) of the taxa within the oxygen minimum zone live in tubes, including *Prionospio* sp. A, ampharetid polychaetes, and mudball cirratulids. It is possible that these organisms use the structures to provide channels for pumping oxygen from above the seafloor (Levin et al., 1997). Certain organisms have adapted to their low-oxygen environment by altering their morphology. For example, spionid and cossurid polychaetes from the Oman Margin have enlarged respiratory surface area, and larger and more branched branchiae (Lamont and Gage, 2000). Within the oxygen minimum zone at about 400 m, the most common species have large numbers of long branchiae or tentacles, which most likely assist in oxygen utilization (Levin et al., 1997). The mussel *Amygdalum*, which occurs in low abundance, has a thin shell. Echinoderms and coelenterates are absent from the community. The general lack of taxa other than polychaetes within the oxygen minimum zone suggests that most molluscs, crustaceans, and echinoderms are intolerant of low-oxygen conditions; this results in the low diversity in these regions (Levin et al., 2000). The general community composition of the oxygen minimum zone in the Arabian Sea conforms with the dysaerobic facies described for bottom-water concentrations of 0.1 to 0.5 ml ℓ^{-1} by Rhoads et al. (1991) and with the oxygen minimum zone macrofaunal structure present at Volcano 7 (Levin et al., 1991, 1997), where oxygen concentrations ranged from 0.1 to 0.2 ml ℓ^{-1}. However, in the near-anaerobic conditions on the Peru margin (O_2 ~0.02 ml ℓ^{-1}), burrowing oligochaetes are the dominant taxa, and no tube builders are present (Levin et al., unpubl.). In addition, at Volcano 7 there is a mixture of burrowing, epibenthic and tube-building taxa (Levin et al., 1991). Therefore, it appears impossible to make generalizations regarding dwelling behavior of low-oxygen macrofauna (Levin et al., 2000).

Below the oxygen minimum zone, between 1250 and 3400 m, macrofaunal densities range from 2485 to 3190 individuals m^{-2} and biomass ranges from ~2 to 10 g m^{-2} (Fig. 7.6; Levin et al., 2000). At 1250 m, amphipods, tanaids, and cumaceans are present (2.7% of macrofaunal individuals). At 3400 m, amphipods, tanaids, and isopods form 31% of the total macrofauna. At 1250 m, the most abundant species was a syllid polychaete, and at 3400 m, a tanaid. Molluscs appear to be present only at depths $\geqslant$1000 m (1.9%), their proportion in the fauna increasing as oxygen concentration increases with depth – 23% at 1250 m and 18% at 3400 m (Levin et al., 2000). In general, low pH and low oxygen concentration create an unsuitable environment for calcified taxa (Levin et al., 2000). The taxa present on the Oman slope are broadly distributed throughout the deep sea (Smith and Demopoulos, Chapter 6, this volume). In the Arabian Sea, outside of the oxygen minimum zone, the macrofauna are not as abundant as within this zone, suggesting that there is a threshold for opportunistic organisms that can tolerate the low oxygen conditions and utilize the abundant food supply in this highly productive region (Levin and Gage, 1998; Levin et al., 2000).

Metazoan meiofauna: Meiobenthos are abundant in the oxygen minimum zone, and have been well studied in the Arabian Sea. However, few of these studies used comparable sampling and laboratory techniques. Nematodes and foraminiferans are the major meiobenthic taxa present, followed by harpacticoid copepods, polychaetes, and turbellarians (Qasim, 1982). Data from core samples (10 cm deep × 3.4 cm^2 area) taken from grab samples indicate that meiobenthic biomass in the oxygen minimum zone between 200 and 1000 m ranges from 2.01 to 42.30 g m^{-2}, and at depths greater than 1000 m the biomass ranges from 16.55 to 119 g m^{-2} (Qasim, 1982). Since it has been documented that the oxygen concentration in the bottom water increases from 0.13 ml ℓ^{-1} at a depth of 400 m to 0.27 ml ℓ^{-1} at 1000 m (Smith et al., 2000), it appears that meiobenthic biomass and abundance follow the same pattern as for the mega- and macrofauna, increasing with increasing oxygen concentration.

Nematode abundance, estimated from sediment samples collected with a multiple corer using 25 cm^2 tubes, is positively correlated with macrofauna abundance. Between 400 and 700 m, nematode abundance ranges from 1700 to 2495 individuals m^{-2}, and the oxygen concentration from 0.13 to 0.16 ml ℓ^{-1} (Cook et al., 2000; Smith et al., 2000). At the lower boundary of the oxygen minimum zone (1250 m) and beyond (3400 m), nematode abundance decreases, ranging from 860 to 494 individuals m^{-2}, respectively (Cook et al., 2000). Bottom-water oxygen concentration does not appear to be the controlling factor for the nematode population – rather, food quality, as measured by the hydrogen index[1] (Patience and Gage, unpublished), appears to be the major predictor of overall nematode abundance in the Oman slope region (Cook et al., 2000).

Protozoa: In the oxygen minimum zone between 200 and 600 m, the dominant foraminifera present include *Bolivina pygmaea, Bulimina* sp., and *Lenticulina iota* (Hermelin and Shimmield, 1990). At 400 m, corresponding to the core of the oxygen minimum zone, the foraminiferan taxa also include allogromiids, bathysiphonids (*Bathysiphon* spp.), hormosinaceans (mostly *Leptohalysis* spp.), saccamminids (*Lagenammina* spp.), spiroplectamminaceans, textulariaceans and trochamminaceans (Gooday et al., 2000). From 600 to 1000 m, *Ehrenbergina trigona, Hyalinea balthica, Tritaxia* sp., and *Uvigerina peregrina* dominate the foraminiferan assemblage. These taxa appear to be closely related; they could be limited by low oxygen concentration, and possibly by the organic-carbon concentration in the sediment (Hermelin and Shimmield, 1990). Foraminiferan taxa found in the oxygen minimum zone appear to be smaller in size (92.9% were <500 μm) and have more elongate tests (160 μm) than foraminifera collected outside the oxygen minimum zone at 3400 m, which had an average test length of 120 μm (Gooday et al., 2000). Below the oxygen minimum zone (3350 m), very large, tubular, agglutinated species can be found, specifically the genera *Bathysiphon, Hyperammina, Rhabdammina* and *Saccorhiza* (Gooday et al., 2000). Foraminiferan densities in the oxygen minimum zone of the Arabian Sea are among the highest reported from an oxygen-poor environment (Gooday et al., 2000). Foraminifera from the Santa Barbara Basin (590 m, O_2 ~0.1 ml ℓ^{-1}) and from the Peru margin (300–1200 m, $O_2 = 0.02$ to 1.6 ml ℓ^{-1}), follow the same trend; in these areas, however, soft-shelled monothalamous taxa are rare and large agglutinated taxa are absent. Foraminifera and metazoans show similar population responses to oxygen stress: species dominance increases, diversity decreases, and the relative abundance of major taxa changes (Gooday et al., 2000).

The benthic flagellates are significantly more abundant in the sediments during the non-upwelling season. Although grazing rates are low, bacterivory at that period has a significantly greater impact on bacterial standing stock in the bottom water than during upwelling (Bak and Nieuwland, 1997). Microbes are fueled by particle flux from the surface waters, and respond to seasonal sedimentation of organic matter (e.g., Pfannkuche, 1993).

Nanobiota: Seasonal deposition of organic matter in the Arabian Sea results in seasonality of benthic microbial production. After the upwelling season, for instance, bacterial abundance and production are high (Ducklow, 1993). Bacterial density, biomass, and cell volume are larger during the August upwelling period than in the non-upwelling period (February). There is no obvious relationship between the biomass and abundance of microbes and the existence of the intense oxygen minimum zone, which is equally present in both seasons (Duineveld et al., 1997; Bak and Nieuwland, 1997). There is a decrease in the biomass and abundance of benthic bacteria and benthic nanoflagellates with increase in depth in sediment, and also with increasing ocean depth. Bacterial densities in the Arabian Sea decrease from 1.5×10^9 cm^{-3} in surface sediments to 0.8×10^9 cm^{-3} at a depth of 10 cm within the sediment (Bak and Nieuwland, 1997). Within the core of the oxygen minimum zone (400 m), average bacterial densities range from 25×10^7 cm^{-3} for the upper 0.5 cm of sediment, to 10×10^7 cm^{-3} at a

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[1] The hydrogen index has been suggested as a proxy for sediment food quality, and is a measure of the hydrogen content (and hence the redox state) of the organic matter. Its units are (mg hydrocarbon)/(g total organic carbon).

depth of 4.5 cm in the sediment (Levin et al., 1997). Colonies of *Thioploca* reach densities of 22 117 m^{-2} (Levin et al., 1997). With increasing seafloor depth, bacterial densities range from 4×10^9 cm^{-3} at 200 m to 0.6×10^9 cm^{-3} at 5000 m (Bak and Nieuwland, 1997).

Trophic types

The most prevalent feeding mode among the macrofauna in the oxygen minimum zone is deposit feeding – that is, the ingestion of sediment and associated organic matter. For the depth range from 400 to 1000 m within the oxygen minimum zone, most of the macrofauna (94%) are tentaculate, surface-deposit feeders. The nemerteans are likely to be scavengers or carnivores, and the mussel *Amygdalum politum* is a filter feeder. Cossurid polychaetes (constituting 1.1% of the fauna) may be the only subsurface deposit feeders present in this region. Below 850 m, subsurface deposit feeders constitute an increasing proportion of the total fauna, the largest figure being recorded at 3400 m (Levin et al., 2000). Subsurface deposit feeders are usually present in deep-sea or organically enriched environments (Levin et al., 1997). However, in organic-rich oxygen minimum zones, opportunistic species that can survive oxygen stress are generally surface-deposit feeders. Organic-rich sediments resulting from high surface production probably contribute to the high dominance of surface-deposit feeders in a relatively dense faunal assemblage, which has been observed (Levin et al., 1997, 2000; Levin and Gage, 1998).

Nematodes generally feed on detrital particles, sediment, and/or bacteria, although some nematodes are carnivorous (Gage and Tyler, 1991). Food availability appears to govern foraminiferal abundance and biomass (Altenbach, 1988; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Gooday et al., 2000). Generally, foraminifera consume phytodetritus, the bodies of small dead animals, bacteria associated with sediment, particulate organic carbon, and potentially dissolved organic carbon (Gooday et al., 1992). Where food is plentiful, foraminifera succeed, but they also must tolerate the reduced oxygen availability that is concomitant with abundance of organic matter (Gooday et al., 2000). The predominance of these organisms in the oxygen minimum zone of the Arabian Sea suggests that the meiofauna, of which they constitute the major part, occupy low trophic levels.

Rates of ecological processes

Very few data exist estimating the rates of key ecological processes in the oxygen minimum zone of the Arabian Sea. Useful data exist for the oxygen consumption of the sediment community (SCOC) in the oxygen minimum zone, specifically from the sediment below the Yemen–Somali upwelling region (~500–800 m). During both the Southwest and Northeast Monsoons, the oxygen consumption of the sediment community ranged from 0.7 to 4.3 mmol m^{-2} d^{-1} when the zone between 70 and 1700 m was covered with water with a low oxygen content (10–50 μM) (Duineveld et al., 1997). These values are 3–7 times higher than reported for oxygenated slopes in the Pacific (Hammond et al., 1996; Smith and Demopoulos, Chapter 6, this volume).

It may be expected that the bioturbation activities of benthos are linked with bottom-water oxygen concentration (Pearson and Rosenberg, 1978; Rhoads et al., 1978; Diaz and Rosenberg, 1995; Smith et al., 2000). In the oxygen minimum zone on the Oman slope, rates and patterns of bioturbation have been evaluated using profiles of ^{210}Pb and X-radiography (Smith et al., 2000). The mixing depths for ^{210}Pb within the oxygen minimum zone, with oxygen concentrations of 0.13–0.27 ml ℓ^{-1}, were half of those on oxygenated slopes in other oceans (mean depths 4.6 cm and 11 cm, respectively). The reduction in the ^{210}Pb mixing depth likely results from the prevalence of surface-deposit feeders and tube builders within this oxygen minimum zone (Levin et al., 2000; Smith et al., 2000). Unlike oxygen minimum zones in other oceans, there does not appear to be enhanced bioturbation at the boundary of the Oman oxygen minimum zone, possibly because of the gradual change in oxygen concentration from 0.13 to 0.27 ml ℓ^{-1} over the breadth of the zone (Smith et al., 2000).

The Western and Central Abyssal Indian Ocean

Habitat and community description

The deep abyssal zone of the Indian Ocean is an area of active deep-sea circulation (Parulekar et al., 1982). It is a habitat with rich benthic biomass. Investigations on deep-sea benthos in the western and central Indian Ocean, in the depth range of 1500 to 6000 m, have revealed abundant biota but low species diversity (Parulekar et al., 1992).

Sediment samples have been collected by grab, and macrofauna (retained on a 500 μm sieve) and meiofauna (retained on a 44 μm sieve) from the deep Arabian Basin and the Central Indian Basins have been quantified (Parulekar et al., 1982, 1992). The fauna from these abyssal sediments (3600–5300 m) are composed of 12 macrofaunal and 3 meiofaunal invertebrate taxa (Parulekar et al., 1982). Specifically, the abyssal macrofauna consists primarily of polychaetes (41.6%), followed by peracarid crustaceans (31.7%), ophiuroids (12.2%), Echiura and Bryozoa (9.7%), molluscs (4.8%), and agglutinating rhizopod protozoans (which were not included in these percentage figures). Macrofaunal densities range from 92 to 462 individuals m^{-2}, and biomass ranges from 0.47 to 13.32 g m^{-2} (Parulekar et al., 1982, 1992). Megafaunal scavengers present include ophidiid fish (Lochte and Pfannkuche, 2000).

The abyssal plains of the Indian Ocean harbor rich meiobenthic assemblages, meiofauna density ranging between 50 177 and 232 912 individuals m^{-2}. These densities are many times greater than densities reported for meiofauna of the central North Pacific and the east and west Atlantic (Wolff, 1977), but are only one-tenth of that observed in the bathyal depths of the northwest Indian Ocean (Thiel, 1966). Meiofaunal biomass ranges from 0.02 g m^{-2} to 0.41 g m^{-2}. Nematodes are the most abundant group, accounting for 53.3% of the individuals, followed by foraminiferans at 17.6% and harpacticoid copepods (16.8%). Kinorhynchs, ostracods, and turbellarians were also present in small quantities (Parulekar et al., 1992). The density of meiofauna decreases with increasing water depth (Parulekar et al., 1982).

In general, manganese nodules from the 3000–4000 m depth range in the abyssal zones are relatively barren with respect to benthic biomass, possibly because of the oligotrophic feeding conditions (Neyman et al., 1973; Parulekar et al., 1982). Benthic tunicates represented 20% of the invertebrate species collected with a trawl in an area with polymetallic nodules (Monniot and Monniot, 1985). Nodules occur at low abundance (1–2 kg m^{-2}) in areas of thick sediments, compared to areas with thin sediments (3.5–5 kg m^{-2}) (Sharma et al., 1997). Meiofauna and macrofauna have been quantified from sediment cores collected from nodule areas. Meiofaunal density ranges from 0.3 to 4.5 individuals cm^{-2}, dominated by nematoda. The macrofaunal density ranged from 8–64 individuals m^{-2}, generally dominated by polychaetes (Sharma et al., 1997). In the abyssal region of the central Indian Ocean in the 3500 to 4500 m depth range, in brown oozy sediments with polymetallic nodules, meiofaunal densities range from 0.4 to 1.5 individuals cm^{-2} (Parulekar et al., 1982). These sediments had almost three times the macrofaunal biomass (5.16 g m^{-2}) of the yellow calcareous oozy sediments without nodules (1.78 g m^{-2}).

The mean benthic population density (meiofauna and macrofauna) from abyssal sediments varies from 233 322 individuals m^{-2} in the 1500–1999 m depth zone to 50 269 individuals m^{-2} in the 5500–5999 m depth zone (Parulekar et al., 1992). The abundance of both macrofauna and meiofauna decreases with increasing water depth. However, the proportions of meiofauna and macrofauna are reversed with increasing depth; the proportion of meiofauna increasing with depth. Benthic biomass in the abyssal Indian Ocean is relatively poor, ranging from 0.11 to 12.75 g m^{-2}, compared to other deep sea habitats in the Indian Ocean (Parulekar et al., 1982, 1992).

It has been suggested that the supply of organic material to the abyssal plains of the deep Indian Ocean results from deep-water circulation transporting organic matter from the shelf and slope to abyssal depths (Parulekar et al., 1982). It is possible to find terrestrial plant debris at depths of 4500 m in the abyssal central Indian Ocean (Parulekar et al., 1982).

The diverse benthic fauna and the high values of standing crop in the western and central Indian Ocean are dependent on high organic production in the overlying water column. The correlation in the abyssal Indian Ocean between the total oxidizable organic content of the water column and the benthic standing crop is statistically significant (Parulekar et al., 1992). In addition, microbial activity and biomass show significant linear correlations with the vertical flux of particulate organic carbon (Lochte and Pfannkuche, 2000). The high biomass on the central Indian Ocean abyssal plain is probably a result of high biological productivity in surface waters (Humphrey, 1972). A close relationship between primary productivity and benthic standing crop was observed (Parulekar et al., 1982), which is not consistent with the suggestion that the deep-water supply of organic matter from the shelf and slope to abyssal depths promotes high standing crops of deep-sea benthos (c.f., Gage, 1978).

The oligotrophic abyss

The seafloor of the Bay of Bengal is characterized by a deep-sea fan cut by many distribution channels of turbidity current fanning out from the north (Curray and Moore, 1971; Ohta, 1984). During present sea-level conditions, a majority of sediments from large rivers (the Ganges and Brahmaputra) are reported to be trapped in the subsiding deltas and on the inner shelf, and thus little sediment and nutrients are transported by the turbidity channels (Curray and Moore, 1971). The Bay of Bengal experiences wind-generated upwelling along the coast, promoting primary productivity. Average primary productivity in the Bay is 109.5 g C m^{-2} y^{-1} (Pant, 1992). The carbonate compensation depth in these waters is ~4500 m; at shallower depths, the calcium-carbonate sediments are covered with thin greenish brown flocculent material.

Limited data from this region come from sediments collected by grab samples; the total benthic biomass (meiofauna and macrofauna) in the Bay of Bengal ranges from 0.11 to 0.38 g m^{-2} (Sokolova and Pasternak, 1962, 1964; Neyman et al., 1973). These abundances appear to be low compared to the rest of the Indian Ocean. Despite the relatively low biomass of deep-sea benthic organisms in the Bay of Bengal, distinct biogenic features can be observed on the surface of the deep-sea floor. Specifically, star-shaped feeding traces produced by echiuran worms can be observed (Fig. 7.7). They live between the depths of 2635 m and 5025 m (Ohta, 1984). As the organism feeds on surface detritus, its proboscis skims the sediment surface of the deep-sea floor radially, leaving a distinctive star-shaped feature. These features are also found in the deep Pacific and Atlantic Oceans (Gage and Tyler, 1991; Gage, Chapter 11, this volume).

Fig. 7.7. Star-shaped echiuran feeding trace from ~4000 m in the Bay of Bengal. Modified from Ohta (1984).

The surface productivity by phytoplankton is poor, and therefore the zooplankton biomass is poor (Pant, 1992). As a result, total transport of organic matter to the sea floor may be expected to be low. Thus, benthic biomass and abundance in the Bay of Bengal appear to reflect the low surface productivity.

CONCLUSIONS AND OUTSTANDING PROBLEMS

The deep Indian Ocean is composed of a variety of habitat types, including abyssal plains, oxygenated slopes and basins, oxygen minimum zones, seamounts, and trenches. This chapter summarizes the available data from a few of these habitats. The general conclusions are that the deep Indian Ocean still remains poorly known, and is waiting to be discovered and understood. We have identified below specific areas that need to be explored within the Indian Ocean, including habitats and ecological rates.

(1) Complete benthic habitat descriptions for seamounts, the Java Trench, and other oxygen minimum zones (e.g., the Bay of Bengal) are not available. In order to understand the productivity of the Indian Ocean and compare it with other oceans, extensive benthic surveys need to be conducted. In addition, the acquisition of reliable data for biomass and abundance from seamounts is important in fisheries. Current knowledge of the deep-sea organisms constituting the Indian Ocean benthos is very limited.

(2) Total energy budgets and biomass estimates for all size classes are not available for any deep-sea habitat in the Indian Ocean. Complete estimates of biomass production for benthic populations are scarce.

(3) Composition, variability, and flux rate of particulate organic carbon to the seafloor is poorly quantified throughout the Indian Ocean. The nature and flux of other food sources to the deep sea, (e.g., phytodetritus, nekton falls), is also unknown for the Indian Ocean. Not only are these important food sources for the deep-sea benthos – quantifying them is necessary for calculating the global carbon budget.

(4) Data on ecological rates, including the benthic response to the intense seasonal (monsoonal) production cycle, are scarce. Bioturbation rates have been evaluated in oxygen minimum zone of the Oman slope, but data for other habitats in the deep sea are very limited. Because the mining of manganese nodules is becoming more important, more intensive research involving the responses of benthic communities to disturbance, both anthropogenic and natural, is imperative.

(5) Chemosynthetic environments. There is recent evidence of hydrothermal venting on the Southwest Indian Ridge (German et al., 1998), and it would be of great biogeographic interest to see if the dominant fauna is more related to the Atlantic or to the Pacific vents. There is also evidence of reducing conditions in sediments near the base of the oxygen minimum zone, where the fauna may gain energy from chemosynthetic primary production.

The Indian Ocean remains an exciting area for pioneering research. A complete understanding of its habitats and processes will not be possible until the outstanding problems mentioned above have been resolved.

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Chapter 8

THE POLAR DEEP SEAS

Andrew CLARKE

INTRODUCTION

At a first glance, the Arctic and Antarctic regions might seem to be rather similar. Both are sited over the geographical poles and are hence subject to extreme seasonal variations in solar radiation; both are cold, receive relatively little precipitation and are dominated by ice. From a biological viewpoint, however, the differences between the two polar regions outweigh their similarities. The Arctic is essentially a landlocked basin allowing only a limited exchange of water with adjacent oceans, and receives an enormous input of freshwater and sediment. The Antarctic is a single landmass isolated on all sides by deep oceans. The two areas thus differ greatly in topography and oceanography; they are also very different in their tectonic and evolutionary history. In this review I shall therefore deal with the Arctic and Antarctic deep seas separately, before describing aspects common to their biology.

First, however, it is necessary to define what is meant by the term ‘deep sea’ in a polar context. Gage and Tyler (1991) considered the deep sea to start at the continental slope. This slope marks the boundary between continental (granitic) crust and oceanic (basaltic) crust. It typically starts at a depth of about 200 metres, with the gradient easing into the continental rise or abyssal plain at around 2000 metres depth. This topographic definition of the deep sea, however, runs into problems in the Southern Ocean where a combination of isostatic adjustment to the mass of the icecap and scouring by ice-sheets during previous glacial maxima means that the continental shelf around Antarctica may be as deep as 500 or even 1000 m in places. As a result many biological studies of the deep sea in Antarctica are actually concerned with the biota of the deep continental shelf rather than truly abyssal or continental-slope organisms. Animals living on the deep continental shelves of the Antarctic will share some physiological features with true deep-sea organisms (since pressure effects on metabolism become apparent at depths as shallow as 500 m: Hochachka and Somero, 1984). In faunistic terms, however, they belong to a continental-shelf fauna rather than a true deep-sea fauna.

In this review I shall therefore use the functional definition of Gage and Tyler (1991), confining the use of the term “deep-sea” to those organisms of the abyssal plain or continental slope. Some comparison with studies of the deep continental shelf around Antarctica will be inevitable, however, for organisms living there share many ecological features with true deep-sea organisms.

Exploration of the polar deep seas

Despite their inhospitable nature, the polar regions have played an honorable role in the history of deep-sea biology. The British explorer John Ross, whilst searching for the North-West Passage in 1818, collected a specimen of the basket-star *Astrophyton* when this was snagged on a sounding line at about 1600 m depth. Thirty years later, James Clark Ross (John Ross’s nephew) and the eminent botanist Joseph Hooker, working from HMS *Erebus* and *Terror* in the Southern Ocean, collected abundant organisms whilst sounding as deep as 1800 m.

These results led directly to the pioneering work of HMS *Lightning* and *Porcupine* in the deep waters of the Atlantic, and then to the seminal work of HMS *Challenger* (1872–76). The circumnavigation by HMS *Challenger* was probably the single most important expedition in the history of oceanography, and laid the foundations for current knowledge of the deep sea. Of particular significance were the studies in the Southern Ocean.

The expeditions that followed are relatively well known [see Gage and Tyler (1991) for a brief historical summary]. Their results are widely available through the comprehensive and thorough expedition reports. In contrast the enormous volume of data from the extensive investigations of the deep sea by biologists of the former Soviet Union are almost unknown in the west. Until recently, they were largely available only in Russian; but the appearance in mainstream western literature of major reviews is now revealing the wealth of knowledge of the deep sea that had been accumulated, including extensive work in polar regions (see, for example, Gebruk et al., 1997). It is likely that the merging of these results with more recent investigations, such as those of USNS *Eltanin*, and German work from RV *Polarstern*, will result in significant advances in understanding of the biology of the polar deep seas. A succinct history of research in this area has been given by Vinogradova (1997).

THE ARCTIC DEEP SEAS

There have always been difficulties in defining the Arctic marine ecosystem. These difficulties are particularly acute for benthic systems in both pelagic and shallow-water environments, where truly polar conditions and assemblages merge gradually into those of boreal and cold-temperate regions.

The Arctic deep-sea environment is, however, fairly precisely circumscribed. It consists of a series of deep basins, isolated from all other deep waters by large areas of shallow sea, and crossed by a series of ridges (Fig. 8.1). We probably know less of the topography of the Arctic than any other ocean basin because the extensive cover of multi-year ice prevents the use of many traditional techniques for determining bathymetry. As a result the names of some of the smaller basins have only recently stabilised, resulting in confusion for biologists researching the older literature. Recent oceanographic studies of the circulation of intermediate depth waters (Rudels et al., 1994) have, however, suggested that functionally there are three major deep water basins (Fig. 8.2).

Traditionally the Arctic has been viewed as consisting of two large basins, the Eurasian and Amerasia Basins, separated by the vast submarine mountain range of the Lomonosov Ridge. Each of these basins is itself divided by ridges (Fig. 8.1). The Amerasia Basin is crossed by the Alpha- and Mendeleev Ridges, which separate the large Canada Basin and the smaller but deeper Makarov Basin. The Alpha–Mendeleev Ridge is the largest submarine mountain complex in the Arctic Ocean, exceeding the Alps in extent. The Eurasian Basin is divided by the Nansen–Gakkel Ridge. This mid-ocean ridge separates the very deep Fram (or Amundsen) Basin from the Nansen Basin. It would appear that the initiation of sea-floor spreading along this ridge transported the Lomonosov Ridge, originally part of the Barents and Kara shelves, to its present position (Weber, 1989).

Surrounding these deep basins are wide and relatively shallow continental shelves. Of particular ecological importance are the series of five epicontinental seas located on the huge European and Siberian continental shelves: the Barents, Kara, Laptev, East Siberian and Chukchi Seas (Fig. 8.1).

All the Arctic basins are deep, typically exceeding 3000 m, and all contain large areas of very flat abyssal plain. Although the deep Arctic basins are isolated from the Pacific Ocean by the broad shallow continental shelves of the Chukchi Sea and the Bering Strait, there is an important deep-water connection through Fram Strait to the deep waters of the Norwegian Sea (Fig. 8.1). The Norwegian Sea is itself separated from the deep North Atlantic by ridges covered by shallower water, running east–west from Greenland to Iceland (the Denmark Strait) and thence to Norway. This topography indicates that the Arctic deep sea cannot be completely prescribed, and that the faunal history of the Norwegian Sea is of considerable significance in understanding the evolutionary history of the fauna of the Arctic basin.

Large-scale oceanography

The topography of the Arctic basin restricts exchange with lower-latitude oceans to two connections, through the very shallow Bering Strait to the Pacific, and through the deeper Fram Strait to the Greenland–Iceland–Norwegian Sea. Zenkevitch (1963) compared the dimensions of these two connections, and estimated the mean annual transport through them as 0.25 Sv through the Bering Strait and ~13 Sv from the North Atlantic. Lewis (1982) computed an overall water, salt and heat budget for the Arctic Basin (Table 8.1). This budget incorporated freshwater inflow from rivers, and outflow of ice, both of which fluxes were small in

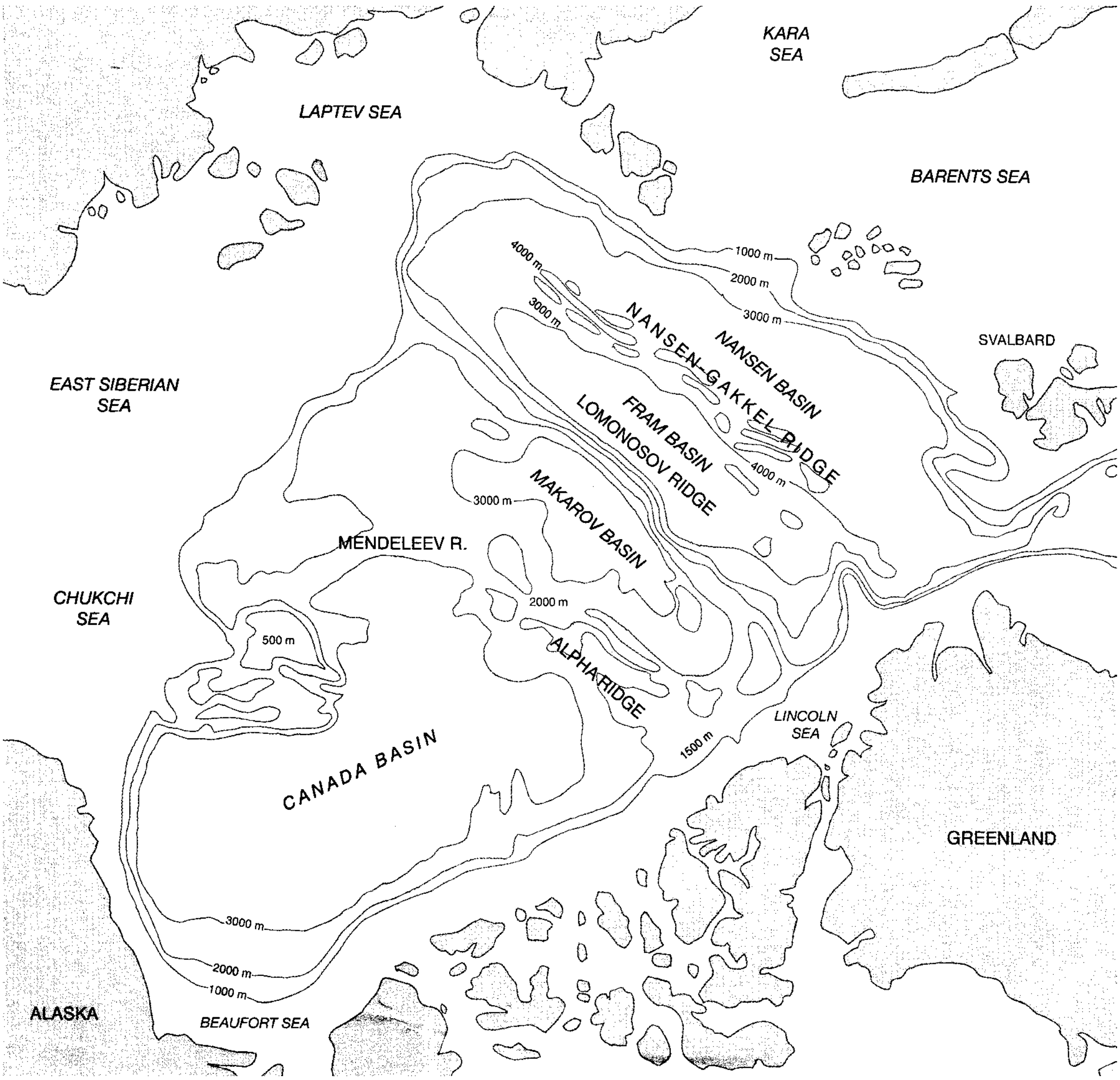

Fig. 8.1. The Arctic basin, showing the major deep-water basins and other topographic features. The Lomonosov Ridge divides the Arctic Ocean basin into the Eurasia and Amerasia basins, which are further sub-divided by the Nansen–Gakkel and Alpha Ridges, respectively. Also shown are the broad expanses of continental shelf underlying the Chukchi, East Siberian, Laptev, Kara and Barents Seas. Depths in metres. Redrawn from Weber (1989).

comparison with the volume of seawater exchanged between the Arctic Basin and the North Atlantic. Subsequent detailed studies have refined the estimates for different components of the overall flux, though considerable uncertainties remain for many of these estimates (see discussion by Samuel et al., 1994).

More recent studies have improved the estimates of exchange. Rudels et al. (1994) have shown that the intermediate-depth waters of the Arctic Basin are supplied from the North Atlantic via two major paths: through Fram Strait and over the Barents Sea. These two branches are of roughly equal strength, estimated at ~2 Sv. Samuel et al. (1994) have estimated inflow from satellite altimeter data and derived an annual mean for the Norwegian Atlantic Current of 2.7 Sv with a seasonal amplitude of 1.8 Sv.

Inflowing currents to the Arctic Basin are steered strongly by topography, and water flowing over the continental shelves is cooled and diluted. Seasonal formation of ice at the perimeter of the Arctic

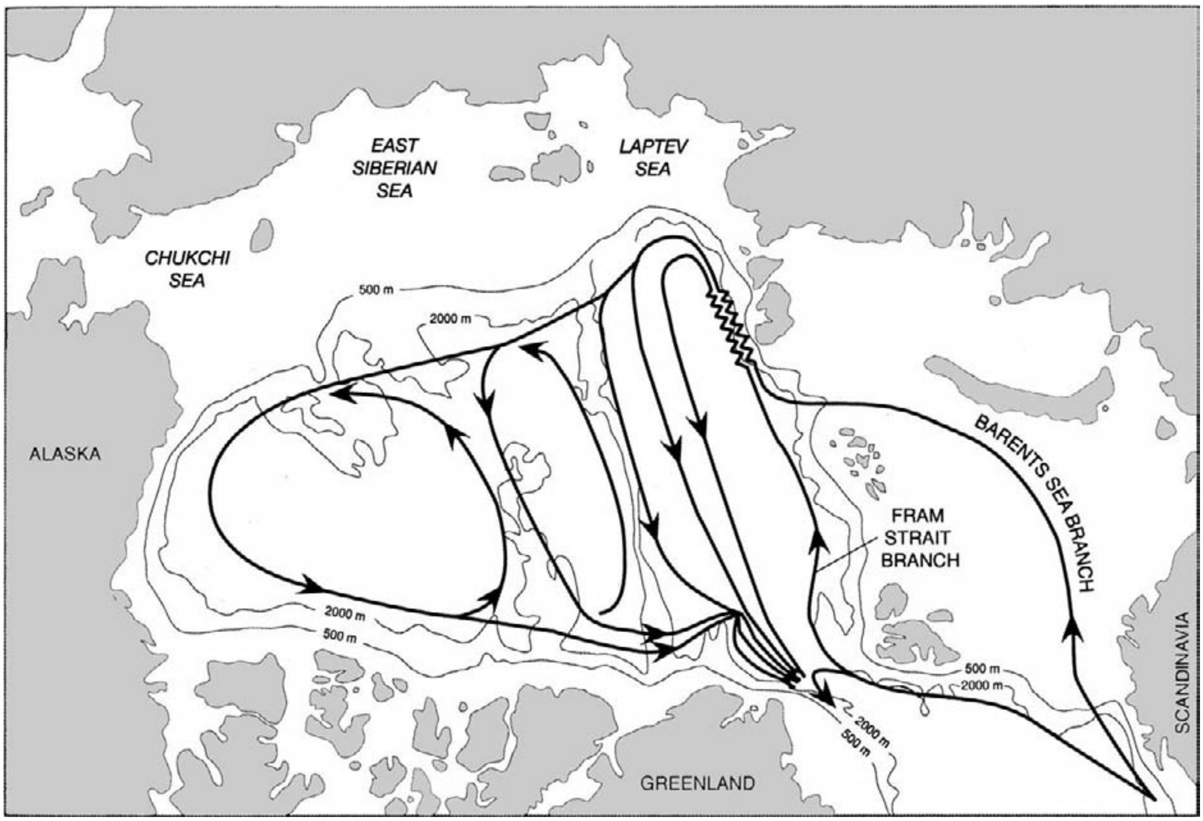

Fig. 8.2. Diagrams showing inferred circulation of water in the Arctic basin at intermediate depths (200 to 1700 m). The influence of undersea topography in steering flow is clear. Redrawn from Rudels et al. (1994).

Basin produces dense, cold water that flows over the continental shelves and sinks to deeper water as cold plumes flowing down the continental slopes. The dominant outflow from the Arctic Basin is at intermediate depths in the East Greenland Current, but deep water circulation within the Arctic Basin is very poorly known.

Although the contribution of freshwater input from rivers is minor in terms of overall water mass balance, it is significant in many other ways. The fresh water forms a surface layer across much of the polar basin, which inhibits vertical mixing and thereby limits exchange with underlying waters (Lewis, 1982). The rivers also deliver large quantities of sediment to the continental shelves, and in some cases also carry significant amounts of pollution into the Arctic Basin.

Much of the Arctic Basin is covered by multi-year ice, which may be regarded as effectively permanent on an ecological time scale. Around the margins the ice grows and melts seasonally, with significant quantities also carried into the North Atlantic on the East Greenland Current. Passive microwave data from satellites indicate that the area of seasonal ice in the Arctic Basin averages $0.88 \times 10^6\,\mathrm{km}^2$. Of the $6.2 \times 10^6\,\mathrm{km}^2$ of permanent ice cover, most is multi-year ice (Gloersen et al., 1992).

Primary production

The perennial ice-cover of the Arctic Basin, and the freshwater lens at the surface together reduce primary productivity in the water column, and also make this difficult to measure. Dunbar (1982) has collated the early measurements. These came almost exclusively from coastal environments, and ranged from 12 to $98\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$; the single estimate for the Arctic Ocean was much lower at $0.6\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$.

Andersen (1989) has provided a thorough survey of primary production in the Arctic Ocean as a whole. Estimates of annual water-column production vary from $<5\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ beneath ice to $>500\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$ in some coastal habitats. Production within ice is

Table 8.1
An approximate water, salt and heat budget for the Arctic Basin[1]

	Volume transport (Sv)[2,3]	Heat transport (GW)[3]	Salt transport[3,4]
Bering Strait			
Water	1.5	3.8	48.6
Ice	negligible	−1.7	negligible
Arctic archipelago	−2.1	13.4	−71.8
East Greenland Current			
Polar water	−1.8	8.4	−61.2
Atlantic water	−5.3	−13.4	−185.0
Ice	−0.1	33.5	−0.3
West Spitsbergen Current	7.1	68.2	248.9
Spitsbergen–Franz Josef Land	−0.1	−1.3	−3.5
Franz Josef Land–Novaya Zemlya	0.7	2.9	24.3
Run-off (riverine input)	0.1	2.1	nil
Total inflow	9.4	–	321.8
Total outflow	−9.4	–	−321.8
Total advective heat	–	124.3	–
Total advective heat loss	–	−16.3	–
Net exchange	0	108.0	0

[1] From Lewis (1982); data are estimated annual means.

[2] $1\,\mathrm{Sv} = 10^6\,\mathrm{m^3\,s^{-1}}$.

[3] Positive values are inflows or heat gains, negative values are outflows or heat losses.

[4] $\mathrm{Tonnes} \times 10^{-3} \times \mathrm{Sv^{-1}}$.

more difficult to measure, and reliable estimates are available only for the spring bloom. This can reach 15 g C m^{-2} y^{-1} in the central Arctic Basin, which is about one-third of the total annual production in this region. The summer bloom of ice-associated algae can be more intense than in spring, but reliable quantitative data are lacking (Andersen, 1989).

The most significant improvements on these early estimates have come from the 1994 joint Canadian/U.S. Arctic Ocean Section. This expedition undertook size-fractionated measures of algal biomass and production in open water leads, and at the ice/water interface, along an oceanographic section running from the shallow waters of the Chukchi Sea to the Nansen Basin, via the North Pole. Maximum daily production rates (mg C m^{-2} d^{-1}) were 2570 over the continental shelf in the Chukchi Sea, 73 in open-water leads over the Makarov Basin and 521 over the Nansen Basin (Gosselin et al., 1997). Production rates were generally lower where ice cover was higher, and at the same time the balance of production switched from larger (>5 μm) to smaller cells. Ice algae contributed just under 60% of total primary production in the central Arctic basin, but only 3% in surrounding areas. Total annual primary production in the central Arctic Ocean was estimated to be 15 g C m^{-2} yr^{-1}, an order of magnitude higher than the earlier estimate cited by Dunbar (1982), and also higher that the estimate of 10 g C m^{-2} yr^{-1} of Wheeler et al. (1996). This increase is a result in part of improved estimates of the contribution from sea-ice algae, but also to inclusion of the previously unmeasured release of dissolved organic matter. There are very few estimates of benthic primary production, although the estimated annual primary productivity near Point Barrow was substantial (>40 g C m^{-2} y^{-1}: Matheke and Horner, 1974).

Away from seeps and hydrothermal vents, the sole source of organic carbon for heterotrophic organisms in the deep sea is surface production (see Chapter 2). Particulate organic matter (POM) produced in surface waters reaches the deep sea through sedimentation, but logistic difficulties have meant that estimates of the flux of particulate organic matter within the Arctic Basin have been very few (Wassmann, 1989; Wassmann et al., 1990, 1991). Recent work utilizing Th/U disequilibrium has suggested a mean flux of particulate organic matter in the central Arctic Ocean of 3 mmol C m^{-2} d^{-1} (Moran et al., 1997).

Although convective processes in polar waters are clearly important in carrying particulate organic matter to deeper water (Carsey and Roach, 1994; Manley and Smith, 1994), it is likely that the most significant process is advection from the productive waters of the continental shelf (Cranston, 1997).

Sediment composition and sedimentary processes

Technical and logistic difficulties have limited studies of Arctic deep-sea sediments. What data there are largely emanate from samples taken from beneath drifting ice stations. These are almost exclusively from areas west of the Lomonosov Ridge, and especially in the Canada Basin; the eastern Arctic basins remain effectively unknown. A thorough review of earlier knowledge was provided by Darby et al. (1989).

The oldest sediments yet collected from the Arctic are Cretaceous in age and come from relatively thin deposits on the Alpha Cordillera (Ling et al., 1973; Clark, 1974). Sedimentary deposits within the basins are considerably thicker, up to 2–3 km deep in areas of the Canada Basin (Hunkins and Kutschale, 1967). All the Plio–Pleistocene sediments examined have proved to be sandy or silty lutites with a variable proportion of gravel-sized clasts (Darby et al., 1989). Photographs, however, reveal the presence of larger clasts, from pebble to cobble size, which are usually not taken in cores (see, for example, Hunkins et al., 1970). Clark et al. (1980) classified the sediments into four types based on the size frequency distribution of the <63 μm fraction. The lithology of these sediments differed from those in other ocean basins in the high proportion (10–30%) of kaolinite and chlorite in the clay fraction (<2 μm), together with the abundant detrital dolomite and calcite in the coarser fractions.

The composition, mineralogy and physical characteristics of Arctic deep-sea sediments point to an important contribution from ice-rafted material. The overall importance of ice-rafting is currently unquantified, but the content of ice-rafted material in sediments of the Arctic abyssal plain has been put at 60–70% (Darby et al., 1989). Aeolian input is low.

Turbidity currents have been a major process for sediment transport in the Arctic deep-sea basins. Their importance is greater closer to the continental shelves, but has probably been important over large areas. Thus, the sediments in the Fram Basin have probably originated from the Lena River, and have been carried into the basin from the Kara and Laptev shelves by turbidity currents. Similarly the Makarov Basin contains turbidites from the East Siberian shelf, and the Canada Basin sediment originated from the McKenzie River region, and was carried by turbidity currents (Weber, 1989). There is no evidence for significant volumes of nonturbidite current-deposited sediments in Arctic abyssal sediments, and the few existing measures of rates of bottom currents in the Arctic deep sea are all low (Galt, 1967).

Microfauna of Arctic deep-sea sediments

Relatively little is known of the microbial fauna or meiofauna of the Arctic deep ocean. Darby et al. (1989) reported organic-carbon contents for the Canada Basin which decreased towards the centre of the basin. The mean value (0.87% dry mass) was significantly higher than in sediments of similar mineralogy from the Atlantic and Pacific Oceans. Cranston (1997) found organic content between 0.3 and 0.5% in the Makarov Basin, with higher levels (1.2%) on the Lomonosov Ridge and in the Amundsen Basin (1.0%). The low hydrogen index (mg H/g C) and the high C/N atomic ratios indicate that most of the organic matter in the sediments of the Arctic deep sea is terrigenous material (Stein et al., 1994; Stein, 1996; Fahl and Stein, 1997). Such material typically has been extensively reworked and consequently is of little nutritive value for benthic organisms.

Concentrations of sediment-bound chlorophyll and phaeopigments are very low (Boetius et al., 1996; Soltwedel and Schewe, 1998). These data indicate that the supply of phytodetritus to the benthos beneath perennial ice cover is very low, and that advection from areas of high production on the shelves is minimal. Mean pigment concentrations were, however, higher in the Amundsen Basin than in the Makarov Basin (Soltwedel and Schewe, 1998). The limited data thus suggest that, in the deep basins of the central Arctic Ocean, organic matter input through the flux of phytodetritus is extremely low and very patchy. A major process contributing to the spatial heterogeneity may be the production of organic matter in spatially restricted areas that are episodically ice-free, followed by sedimentation of phytodetritus (Soltwedel and Schewe, 1998).

Bacterial numbers and biomass are also very low in the central basins of the Arctic Ocean. Soltwedel and Schewe (1998) reported $3.2–3.7 \times 10^8$ cells ml^{-1}, equivalent to 5–6 $\mu g\,C\,ml^{-1}$, in sediments from the Amundsen and Makarov Basins. These data are somewhat higher than those reported by Kröncke et al. (1994), but nevertheless indicate that bacterial biomass in Arctic deep-sea sediments is very low. Soltwedel and Schewe (1998) referred to the central Arctic deep-sea basins as a benthic desert. Almost nothing appears to be known of the non-bacterial microbial fauna or the meiofauna of the central Arctic basins (Pfannkuche and Thiel, 1987).

The Arctic deep-sea macrofauna

Whilst the fauna of the continental shelves of the Arctic Ocean has become relatively well known through the extensive work of biologists from Canada, North America, Scandinavia and Russia, the abyssal fauna remains little known (Paul and Menzies, 1974). Key exploratory studies were the cruises of the Soviet research vessels *Sadko* and *Sedov* between 1932 and 1938, Soviet studies of the central Arctic basin from the *Sedov* in the period 1937 to 1940, and the work of

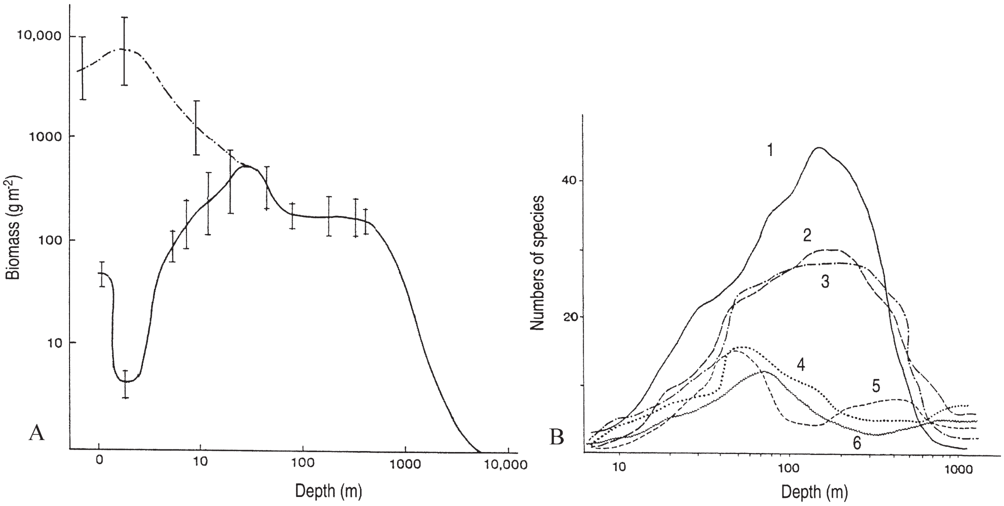

Fig. 8.3. A. Variation in benthic biomass (g m^{-2}; fresh mass) with depth. Data for high Arctic and boreal environments plotted separately. Note logarithmic axes. Redrawn from Golikov and Scarlato (1989). B. Species richness of echinoderms (echinoids, arteroids and ophiuroids, all taxa pooled) with depth in various geographic regions of the Arctic basin. 1, Southern Barents Sea; 2, Northern Barents Sea; 3, Kara Sea; 4, Laptev Sea; 5, East Siberian Sea; 6, Chukchi Sea. Note logarithmic abscissa. Redrawn from Anisimova (1989).

the Danish *Ingolf* expedition between Jan Mayen and Iceland. The latter work was outside the Arctic Ocean proper, but was extremely important in unravelling the links between the abyssal faunas of the Arctic and North Atlantic. Subsequently important insights have been gained from photographs (Ewing et al., 1969; Hunkins et al., 1970), work from drifting ice islands, and recent expeditions such as the Arctic Ocean Section and dedicated cruises by the German research vessel *Polarstern*. Despite all this work, the Arctic deep sea remains one of the least studied habitats on the face of the globe.

Extensive work at lower latitudes has established that abyssal depths tend to support a lower macrofaunal biomass and fewer species than habitats on the continental slope or shelf (reviewed by Gage and Tyler, 1991). Detailed work by Soviet biologists has suggested a similar pattern in the Arctic Ocean (Fig. 8.3). The species richness of echinoderms (Anisimova, 1989), bivalves (Fedyakov and Naumov, 1989), prosobranch gastropods (Golikov, 1989), bryozoans (Gontav and Denisenko, 1989) and cumaceans (Vassilenko, 1989) have all been shown to be very low in the Arctic deep sea compared with the nearby shelves. In most cases peak species richness is found in the depth range from 100 to 200 metres (Fig. 8.4). A similar pattern of decreasing species richness with depth has been described for asellote isopods by Svavarsson et al. (1993), although if the analysis was restricted to true Arctic species a peak in species richness at about 1000 m depth was suggested. In contrast, Brandt (1997) found that, in the Greenland Sea, the species richness of cumaceans and isopods was greater in deeper waters.

These observations pose the question as to how the fauna of Arctic deep seas compares with that of similar depths elsewhere. Menzies et al. (1973) have compared the taxonomic richness of the fauna of the Eurasia Basin with that of the deep sea off Costa Rica. Taxonomic richness at the level of class was significantly lower in the Eurasia Basin, although it is possible that further work will establish the presence of taxa previously thought to be absent. The number of higher taxa is a reasonably good predictor of species richness in the sea [Roy et al., 1996; but see Prance (1994) for a contrary view of tropical terrestrial plants]. This would suggest that the species richness of the Arctic deep sea will prove to be low.

Marshall (1982) has emphasized that the species richness of the bathyal macroinvertebrate fauna (down to 2000 m depth) is over 500, exceeding that of the abyssal fauna (below 2000 m) by a factor of about four. The most comprehensive studies of the Arctic deep-sea fauna are those of Guryanova, all published in Russian. Using all available data [notably species lists produced by Gorbunov (1946), Koltun (1964) and Guryanova (1970), together with western data], Guryanova concluded that the Arctic deep sea fauna is relatively young, and probably of Pleistocene age.

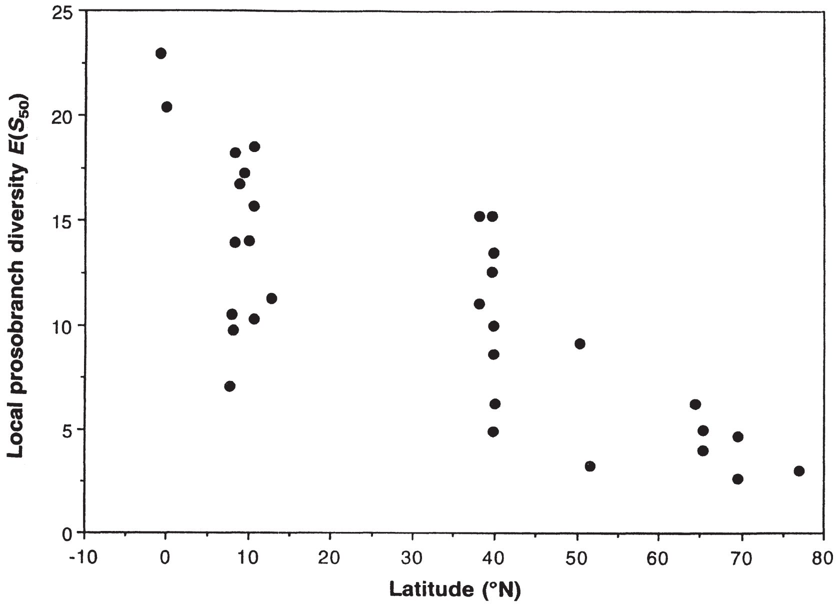

Fig. 8.4. Relationship between species diversity of deep-sea prosobranch gastropods and latitude for the North Atlantic and the Norwegian Sea. Diversity is expressed as the expected number of species E (Sn), with $n = 50$ individuals (Hurlbert, 1971). Diversity in this group is negatively correlated with latitude, and the relationship is statistically significant ($P < 0.001$). Redrawn from Stuart and Rex (1994).

The best known groups are the amphipod and isopod crustaceans, and echinoderms. These groups have a high degree of endemism at the species level, but very low endemism at the genus and family level (Guryanova, 1970). The diversity is lowest in the central Arctic basin (Clough et al., 1997), and the strongest faunal affinities are with the Norwegian Basin, suggesting continuing invasion from the North Atlantic.

Fedyakov and Naumov (1989) listed 183 species of bivalve molluscs, of which 44 species were found in the Norwegian Basin and 35 species in the central Arctic Basin. Deep sea bivalves appear to be generally distributed in all the deep-sea basins, and characteristic species of the central Arctic Basin are *Ledella tamara, Nucula zophos* and *Tindaria derjugini.* Echinoderms are typically important members of abyssal faunas, and key Arctic species are the widespread echinoid *Pourtalesia jeffreysi* and the ophiuroid *Ophiopyren striatum* (Anisimova, 1989).

Quantitative data on biomass and diversity have been provided for Arctic deep-sea macrofauna by Kröncke (1994, 1998). Samples were collected by a box-core technique along transects across the Amundsen and Makarov Basins. Box-core samples are excellent for quantitative data on species abundance, but the small areas sampled mean that many large, infrequent taxa are missed. Thus the species list provided by Kröncke (1998) contains many polychaetes and small crustaceans (cumaceans, tanaiids, isopods and amphipods) but only a single echinoderm (*Ophiura robusta*).

Biomass values were very low in the deep basins (0.025 to 3.445 g fresh mass per square metre), but somewhat higher at the shallower stations. Species richness was also very low in the deep basins (1 to 11 species in a sample of 0.02 m^2) and non-overlapping k-dominance plots showed clearly that faunal diversity was lowest in the deepest basins. Comparison was made difficult, however, by the very low absolute number of species from the deeper stations.

Are Arctic deep-sea faunas impoverished?

It has long been established for many groups of terrestrial plants and animals that there is a marked cline in richness at several taxonomic levels (species, genera, families) from the tropics to the poles. Following the seminal work of Thorson (1957), it has also long been assumed that a similar latitudinal cline in taxonomic diversity exists in the sea. Although the data are very convincing for some well-studied groups (notably gastropod and bivalve molluscs), it is not yet certain that this will prove to be a general feature of all marine organisms or of both hemispheres (Clarke, 1992; Clarke and Crame, 1997).

Most of the data pertinent to a discussion of latitudinal diversity clines in the sea come from shallow or continental-shelf waters (Kendall and Aschan, 1993; Kendall, 1996). Recently, however, Rex and colleagues have argued that a latitudinal cline in diversity is to be found in the deep sea (Rex et al., 1993, 1997; Stuart and Rex, 1994). A particularly striking cline is exhibited by prosobranch gastropods where the number of species to be expected in a sample of 50 individuals decreases from >20 in the abyssal equatorial Atlantic to <5 in the Norwegian Deep (Fig. 8.4). Although no data were included for the Arctic Ocean itself, the latitudinal cline is very marked. Similarly distinct clines have been shown in the northern hemisphere for deep-sea isopods and bivalves (Rex et al., 1993). These clines are, however, particularly strongly influenced by the data for the Norwegian Sea (which has a genuinely depauperate fauna: Dahl et al., 1976; Gray, 1994). For some taxa (for example bivalves) removing the data from the highest latitudes leaves a pattern with no apparent latitudinal variation; for others (for example gastropods: Fig. 8.4) a strong cline remains. There are also statistical problems in the use of rarefaction to estimate diversity from small samples, and the difficulty of attaching a suitable confidence interval (Gotelli and Graves, 1996; Svavarsson, 1997).

As with so many aspects of deep sea biology, the question of the existence of a latitudinal cline in diversity for all taxa is one where the hypotheses exceed the data with which to test them. Nevertheless the most careful analysis of the existing data does suggest a strong latitudinal cline in the diversity of deep-sea faunas (Rex et al., 1993, 1997). This would suggest that the low taxonomic richness suggested by the limited data for the Arctic deep-sea fauna is explicable, at least in part, by global-scale processes. The explanation for the latitudinal cline in diversity (if indeed there is a single explanation) is not yet clear [see discussion by Clarke and Crame (1997)], but the evolutionary history of the fauna is clearly important.

Faunal affinities and evolutionary history

The evolutionary history of the Arctic fauna has been reviewed by Menzies et al. (1973), Golikov and Scarlato (1989), and Dunton (1992). It is now well established that the shallow-water fauna of the Arctic continental shelf is relatively young, and comprises species of both Pacific and Atlantic affinities as well as some endemics (Table 8.2).

Table 8.2
Biogeographic affinities of shallow water (0–50 m) and abyssal faunas of the Arctic Ocean[1]

Region	n[2]	Biogeographic group[3] (% fauna)			
		A	B	C	D
Chukchi	150	9	6	27	58
Beaufort	371	8	13	15	64
Canadian Archipelago	168	5	20	9	66
Barents	186	14	15	8	63
Laptev	152	12	19	10	59
East Siberian	ND	9	5	16	70

[1] Shallow water data from Dunton (1992), where original sources cited; abyssal data from Menzies et al. (1973).
[2] n = number of species; ND, no data.
[3] A, Arctic endemics; B, Atlantic boreal arctic; C, Pacific boreal arctic; D, boreal Arctic and cosmopolitan.

The primaeval Arctic Ocean originated in the Mesozoic as a large embayment of the North Pacific. The habitat and fauna appear to have been cool-temperate. In the late Cretaceous there were connections to the warmer waters of the subtropical Gulf of Mexico and the Tethys Sea, though there appears to have been only limited faunal exchange (Zonenshain and Natapov, 1989; Marincovich et al., 1990). The connection to the Pacific was closed by tectonic movements at the end of the Cretaceous, and a shallow-water connection was not re-established until the late Pliocene (3–3.5 Ma BP). A deep-water (abyssal) connection to the Pacific has never been re-established, and the Arctic abyssal fauna contains no taxa with an identifiable deep-water Pacific origin (Zenkevitch, 1963; Dunton, 1992).

The Arctic was also connected to the northern parts of the developing North Atlantic Ocean, although the timing of deep-water connections is still a matter of debate. Nevertheless a distinct boreal province developed during the Oligocene, and this is evident well into the late Miocene. A further cooling appears to have taken place about 12 Ma BP, stimulating speciation in typical cold-water taxa.

The sudden arrival of typical Pacific molluscs in the Pliocene deposits of Iceland indicates that the Bering land bridge was flooded about 3–3.5 Ma BP (Marincovich et al., 1990). The re-establishment of shallow water connections with the North Pacific allowed significant migration of Pacific species across an

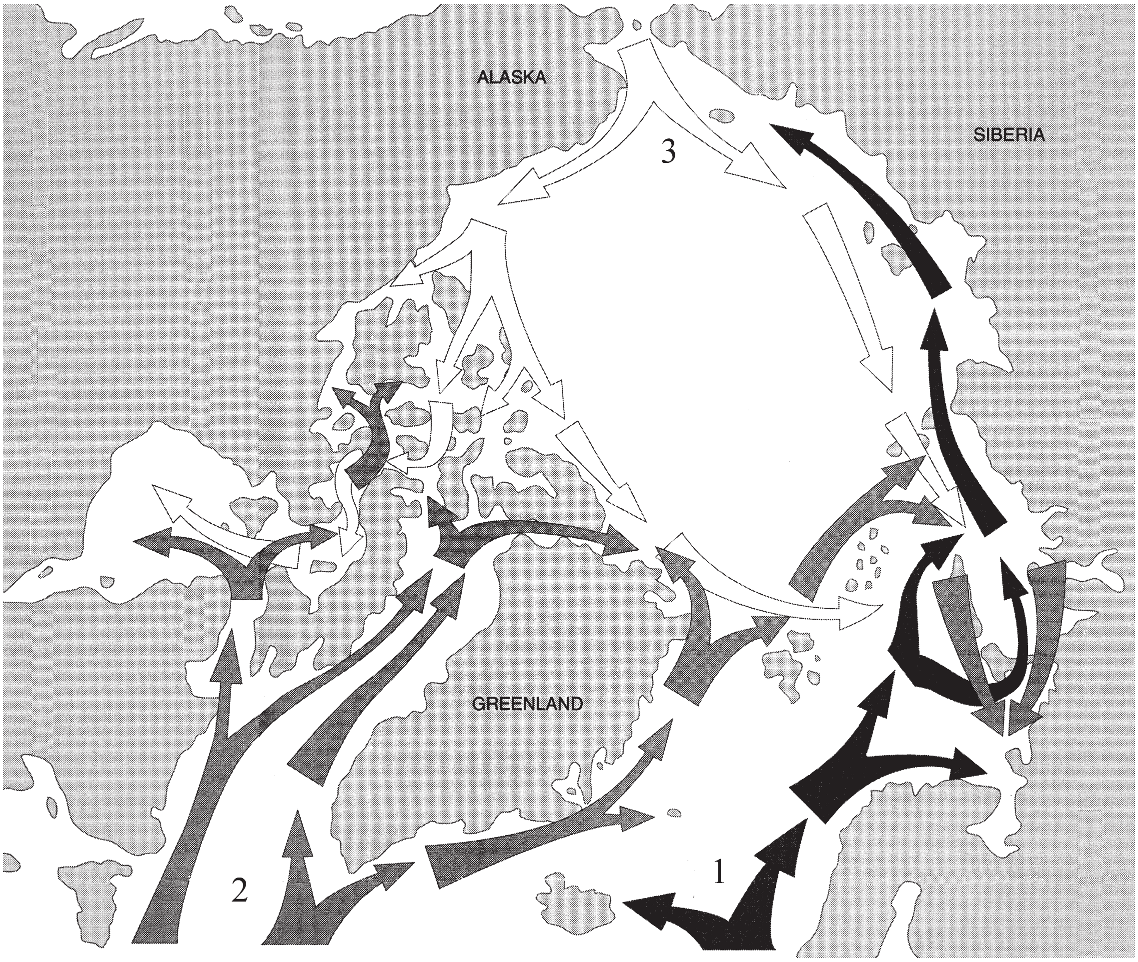

Fig. 8.5. Suggested routes of dispersal of lower latitude bivalve molluscs into the Arctic Ocean. 1, Migration from the European Atlantic shelf; 2, migration from the American Atlantic shelf; 3, migration from the Pacific shelf. These patterns are broadly similar to those proposed by Zenkevitch (1963) for the fauna in general. Redrawn from Fedyakov and Naumov (1989).

ice-free Arctic Ocean, and it is likely that colonization is continuing today.

The present-day Arctic shallow-water fauna is thus the result of colonization by both Pacific and Atlantic taxa (Fig. 8.5), but also reflects the impact of processes associated with repeated Pleistocene glaciations. Reconstructions of the height of glaciation suggest a substantial drop in sea-level, exposing vast areas of continental shelf. During the many glacial cycles during the Pleistocene, it now appears certain that Arctic continental-shelf faunal assemblages were almost completely eradicated (Golikov and Scarlato, 1989; Dunton, 1992). The current assemblages were formed by survivors from refugia in unglaciated shelf areas of the East Siberian and Beaufort Seas, or deeper (abyssal or bathyal) waters of the Eurasian sector. Nesis (1984) suggested that differences in the bathymetric ranges of the fauna of the Pacific Arctic (typically stenobathic[1]) and that of Atlantic Arctic (typically eurybathic[1]) can be explained by the different impacts of glaciation in the two regions. In the Pacific Arctic much of the continental shelf was exposed and unglaciated, suggesting that shallow-water refugia may have been available. In the Atlantic area, the continental shelves were covered by ice shelves which may have descended deep into the ocean. This suggests that abyssal waters may have played an important biogeographic and evolutionary role during the Pleistocene glaciation of

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[1] See Glossary, p. 477.

the Arctic Ocean. Vinogradova (1997) has concluded that the deep-sea fauna of the central Arctic basins is essentially Pleistocene in age, having been formed primarily as the consequence of repeated descent into deep water of shelf fauna driven by changes in temperature, glaciation and sea-level.

Relatively little is known of the biogeographical affinities of the Arctic abyssal fauna, although the isopod fauna contains a majority of genera with close affinity to cosmopolitan abyssal genera. Of the rest, 25% of the genera are found only in the North Atlantic, and 10% are found only in North Pacific (Menzies et al., 1973). The isopod fauna shows the expected bathymetric zonation, the deeper fauna being dominated by Asellota.

In summary, the Arctic abyssal fauna appears to contain elements that reveal ancient connections to the deep-sea faunas of both the Pacific and Atlantic. The Arctic abyssal fauna has, however, long been isolated from the Pacific, and although there remains a deep-water connection to the Norwegian Basin, there is no contiguity to the abyssal North Atlantic. The species richness appears to be low. Although the Arctic deep sea probably acted as an important refugium during glacial maxima it would appear that the Pleistocene glaciation was the cause of considerable extinction within the abyssal fauna as well as on the continental shelf.

THE ANTARCTIC DEEP SEA

The Antarctic is a large land-mass surrounded by a deep ocean. It thus forms almost a mirror image of the Arctic basin. The Southern Ocean surrounding Antarctica is defined oceanographically as those waters south of the Antarctic Polar Front (Fig. 8.6). Referred to as the Antarctic Convergence in the earlier literature, this marks the northernmost limit of cold surface waters.

The Antarctic Polar Front is a particularly well-marked oceanographic feature, and one which defines the geographical range of many Southern Ocean zooplankton (Hardy and Gunther, 1935; John, 1936; Angel, 1997). It is, however, essentially a surface feature which has less relevance to the distribution of mesopelagic or benthic fauna. The mesopelagic fauna of the Southern Ocean has been little studied, but it contains species known to be widespread (Clarke and Holmes, 1987). The benthic fauna of Antarctica also contains species known from South America (Dell, 1972; Arntz et al., 1994).

From a benthic perspective, two features of Southern Ocean topography are important. The first is the unusually deep nature of the continental shelves around Antarctica, and the second is the relationship of the deep-sea floor to surrounding ocean basins.

The continental shelves around Antarctica are typically over 500 m deep and often reach >800 m at the edge of the continental shelf. In many areas there are deeper basins within the shelves, and in a few places these may reach 1000 m. Two factors appear to have been important in deepening the continental shelves around Antarctica. The first is a general isostatic depression caused by the enormous mass of continental ice, and the second is scouring by ice-shelves as they extend seawards at glacial maxima. The relative importance of these two processes is still a matter of some debate, but recent geophysical evidence has shown clearly that previous extensions of the ice-sheet have scoured vast quantities of sediment from the inner continental shelves and deposited these at the edge and on the continental slope (Anderson, 1990; Anderson et al., 1991).

Deep-water topography

Even a casual glance at a bathymetric map of the Southern Ocean will reveal vast areas of seabed at abyssal depths (Fig. 8.7). These form effectively four basins. The Atlantic–Indian basin lies to the north of Dronning Maud Land, from the northernmost Weddell Sea (roughly longitude 30ºW) to its easternmost boundary at the Kerguelen Plateau (roughly 60ºE). This basin is effectively the southernmost section of the deep Atlantic Ocean, although the Atlantic–Indian ridge separates it from the Agulhas Basin to the north.

Further to the east, running roughly from the Kerguelen Plateau to longitude 150ºE, is the shallowest of the four basins, the South Indian Basin. This is separated from the main Indian Ocean basin by the Southeast Indian Ridge. The southern Pacific Ocean is more complex close to Antarctica in that these are two deep basins, the Southeast Pacific and Southwest Pacific Basins, separated by the Pacific–Antarctic Ridge (Fig. 8.7).

This topography would suggest that the faunal characteristics of each of these basins would contain individual Indian, Pacific or Atlantic Ocean elements. Superimposed on these would be features associated

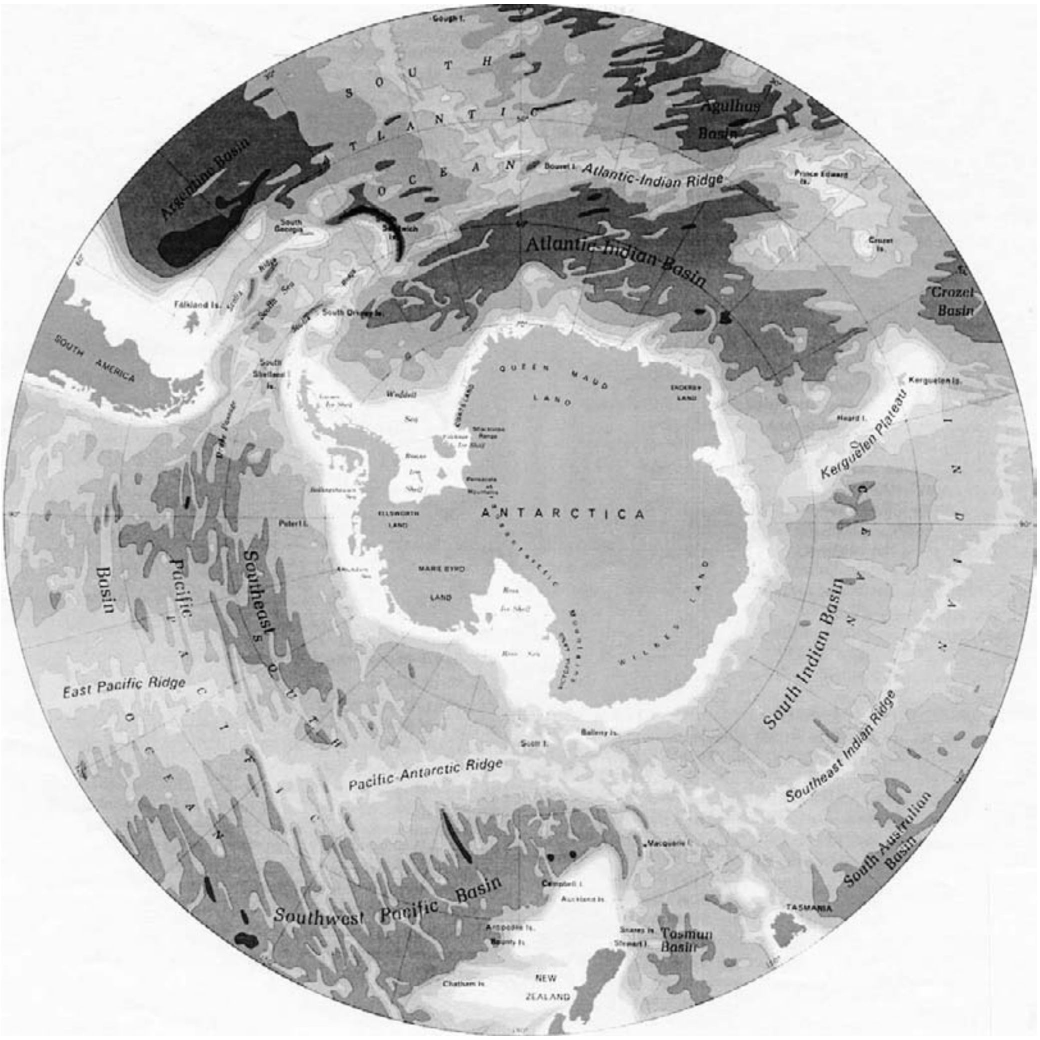

Fig. 8.6. The major deep-water basins around Antarctica. Depth contours at intervals of 1000 m, shown in eight shades of grey from 0–1000 m (palest) to 7–8000 m (darkest). Note the extensive Atlantic-Indian Basin, the shallower South Indian Basin and the two basins in the Pacific, separated by the Pacific-Antarctic Ridge. Reproduced from Goodell et al. (1973).

with the ecological influence of the Antarctic, and the tectonic, glacial and evolutionary history of the Southern Ocean.

Large-scale oceanography

The broad features of water circulation of the Southern Ocean are now well known. It is basically a three-layer system, in which water that is cooled and diluted at high latitudes spreads outwards (northwards) at the surface and at the bottom. At the same time water moves southward at intermediate depths and serves to replenish salt and heat.

The northward boundary of cold surface waters forms the Antarctic Polar Front. Although there is a net transport of surface water northward from the Antarctic continent, these surface waters are dominated by the continuous eastward flowing Antarctic Circumpolar Current (ACC). This is a deep-reaching current driven by the strong prevailing westerly winds, and in places it can be topographically constrained (for example in Drake Passage and in the Scotia arc region). The southward-flowing warm circumpolar deep water (CDW) is found at intermediate depths, and may constitute the most voluminous water mass in parts of the Southern Ocean.

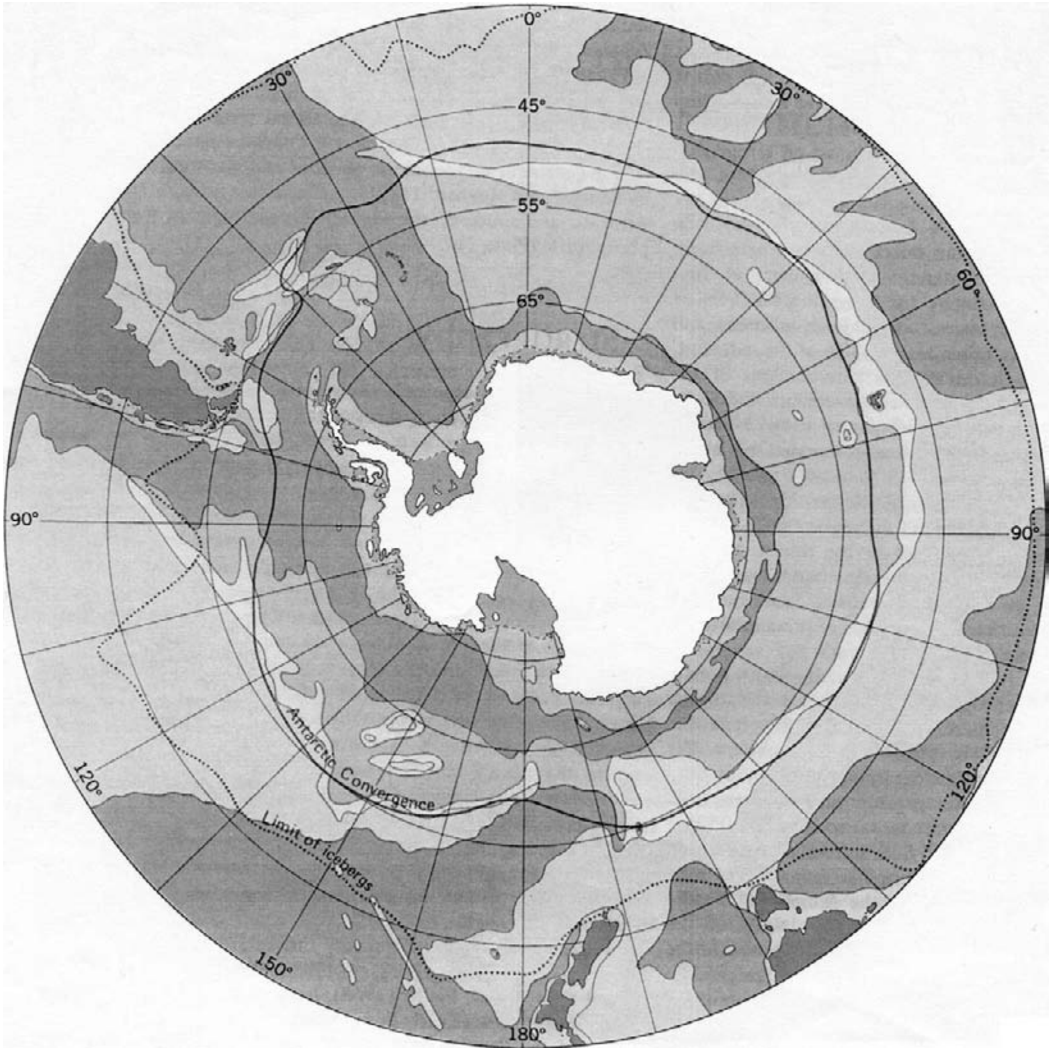

Fig. 8.7. The distribution of the main sediment types around Antarctica. The distribution is effectively circumpolar with the major sedimentary facies lying in broad swathes around Antarctica. Closest to the continent are submarine hills and glacial marine sediments. Outside this, and dominating the western South Atlantic, is a narrow band of clay-silt (dark grey) and surrounding this a broad band of siliceous ooze (pale grey). Reproduced from Goodell et al. (1973).

The third major Southern Ocean water mass is the most enigmatic. Antarctic Bottom Water (ABW) is intensely cold and highly saline. It has long been known that the Weddell Sea is a major source of bottom water, although there is also strong evidence for bottom-water formation in the Ross Sea and Adelie Land. Because of its high density, bottom water sinks to the deep-sea floor down the continental slope. Here the influence of the earth's rotation deflects the movement to the left, and the bottom water flows approximately parallel to the isobaths as a contour current. When bottom water eventually reaches the abyssal plain it spreads laterally along the bottom of the basins. Exchange between basins appears to be restricted by the ridges, and is limited to gaps and fracture zones (Patterson and Whitworth, 1990).

Bottom water appears to form through near-boundary processes. Sea-ice formation is important in producing high-salinity water, and it is clear that there are complex interactions with ice-shelves (Carmack, 1990), although the precise details of these interactions currently remain obscure. Antarctic Bottom Water is rich in oxygen, and this is important in preventing anoxia in the world's deep seas.

Sediment composition and sedimentary processes

Many of the early expeditions to the Southern Ocean took samples of the seabed (Philippi, 1910; Pirie, 1913; Wüst, 1933; Douglas and Campbell-Smith, 1930), and 142 samples were taken as part of the *Discovery* investigations (Neaverson, 1934). More recent data have come from bottom samples and photographs acquired by USNS *Eltanin*, RV *Conrad* and USCGC *Glacier*, mainly under the auspices of Operation Deep Freeze (Bullivant, 1959, 1967; Anderson, 1990), and also by Russian (Lisitzin, 1962, 1970) and French (Dangeard et al., 1977) expeditions.

In common with abyssal plains elsewhere, those around Antarctica are composed primarily of soft sediments. They differ from sediments in most deep-sea areas in two primary ways: the low temperatures of the surface waters mean that these sediments are primarily siliceous rather than the carbonates typical of lower latitudes, and there is a strong influence of glacial processes.

Close to the Antarctic continent the sediments contain an abundant silt fraction comprised of rock flour with coarse, poorly sorted debris, and contain little calcite or biogenic debris. These sediments were termed glacial-marine by the Deutsche Südpolar-Expedition (Philippi, 1910) and they form a wide circumpolar band around Antarctica. Goodell et al. (1973) proposed a more rigorous definition of glacial-marine sediments, and distinguished four more or less concentric zones around Antarctica, distinguished primarily on textural grounds (Fig. 8.7). In general there is a decrease in the proportion of coarse material with increasing distance from the continental source, and the outermost of the four zones corresponds to the pelagic clays of the abyssal plain. The northernmost limit of glacial-marine sediments is related to the 0°C surface isotherm, since this influences the rate of iceberg melting.

In the Southern Ocean icebergs are the major mechanisms of ice-rafted transport of sediment. In contrast to the Arctic, sea-ice is of relatively little importance for transport of terrigenous material, largely because the extensive development of ice-shelves effectively precludes the capture of sediments by sea-ice. Ice-shelves also greatly reduce the importance of riverine and aeolian input to the Southern Ocean compared with the Arctic. Nevertheless the input of sediment from Antarctica to the southern Pacific is substantially greater than from other nearby continents (Edwards, 1968; in Anderson, 1990).

Beyond the limits of significant ice-rafted input, the glacial-marine sediments merge gradually into biogenic oozes. The low temperatures of surface waters in the Southern Ocean mean that coccolithophorids are absent, and primary production is dominated by diatoms. Since dilution by non-biogenic material is almost non-existent, and the low temperature and the depth of the abyssal plain tend to induce dissolution of carbonates, the biogenic oozes of the Southern Ocean are almost exclusively siliceous. The boundary between siliceous oozes and the carbonate oozes formed in warmer sub-polar surface waters is dictated largely by the position of the Antarctic Polar Front, and previous positions of the Polar Front can be inferred from the switch between siliceous and carbonate sediments in cores.

The lack of substantial riverine or aeolian input means that rates of abyssal sediment accumulation around Antarctica can be very slow, often less than 1 cm per thousand years (Osmond et al., 1971). Vertical flux has been measured in the Southern Ocean by the use of sediment traps (reviewed by Honjo, 1990). These measurements reveal a strong seasonal component, with important contributions from grazing by zooplankton as well as aggregation processes. Almost all such measurements have, however, been over the continental shelf, where rates of primary production, and hence sedimentation, are considerably greater than in the pelagic areas over the abyssal plains.

Terrigenous material may also be delivered to the abyssal plain by turbidity currents flowing down the continental slope or along submarine canyons. This process appears to have been especially important in the Amundsen and Bellingshausen Seas, where there are large deep-sea sediment fans (Dangeard et al., 1977; Wright et al., 1983).

Drop-stones

Although much of the terrigenous material transported away from Antarctica is in the form of fine to coarse sediment, icebergs can also carry larger clasts and boulders. Large ice-rafted boulders (drop-stones) are important in providing isolated patches of hard substratum on the otherwise soft abyssal plain of the Southern Ocean. These drop-stones are released once the icebergs encounter water warm enough to induce bottom melting. The density of these drop-stones declines northwards, and their distribution influences the population dynamics of encrusting taxa in the Southern ocean. Unfortunately very little is known of either the distribution or the fauna of these drop-stones.

Hydrothermal vents

One habitat which was unknown before the mid-1970s and which is currently the subject of intense investigation is that of hydrothermal vent fields (Gage and Tyler, 1991). The tectonic history of the Southern Ocean suggests that hydrothermal vent fields are very likely to exist, especially in the eastern Scotia Sea or the South Shetland Islands. As yet, however, none has been described.

Primary production

For many years the Southern Ocean was considered to be highly productive. It is now known that this conclusion was the result of a strong seasonal and spatial bias in sampling (Smith and Sakshaug, 1990). More extensive oceanographic measures and especially remotely-sensed ocean colour data have shown that the bulk of the Southern Ocean is oligotrophic. Standing-crop chlorophyll biomass can reach high levels ($>40\,\mathrm{mg\,m^{-3}}$) in nearshore waters, or in the marginal ice zone, but otherwise levels are low. A representative figure for annual production in pelagic waters of the Southern Ocean is considered to be about $16\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Holm-Hansen et al., 1977).

As with the Arctic Ocean, considerable primary production is associated with sea ice. In the Southern Ocean the marginal ice zone may fix carbon at rates five times those of the open ocean (Smith et al., 1988).

Primary production in the Southern Ocean rarely results in the depletion of macronutrients (N, P, Si) to levels which would be regarded classically as limiting. There is currently an intense, and as yet unresolved, debate as to the relative influence of light limitation through vertical mixing, grazing and limitation by micronutrients (especially iron) in limiting Southern Ocean production.

Overall, present knowledge of primary production and vertical flux suggests that biogenic production in surface waters is low, and that input to the deep-sea system is also likely to be low, reflecting the generally oligotrophic nature of the overlying ocean. Low surface production is likely to lead to low productivity in the underlying benthos (Rowe, 1971). There are very few estimates of secondary production in the deep sea, although model calculations suggest that macrobenthic production in the Southern Ocean decreases exponentially with water depth (Brey and Gerdes, 1998).

The Southern Ocean deep-sea fauna

Although the deep sea forms the single largest benthic habitat in the Southern Ocean, very little is known of its biology. Sampling has largely been confined to the continental shelves and slope, although some truly abyssal material has been collected. Most significant has been the extensive work by Russian biologists [still largely inaccessible to western scientists, but recently summarized by Vinogradova (1997)] and the series of collections made in the Atlantic and Pacific sectors by USNS *Eltanin* in the 1960s (Menzies et al., 1973).

The unusual depth of the continental shelves around Antarctica means that many organisms elsewhere associated with shelves are, in the Southern Ocean, living at depths traditionally regarded as deep-sea (for example, down to 900 m in some deep basins). Indeed at such depths, organisms necessarily display physiological adaptations to pressure which parallel those found in true deep-sea organisms in other oceans. From the perspective of faunal evolution, however, such assemblages are best regarded as associated with the continental shelf (albeit unusually deep), rather than with the deep sea *sensu stricto*. Around Antarctica the true deep-sea fauna should be regarded as that living at 2000 m or deeper, although recent sampling has shown that some abyssal species extend up the continental slope to the shelf-break at 1000 m (Brandt, personal communication). Unfortunately the deep-sea fauna has been sampled only sporadically, and knowledge of the deep-sea assemblages remains a major gap in understanding of the Southern Ocean.

Ekman (1935, 1953) was the first to propose that the Antarctic deep-sea fauna forms a discrete biogeographic entity, relatively isolated from deep-sea faunas elsewhere. The northern boundary of the Antarctic deep-sea was suggested to fall around latitude 40°S, emphasising the minimal impact of the surface Antarctic Polar Front on deep-sea faunas. Ekman based his conclusion on the distribution of sponges, but the concept of a uniform Antarctic abyssal fauna was later supported by analyses of asteroids and polychaetes [see discussion by Vinogradova (1997)].

Further subdivision of the Antarctic deep-sea fauna depends critically on the depth range considered (Vinogradova, 1959, 1979, 1997). It has long been recognized that species with wide bathymetric ranges also tend to be widely distributed geographically. Thus, whilst Zezina (1997) considered the Antarctic to form a uniform biogeographic zone in the bathyal regions, Vinogradova (1997) has subdivided the Antarctic deep sea into two major subregions, namely the Antarctic–Atlantic and the Antarctic–Pacific–Indian regions. Finer division of the latter into Pacific and Indian subregions is also possible.

The lower continental slopes around Antarctica harbour a range of echinoderms, including ophiuroids, crinoids, asteroids and echinoids. There are fewer sponges and gorgonians than on the deep continental shelf, but pennatulids and bryozoans are still present. As is typical of the lower continental slope elsewhere, there is a shift from assemblages dominated by sessile suspension feeders to one consisting primarily of motile forms. Biomass also decreases sharply with depth (Menzies et al., 1973).

Sokolova (1997) has provided a detailed analysis of the trophic structure of deep-sea faunas, emphasizing the unusual importance of zooplankton to deep-sea benthos in Antarctica. Although the connection between high euphausiid biomass and high biomass in the benthos beneath has long been recognized for continental shelves (Dearborn et al., 1986), Sokolova (1994) has emphasized the importance of zooplankton to the abyssal fauna (a phenomenon she termed a dead body rain). This appears to be a feature unique to Antarctica, where high zooplankton biomass overlies deep water.

The abyssal zone deeper than 3500 m contains large taxa typical of deeper waters elsewhere, including the holothurian *Scotoplanes* and the pennatulid *Umbellula.* The deepest waters contain cosmopolitan taxa including the holothurians *Psychropotes, Peniagone, Pseudostichopus, Scotoplanes* and *Benthodytes,* the ophiuroid *Ophiomusium,* the echinoid *Phormosoma,* the tunicate *Culeolus* and the pennatulid *Umbellula.*

The sparse data that exist would thus suggest that the deep-water basins around Antarctica thus contain faunal assemblages similar in structure to those elsewhere. The patterns of deep-water flow around Antarctica and the history of glaciation suggest, however, that there may also be strong affinities with the Antarctic shelf fauna. The most detailed analyses of this have been for isopods.

The Southern Ocean isopod fauna

Isopod crustaceans are particularly well represented in the deep sea, and on the Antarctic continental shelf (Table 8.3). This has led to much speculation as to the faunal links between high southern latitudes and the deep-sea, and isopods have been a pivotal group in discussions of the evolution of the abyssal fauna.

Table 8.3
Number of isopod genera represented in continental shelf faunas from different regions in the world[1]

Region	Number of genera
Antarctica	55
Peru	11
Puerto Rico	19
California	23
Carolina and Georgia	25
Arctic	16

[1] From Menzies et al. (1973), where original sources cited.

Kussakin (1973) advanced the view that the deep-sea isopod fauna resulted from colonization by shallow-water forms, particularly those from high latitudes. Kussakin linked this move into deeper water from around the late Cretaceous, when high southern latitudes in particular began to cool. In contrast, Hessler and Thistle (1975) argue that the distribution of eyes amongst deep-sea paraselloidean families suggests strongly a long period of evolution *in situ.* Present day distributions of these isopods provide no suggestion of a shallow-water origin.

Menzies et al. (1973) have divided the isopod fauna of Antarctica into three groups: shelf (5–100 m), archibenthal (deeper continental shelf, 101–800 m), and abyssal (801–5500 m). Their analysis shows that representatives of all three groups are found at all depths, providing powerful evidence for complex evolutionary patterns with some taxa moving into deeper water (evolutionary polar submergence) and other taxa colonising the shelf from the deep-sea (evolutionary polar emergence) (Fig. 8.8).

Brandt (1991, 1992) has undertaken a thorough analysis of the Southern Ocean isopod fauna, including phylogenetic analyses of families with both shelf and deep sea representatives. She demonstrated that

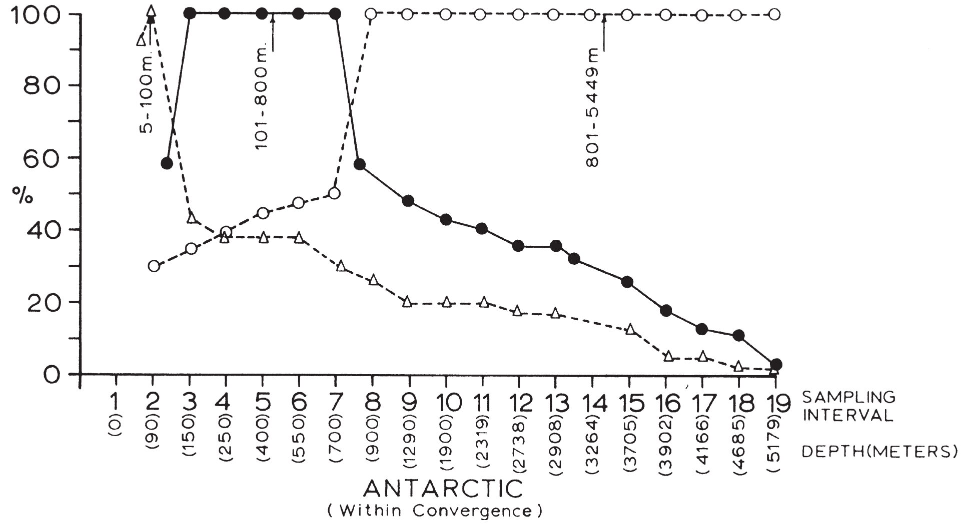

Fig. 8.8. Distribution of isopod genera, divided into three depth groups, as a function of depth. The groups are shallow shelf (5–100 m, triangles), deeper shelf (archibenthal: 101–800 m, solid circles), and abyssal (801–5500 m, open circles). Note the relative rapid change in assemblage contribution at about the shelf–slope transition (900 m). Redrawn from Menzies et al. (1973).

the families Serolidae, Arcturidae, Stenetriidae, Acanthaspidiidae, Munnidae, Paramunnidae, Dendrotiidae, Haplomunnidae and Pleurocopidae have moved into the deep sea from the continental shelves of Gondwana. In contrast, the families Munnopsidae, Nannoniscidae, Desmosomatidae and Ischnomesidae have moved from the deep sea onto the Antarctic continental shelves.

Andriashev (1953) (in Merrett and Haedrich, 1997) has also shown a complex evolutionary history for the deep-sea fish fauna, which comprises a mixture of taxa with a long evolutionary history in the deep sea with more recent colonists. The complex evolutionary history shown for the deep sea fish and isopod faunas is likely to prove a general model for the Antarctic deep sea fauna as a whole. The explanation for this complex history lies in the geological, climatic and evolutionary history of Antarctica.

The evolution of the Antarctic marine fauna

It is now generally accepted that the marine fauna of the Antarctic continental shelf has a long history of evolution *in situ* (Dell, 1972; Knox and Lowry, 1977; Lipps and Hickman, 1982; Clarke and Crame, 1989, 1997). The phylogenetic analysis of the Southern Ocean isopod fauna by Brandt (1991, 1992) has shown clearly that the older groups have an evolutionary history extending back to before significant fragmentation of Gondwana. The ancestral taxa appear to have been present on the continental shelves of Gondwana by 80–90 million years ago, and these gave rise to the present species of Serolidae and Arcturinae. Species of other families have either moved onto the continental shelves from the deep sea, or evolved *in situ* through the climatic changes of the Tertiary and the fragmentation of Gondwana. Evolutionary rates in Southern Ocean taxa appear to be similar to those elsewhere (Crame and Clarke, 1997), and there is strong evidence for rapid speciation in some taxa (Arnaud and Bandel, 1976; Watling and Thurston, 1989; Clarke and Johnston, 1996; Eastman and Clarke, 1998).

Biogeographic analyses indicate that taxa have migrated to and from Antarctica along the Scotia arc, and also to and from the deep sea (Menzies et al., 1973; Knox and Lowry, 1977; Brandt, 1991, 1992). Exchanges between the shelf, slope and deep-sea faunas in Antarctica are likely to have been aided by the generally deep nature of the continental shelves around Antarctica. This would require the shelf fauna to be adapted to greater hydrostatic pressures than would be typical for shelf faunas elsewhere. It has long been suspected that the shelf faunas of Antarctica contain many taxa with an unusually wide bathymetric range (Menzies et al., 1973) and this has recently been confirmed by an analysis of data available for the whole fauna (Brey et al., 1996).

It is likely that a key factor in the eurybathy shown by the fauna of the Antarctic continental shelf has been glacial history. Periodic extensions of the continental ice sheets at previous glacial maxima will have covered large areas of the continental shelf, and forced the fauna to move into the deeper waters of the continental slope or become locally extinct (Clarke and Crame, 1989; Brey et al., 1996). Such extensions and retractions of the ice sheet are likely to have been a powerful evolutionary forcing mechanism, driving both speciation and extensive exchange between shelf, slope and possibly even abyssal faunas (Clarke and Crame, 1989). A critical point, as yet unresolved, is whether previous glacial maxima ever resulted in a complete eradication of continental shelf habitat. Glaciological and geophysical evidence currently remains equivocal, although Brandt (1991, 1992) concluded from her phylogenetic analysis of the Southern Ocean isopod fauna that some shallow water refugia always remained colonised.

Although the Southern Ocean is contiguous with each of the other main oceans, the degree of faunal similarity varies (Table 8.4). The Antarctic deep-sea fauna shows stronger affinities with the Atlantic and Indian Oceans than with the Pacific Ocean. It is possible that this reflects in part, present day patterns of deep-water flow. This can only be part of the explanation, however, for the disposition of deep-water temperature and currents has changed significantly through time.

Table 8.4
Zoogeographical similarities between the Antarctic deep-sea and other oceans[1]

Depth range of deep-sea species in the Antarctic	% of these species whose geographic range also includes		
	Atlantic Ocean	Indian Ocean	Pacific Ocean
Both above and below 2000 m	70	60	27
Below 2000 m only	15	40	4.3
Below 3000 m only	6	10	2.5
Below 4000 m only	0	0	0

[1] Data from Vinogradova (1959) and Menzies et al. (1973).

CONCLUDING REMARKS: THE INFLUENCE OF HISTORY

The deep-sea is today generally cold and well-oxygenated (Gage and Tyler, 1991), prompting frequent comparisons with the polar regions. Furthermore, much of the water which bathes the deep sea currently originates in polar regions.

Many of the early views of the deep-sea fauna were predicated on the apparent constancy of the deep-sea environment (for example Zenkevitch, 1966). We now recognise that the deep-sea shows marked variability over a wide range of temporal scales (Gage and Tyler, 1991). Thus Mesozoic bottom temperatures appear to have been warm throughout the world (Menzies et al., 1973) and the present deep-sea fauna must have evolved its present low temperature adaptation during the Tertiary cooling (and in particular during the early Oligocene, when bottom temperatures cooled sharply, possibly caused by the onset of bottom water formation at high latitudes). This adaptation will have happened in parallel with a similar thermal evolution in shallower high-latitude waters (Clarke and Crame, 1997). In the sense of temperature, there could therefore not have been any pre-adaptation of polar shelf faunas to the deep sea; the shelf seas and deep waters were cooling broadly in parallel. This parallel evolution to cooling seawater temperatures would not have taken place in temperate and tropical shelf environments. These remained warm, although the geographical spread of three zones would necessarily have contracted throughout the Tertiary as the meridional temperature cline of surface water temperature steepened.

The deep water physiology of the Antarctic continental shelf faunas will also have evolved through the Tertiary as the buildup of continental ice and the gouging of extending ice shelves deepened the habitat. The apparent close faunal links between the Antarctic shelf fauna and that of the Southern Ocean deep sea may thus be the result, at least in part, of a shared thermal history rather than pre-adaptation.

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Chapter 9

THE PERIPHERAL DEEP SEAS

Paul A. TYLER

INTRODUCTION

The major oceans of the world occupy over 50% of the surface of the planet. It is in these major oceans that the greatest depths are found and in which the greatest research effort has been concentrated (see Chapters 5 to 8). There are, however, a number of seas peripheral to the main oceans that have basins of oceanic-depth, are of great interest and have been considered worthy of study. The largest of these is the Mediterranean, which itself has peripheral seas. The 'newest' ocean is the Red Sea, with its bottom water warmer than the surface waters as a result of hydrothermal activity. In the Americas, the Caribbean has many features similar to those of the Mediterranean, whilst the Gulf of Mexico is the only deep peripheral sea known to have deep chemosynthetically-supported communities. The deep basins of the Indonesian seas were the only deep peripheral seas to be sampled by the *Challenger*. In the Far East are the Sea of Okhotsk and the Sea of Japan with their deep basins, the former linked with the main Pacific and the latter with very limited exchange.

Because these seas border the main ocean, they are relatively close to land and the local climate has discernable effects either in the local hydrography, or through contributions of allochthonous organic matter from terrestrial vegetation. Major rivers, as well as aeolian particle transport, may also have a significant impact on sedimentation. In nearly all cases, however, the deep-sea ecosystem within these peripheral seas is driven by the vertical flux of surface production to the seabed. A notable exclusion is the Black Sea. This sea is omitted as it is anoxic below ~250 m and does not have a 'deep-sea' metazoan fauna. Recent reviews of the Black Sea have been published by Izdar and Murray (1991) and Ivanov and Oguz (1997).

The deep peripheral seas can be examined from a variety of perspectives. Their morphology is a function of their geological history, whilst their hydrography is driven by heat and salt balance as well as by influx of oceanic waters from the major oceans. In the Mediterranean and Red Seas evaporation far exceeds freshwater influx (Table 9.1), and thus surface waters become dense by increasing salinity. In the Mediterranean the deep water forms when this saline surface water undergoes winter cooling. In the Caribbean Sea and the Gulf of Mexico evaporation exceeds freshwater inflow to a lesser extent (Table 9.1), and the influx of water from the Atlantic has an effect on both these areas. On the other hand the Gulf of Mexico makes a significant contribution to the Atlantic in the form of the Gulf Stream. Also in warm latitudes are the deep basins of the Indonesian Seas, where evaporation exceeds precipitation but there is a strong seasonal component forced by the monsoon. In the Sea of Japan evaporation is less than freshwater inflow, and severe winter cooling is required to form deep water. Lastly in the very cold Sea of Okhotsk (Okhotskoye More) there is great freshwater input but the extreme winter cooling, which results in freezing of the surface waters, determines the formation of deep water.

HYDROGRAPHY AND PHYSICAL PROPERTIES

The Mediterranean Sea

Morphology

The Mediterranean is the largest of the seas peripheral to the main oceans, and consists of two deep basins, the western and eastern basin separated by the Straits of Sicily, a sill of ~400 m depth. The western extremity of the Mediterranean is the Strait of Gibraltar with a sill depth of 350 m separating the deep

Table 9.1
Characteristics of the main peripheral seas

Sea/sub region	Max depth (m)	Sill depth	Main characteristics	Area (km^2)	Volume (km^3)
Mediterranean			Warm: evaporation $>$ fresh-water influx	2510×10^6	3771×10^6
West	3730	350[1]			
East	5093	400[2]			
Red Sea	>2000	200	Hot: evaporation $\gg$ fresh-water influx	0.45×10^6	0.251×10^6
Caribbean Sea	–	–	Warm: evaporation $\geqslant$ fresh-water influx	2.62×10^6	
West	7600	1500[3]			
East	5400	2800/1815			
Gulf of Mexico	3400	1500[3]	Warm: evaporation $\geqslant$ fresh-water influx	1.543×10^6	2.322×10^6
Indonesian archipelago	7000	2000	Warm: evaporation $<$ fresh-water influx	Boundary not distinct	
Sea of Japan	4036	130	Cold: evaporation $<$ fresh-water influx	1.01×10^6	1.36×10^6
Sea of Okhotsk	3657	2318	Cold: evaporation $\ll$ fresh-water influx	1.58×10^6	1.23×10^6

[1] Strait of Gibraltar [2] Straits of Sicily [3] Strait of Yucatan

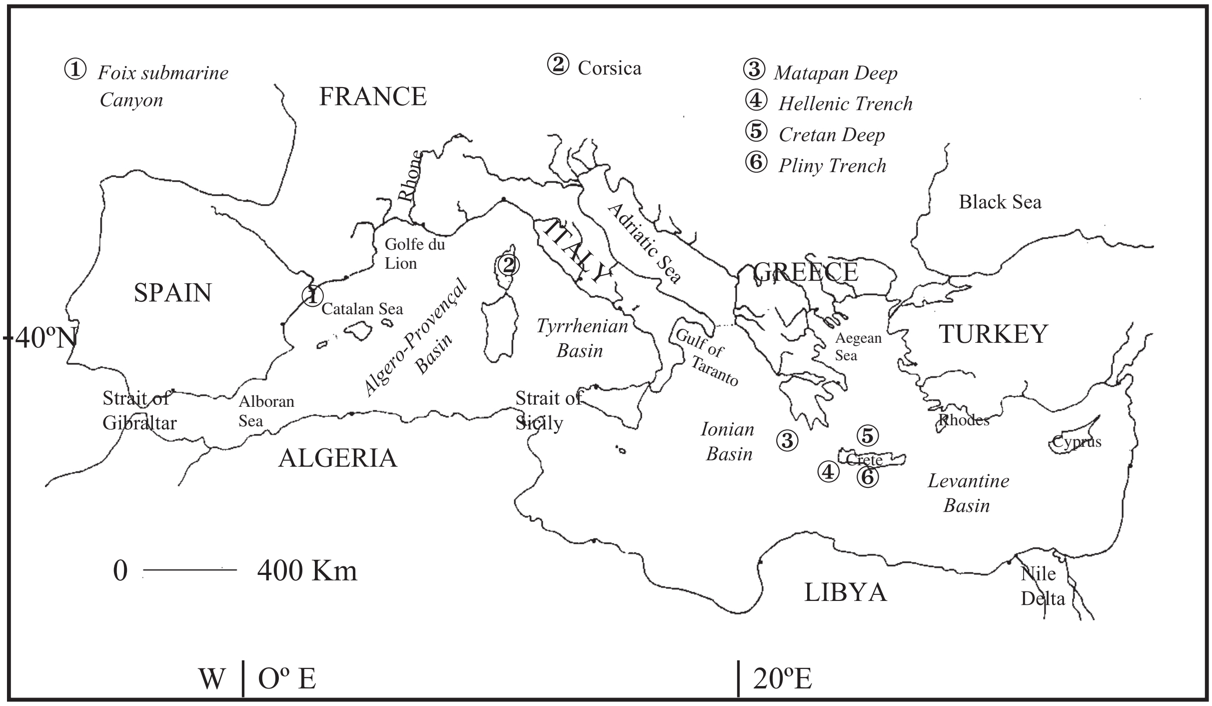

Fig. 9.1. Mediterranean Sea: Geography (in roman characters) and oceanographical features (in italics) referred to in the text.

waters of the Mediterranean from those of the Atlantic (Fig. 9.1).

Within the western basin are a series of sub-basins, including the Algero-Provençal Basin (maximum depth 3420 m) and the Tyrrhenian Basin (maximum depth 3730 m). The deep eastern basins form another series including the Ionian Basin (maximum depth 5093 m) and the Levantine Basin (4384 m). Peripheral seas bordering the Mediterranean include the Adriatic Sea (max depth 1216 m) and the Aegean Sea (max depth >2500 m), the latter leading through the Bosporus to the Black Sea, which has a maximum depth of

~2500 m, and where the waters below a depth of 250 m are anoxic (Fredj and Laubier, 1985). The surface properties of the Mediterranean were reviewed in Volume 26 of this series (Miller, 1983; Ben-Tuvia, 1983).

The Mediterranean Sea has a complicated geological history, being trapped between Africa and Europe, and its present deep-sea fauna reflects part of this geologic history. The Mediterranean was derived from the Tethys Ocean, which itself was formed when Pangea split ~200 My ago (Maldonado, 1986). The shape of the Mediterranean that one recognizes today was created ~40 My ago, although there remained a deep connection between the Mediterranean and the Atlantic Ocean. In the eastern Mediterranean the Hellenic Trench system southwest of the island of Kriti (Crete) represents the last fragments of the Tethys Ocean as it is subducted beneath the European Plate. The African continental crust is now reaching the Hellenic Trench (Maldonado, 1986). The youngest basin is the Pliocene/Quaternary Aegean Sea. In the western Mediterranean there has been extensional rifting and new oceanic crust has developed, the oldest oceanic crust being the Oligocene Balearic Sea.

In the late Miocene (Messinian), the Mediterranean became separated from the Atlantic by the orogenic closure of the Strait of Gibraltar, and this started the so-called ‘Messinian Salinity Crisis’. The Mediterranean was formed from a number of large lakes which ultimately dried out leaving thick evaporite deposits (Cita and Ryan, 1973). Estimated drying times have been as little as 1000 y, and there have been suggestions this may have occurred up to 17 times (Maldonado, 1986). The latest inundation of the Mediterranean occurred at the beginning of the Pliocene, approximately 5 My ago.

Hydrography

The main surface inflow of Atlantic surface water to the Mediterranean Sea is through the Strait of Gibraltar (36 salinity), driven by water-level differences between the two water bodies. This water flows via two cyclonic gyres in the Alboran Sea along the North African coast, with branches feeding cyclonic loops extending northwards in the western basin (Fig. 9.2a). As the surface water flows eastwards, excess evaporation over precipitation increases the salinity to 39. Formation of intermediate and deep water takes place during winter along the northern borders of the Mediterranean, in both basins, under the influence of cold katabatic winds blowing off the continental landmass to the north. When cold winds blow down the Rhône valley the water column in the northern Mediterranean becomes cold, and up to one-third of the deep water can be formed in a single event. Levantine Intermediate Water (LIW) is formed off the island of Rodhos (Rhodes) (Fig. 9.2a) when winter cooling increases the density of high-salinity water, and this water sinks to a depth of ~400 m. Levantine Intermediate Water extends as a midwater water mass westwards from its source and bifurcates with a branch flowing both north and south of Crete (Fig. 9.2b) (Tomczak and Godfrey, 1994).

The northern branch of Levantine Intermediate Water flows into the Adriatic Sea at intermediate depths (Fig. 9.2b). Under the influence of winter cooling the surface and intermediate waters of the Adriatic mix and form a deep-water mass down to the seabed at 1000 m (Fig. 9.2a). This deep water overflows the 700 m-deep sill at the entrance to the Adriatic Sea and flows southeastward into the deepest part of the eastern basin of the Mediterranean Sea. More recently, there has been evidence that the densest waters of the eastern Mediterranean are formed in the Aegean Sea (Klein et al., 1999; Lascaratos et al., 1999) with a formation rate[1] of 1 Sv, which is three times the rate of formation in the Adriatic Sea. A new dense water mass has recently been identified (Fig. 9.2a). It is formed in the Aegean [called Cretan Sea Overflow Water (Klein et al., 1999), leading to Cretan Deep Water (Tsimplis et al., 1999)], is warmer but more saline than that formed in the Adriatic, and has replaced about 20% of the deep water in the eastern Mediterranean over the past decade. This subtle change in the origin of the deep waters is attributed to the very cold winters of 1987 and 1992–1993, which created favourable conditions for deep-water formation in the Aegean (Lascaratos et al., 1999). This regime shift is also believed to be a long-term impact from the building of the High Aswan Dam, which reduced freshwater inflows from the Nile into the eastern Mediterranean, leading to increased salinity, and thus density. Past and present circulation patterns and deep-water formation in the eastern Mediterranean have been reviewed in detail by Malanotte-Rizzoli and Hecht (1988) and Lascaratos et al. (1999).

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[1] A special unit, the Sverdrup (abbreviation Sv), is used for formation and movement of water masses in the ocean. It is defined as $10^6\ m^3\ s^{-1}$.

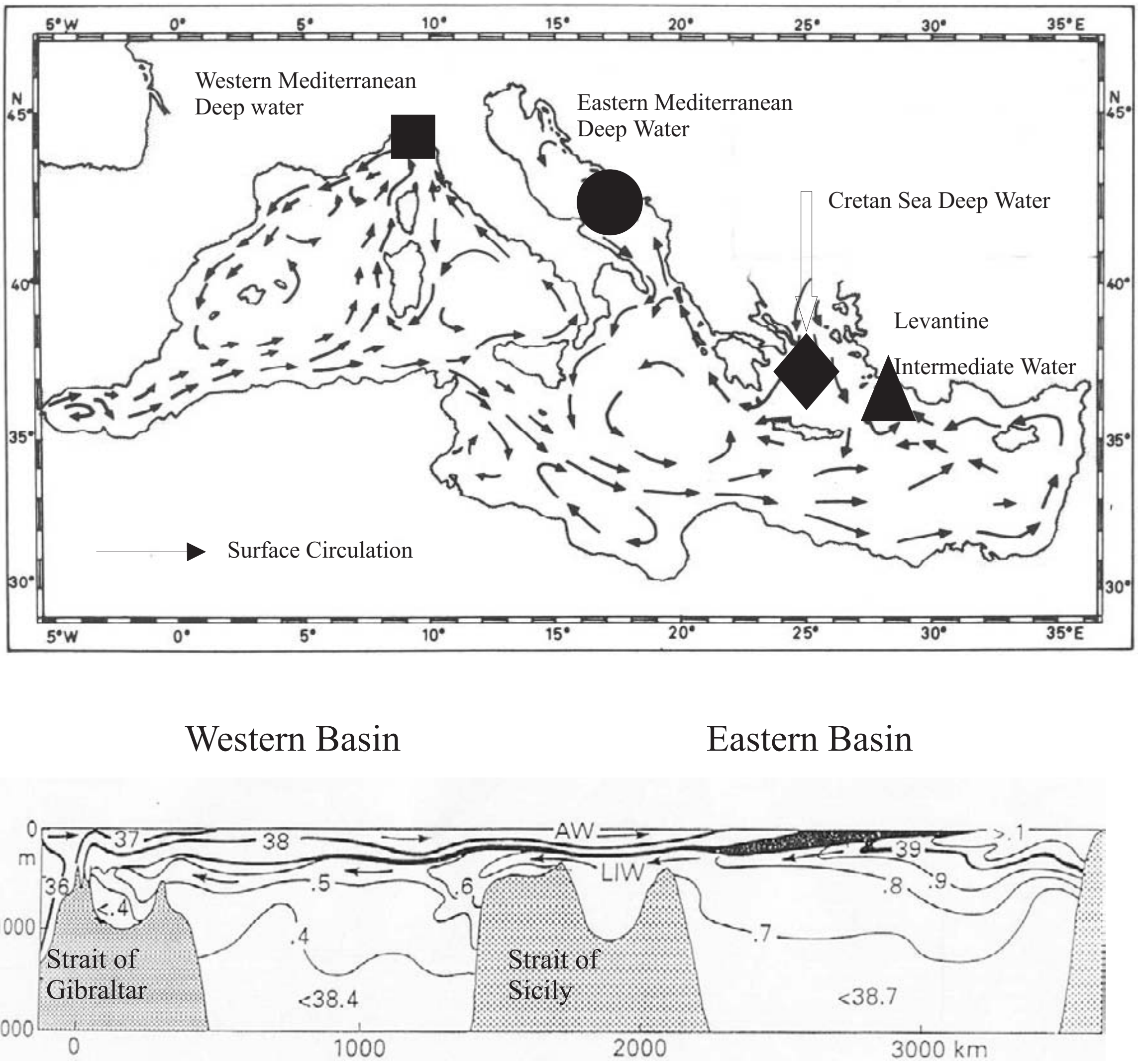

Fig. 9.2. Mediterranean Sea (a) surface circulation pattern with points of intermediate and deep water formation. Triangle, Levantine Intermediate Water; square, Western Mediterraean Deep Water; circle, Eastern Mediterraean Deep Water; diamond, Cretan Sea Deep Water. Modified from Miller (1983). (b) West–east vertical profiles to main water masses and general westward subsurface flow. Abbreviations: AW, Atlantic Water; LIW, Levantine Intermediate Water. Modified from Wüst (1960).

The Levantine Intermediate Water passing to the south of Crete flows westwards, through the Straits of Sicily, with branches extending northwards. In the Golfe du Lion, off the southern coast of France, winter cooling of surface waters by the Mistral cools the water resulting in convective mixing as deep as 2000 m. This dense water sinks and fills up the deep basins of the western Mediterranean (Fig. 9.2a,b) (Send et al., 1999). Lastly both branches of LIW and waters from the deeper parts of the western basin overflow over the Gibraltar Sill at depth and sink to ~1600 m in the Atlantic as an intermediate water mass. Inflow at the surface over the Gibraltar Sill is at a rate of 53 000 km^3 y^{-1}, whereas the deep outflow is at a rate of 50 500 km^3 y^{-1}, resulting in a water loss of 2500 km^3 y^{-1} by evaporation.

Although the formation of deep water masses in the Mediterranean results from winter cooling, the deep-water temperature in the deepest parts of the western and eastern basin still exceeds 13ºC and salinity is 38.5 to 38.6 (Carpine, 1970). With the exception of the Red Sea and the occurrence of very hot waters round isolated hydrothermal vents, these represent the warmest abyssal water in the world's oceans. Minimum oxygen levels are 3.5 ml ℓ^{-1} in the eastern basin, whilst in the western basin values usually exceed 4.0 ml ℓ^{-1}. There is recent evidence that shows there is seasonal variation in oxygen content, at least in intermediate waters (Souvermezoglou et al., 1999).

Deep water sediments

The sediments of the deeper parts of the Mediterranean are soft, consisting of firm red or blue clayish muds (Emelyanov, 1972; Nairn et al., 1978; Pérès, 1985) resulting from river input, and aeolian dusts blowing over the sea from North Africa. Riverine input has increased as a result of deforestation of the catchments feeding rivers entering the Mediterranean. Exceptionally low surface productivity leads to a very slow rate of accumulation of biogenous sediments, particularly in the eastern Mediterranean. However, biogenous sediments dominate eastwards, with an increase in the calcium carbonate content. Oozes are formed from Foraminifera, coccolithophorids and pteropods. Terrigenous deposits arise from riverine input, especially from the Rhône, which gives rise to a deep-sea fan (Bellaiche et al., 1983; Fredj and Laubier, 1985). The calcium carbonate compensation depth may vary from 1000 to 2500 m, which is much shallower than in the major oceans because of the high *in situ* temperature (see Chapter 3). The Nile made a significant terrigenous contribution between Cyprus and Syria, but this source has all but ceased with the building of the High Aswan Dam. Values for organic carbon in deep-water sediments range from 0.2 to 1.6% with typical values of 1.14% west of Corsica and 0.9% off Monaco (Carpine, 1970). Hard substrata are relatively rare, consisting of ahermatypic corals; at bathyal depths these appear to be in decline. The main areas of rock outcrop are near the coasts. Lastly, there is evidence for mud volcanoes and hypersaline lakes in the eastern Mediterranean (Corselli and Basso, 1996). It should be noted, however, that Fredj and Laubier (1985) doubted the importance of the different sediment types in the soft-substratum deep-water ecology of the Mediterranean.

Surface production and vertical flux of organic matter

Up to the 1980s relatively few data were available quantifying both total surface production and vertical flux to depth (Table 9.2). Surface biomass and productivity, for the western Mediterranean, has been estimated from satellite imagery (Morel and André, 1991; Arnone, 1994). Surface productivity over deep water varies seasonally, with maximum production of ~400 mg C m^{-2} d^{-1} in May of each year and a minimal production of <120 mg C m^{-2} d^{-1} in November (Morel and André, 1991). Phytoplankton biomass decreases rapidly away from shore, with a maximum biomass over the Alboran Sea and minimal in the central western Mediterranean (Arnone, 1994). Arnone also noted that subregions of the western Mediterranean with energetic circulation have higher chlorophyll concentrations. If one assumes that 1% of surface production reaches a depth of 2000 m, then the maximum vertical flux will be 4 mg C m^{-2} d^{-1} to the deep sea. Empirical data for vertical flux in the Mediterranean are sparse and highly localized. Off Corsica, sediment traps moored at a depth of 200 m collected a mass flux of material varying from 8 to 335 mg m^{-2} d^{-1} of which between 8 and 15% was organic matter (Buat-Ménard et al., 1989). Much of the flux, particularly in late January and early February, was in the form of faecal pellets. Fowler et al. (1991) measured particle flux at 200 m depth off Monaco. Maximum particle flux occurred in late winter and early spring although the organic-carbon flux, equivalent to 42% of surface production, followed the spring phytoplankton bloom. Fowler et al. (1991) showed that organic-carbon flux varied from 26.4 mg C m^{-2} d^{-1} in winter to 93.7 mg C m^{-2} d^{-1} during the spring phytoplankton bloom. Much of the organic-carbon flux consisted of copepod faecal pellets, although Andersen and Nival (1988) have suggested that salps were the main producers of these pellets. Sink rates in this region had been estimated at 29 m d^{-1} (Fowler et al., 1987). In the Golfe du Lion and the Catalan Sea vertical flux was highly seasonal (Danovaro et al., 1999), although this seasonal variation was damped in the Foix submarine canyon south of Barcelona (41°N, 2°E) (Puig et al., 2000). Buscail et al. (1990) recorded values of 92.7 mg C m^{-2} d^{-1} at a depth of 645 m in the open sea of the Golfe du Lion. About 10% of surface production (~15 mg C m^{-2} d^{-1} in the Golfe du Lion) reaches a depth of 1000 m. Monaco et al. (1990a,b, 1999) have shown that there appears to be preferential downward transport within canyons in the Northwest Mediterranean.

Between Crete and the island of Antikythira in the eastern Mediterannean the EU-funded PELAGOS programme, using sediment traps to a maximum depth of 1345 m, found that the total mass flux varied from

Table 9.2
Data for vertical flux in peripheral seas or (in its absence) data for surface production[1]

Peripheral sea/region	Depth of trap (m)	Mass flux (mg m^{-2} d^{-1})	Organic carbon flux (mg C m^{-2} d^{-1})	Surface production (g C m^{-2} d^{-1})	Reference
Mediterranean					
Golfe du Lion	600	30 to 20 000	100 (mean) 200 (maximum)		Monaco et al. (1990a,b)
	645		92.7		Buscail et al. (1990)
Off Calvi, Corsica	200	6000	26.4 to 93.7	121 to 155	Fowler et al. (1991)
Capo Cavallo	200	8 to 335	8 to 15% of mass flux		Buat-Ménard et al. (1989)
Rhône margin	600	3410 (spring maximum)	27 (mean)		Monaco et al. (1999)
Catalan Sea		10 to 50 000			Danovaro et al. (1999)
Cretan Sea	1515	50 to 210	3.15 (mean)		Danovaro et al. (1999)
Antikythira Strait					
Aegean	965	203 (39–361)			Kerhervé et al. (1999)
Ionian	880	96 (11–183)			
Ionian	1345	299 (209–390)			
Caribbean Sea					
Southeast				0.5	Richardson and Young (1987)
Northwest				0.15–0.25	
Central				0.1–0.15	
Gulf of Mexico				>0.06 to >0.18	Müller-Karger et al. (1991)
Indonesian seas					
Banda, Flores, Seram, Sulawesi, Makassar				1.2 (all year) 0.5 (NW Monsoon) 1.15 (SE Monsoon)	Kinkade et al. (1997)
Sea of Japan					
Central				0.21 (winter) 0.08 (summer)	Terazaki (1999)
				0.25 to 0.5	Nishimura (1983)
Sea of Okhotsk					
Southeast				0.25 to 0.5	Nishimura (1983)

[1] No data on the Red Sea.

1 to 1273 mg m^{-2} d^{-1} (from a surface production of 19 to 60 mg C m^{-2} d^{-1} – half that in the western Mediterraean) (Danovaro et al., 1999; Kerhervé et al., 1999). Lowest fluxes were in the summer and autumn when stratification in the water column was at its deepest. The generally low values recorded emphasized the highly oligotrophic nature of this area (Kerhervé et al., 1999).

The flux of material to deep water in the whole Mediterranean is compounded by the high deep-water temperatures, which accelerate biodegradation of sinking organic particles. In addition, the primary production in the Mediterranean is dominated by picoplankton (0.2–2 μm).

The Red Sea

Morphology

The Red Sea forms the newest of the deep seas, although, in geological terms, an ocean (Braithwaite, 1987). The Sea is a rift valley orientated NE–SW, ~2000 km long but only 270 km wide; but it has a maximum depth of >2720 m in the 30-km-wide central graben (Fig. 9.3a). The northern end is blind,

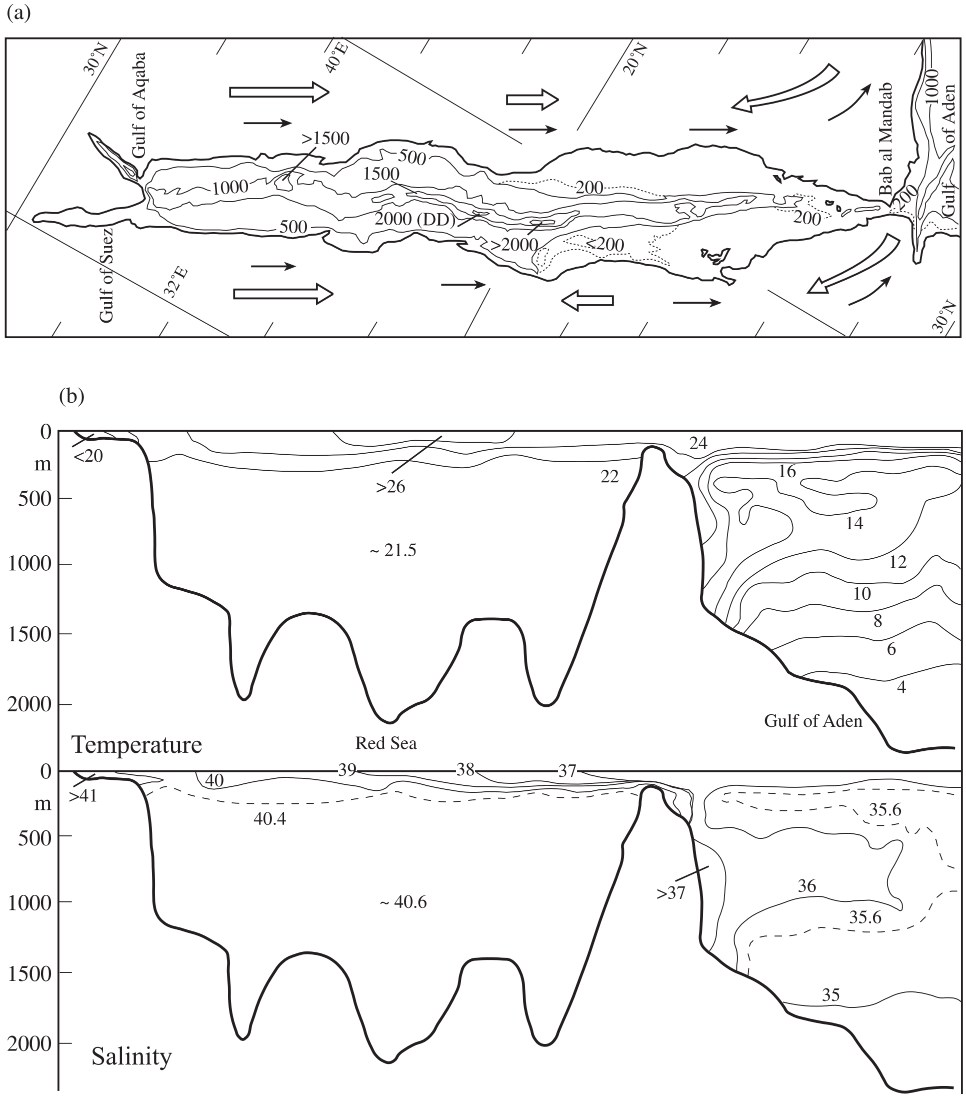

Fig. 9.3. Red Sea. (a) Bathymetry and winds. Open arrows show the direction of winds in winter, solid arrows in summer. DD identifies the position of the Discovery Deep and the adjacent Atlantis II Deep and Valdivia Deep. (b) Vertical profiles of temperature and salinity. Redrawn from Tomczak and Godfrey (1994).

bifurcating to form the Gulf of Suez and the Gulf of Aqaba. The southern end of the Red Sea is just 29 km wide, and is bounded by the 322m-deep sill of the Bab al Mandab. The shelves are narrow, except in the south, and the continental slope steep. The deep part of the Red Sea consists of a series of basins (Fig. 9.3a), which were discovered during the Swedish Deep Sea Expedition of 1948 (Bruneau et al., 1953), the most complex of which are those associated with the Atlantis II Deep (21º22.5′N, 38º4.5′E) and the Discovery Deep (21º17′N, 38º4.9′E), discovered by the *Atlantis* in 1962/63. The characteristics of the shallow part of the Red Sea are reviewed in Volume 26 of this series (Ross, 1983).

Hydrography

The Red Sea is flanked on both sides by hot dry deserts, and as a result the surface waters are warm and salty (Table 9.1). The deeper parts of the Red Sea are more saline (>40 salinity) and hotter (~22.6ºC) (Fig. 9.3b,c) than most other deep-sea areas (Bäcker and Schoell, 1972) as a result of the flow of hydrothermal fluid from the seabed. Open-water circulation shows southward flow at depths of ~250 m and >1000 m, with northward flow at ~500 m. Deep water is formed in the northern Red Sea, especially in the Gulf of Suez, although the Gulf of Aqaba makes a contribution. This new deep water is immediately injected under the pycnocline, at a rate of 0.11±0.02 Sverdrup, forming a southward-flowing current (Cember, 1988). Deep-water residence time is about 36 y. Flow of the dense brine water in the deeps of the Red Sea is driven by local topography with the temperature decreasing away from the brine source (Karbe, 1987).

Compared to the surface and intermediate waters of the Red Sea, the brines of the deep waters are enriched in manganese, iron, zinc, cadmium and copper, but depleted in magnesium, iodine, sulphate and nitrate. Concentrations of hydrogen sulphide and carbon dioxide differ between the various deep basins. As a broad rule, the high-density discontinuity between the brines and the overlying waters has prevented convective mixing. In the intervening years since their discovery in the early 1960s there has been little change in the salinity and temperature of most of the deeps (23.5 to 44.6ºC and 144 to 270 salinity) with the exception of the Valdivia Deep (21º20.5′N, 37º57′E), where the temperature has increased by 4.1ºC and the salinity by 10. This change is attributed to variation in the brine discharge (Anschutz et al., 1999). Only the Atlantis II Deep has been surveyed on a regular basis. Recent observations (Blanc and Anschutz, 1995) suggest that the two-layer stratification recorded originally has been supplemented by two additional upper convective layers, possibly as a result of the rate of heat input remaining constant (Anschutz and Blanc, 1996). From these data Blanc and Anschutz (1995) estimate that the hydrothermal discharge is in the order of $200\,\ell\,s^{-1}$.

Deep-water sediments

The majority of sediments of the Red Sea are poorly-sorted biogenous carbonates in the form of foraminiferal, pteropod and heteropod oozes (Berger, 1978). Coccolithophorids also contribute significantly to the sediment. Siliceous oozes are less common. The inorganic fraction consists of quartz, feldspar and mica derived from wind-blown particles from the deserts of Arabia and Africa. The dominant size range of the particles is in the <63 μm fraction, and the organic-matter content is <1%. Sediments in the very deep parts of the Red Sea have a hydrothermal origin and arise from the deep-water brines (Karbe, 1987). Within the deeper parts of the Red Sea the sediments are marls with a strong hydrothermal imprint giving rise to a multi-coloured layered structure. Oxidized sediments contain limonite, haematite and manganite, whilst those under reducing conditions contain pyrite and chalcopyrite, minerals found at hydrothermal vents forming chimneys. Other deposits contain ferrous sulphide, sphalerite, iron montmorillonite and manganosiderite. The sediment sequences vary greatly both within and between deeps (Karbe, 1987). Monin et al. (1981) have presented visual observations of the sea bed in the deeper parts of the Red Sea. These observations reveal a mosaic of rock outcrops with numerous basalt fragments dusted with sediment, step-like scarps of ~4 m amplitude, as well as decimetre-scale ripples believed to represent the brine surface.

Surface production and vertical flux

Throughout the Red Sea surface primary production is low, mainly owing to the low levels of inorganic nutrients (see Table 9.2). Vertical flux of organic matter is in the form of a ‘ladder of migrations’ (Weikert, 1982)[2] but the transport of organic matter below 1100 m depth by sinking is very limited owing to the rapid decay of organic matter in the high water temperatures. For the Atlantis II Deep, Weikert (1982) gave values for particulate organic matter of $<100\,\mu g\,\ell^{-1}$ below 750 m and even less at greater depths; but he was unsure of the reliability of his data.

Caribbean Sea

Morphology

The Caribbean Sea, underlain by oceanic crust (Matthews and Holcombe, 1985), consists of the eastern and western basins, separated by the Jamaica Rise at depths of 1500 m (Fig. 9.4). The eastern basin, with a maximum depth of 5400 m, is divided into the Venezuela Basin and the Colombia Basin by the Beata Ridge, although the Aruba Gap connects the Venezuela and Colombia Basins at a depth of 4078 m. The Venezuela Basin is separated from the smaller Grenada Basin to the east by the Aves Ridge and has the Muertos Trough along its northern side (Matthews and

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[2] The ‘ladder of migrations’ is a term used for the overlapping depth distribution (including vertical migration) of different species of zooplankton. This ‘ladder’ allows the rapid removal of organic particulates into deep water.

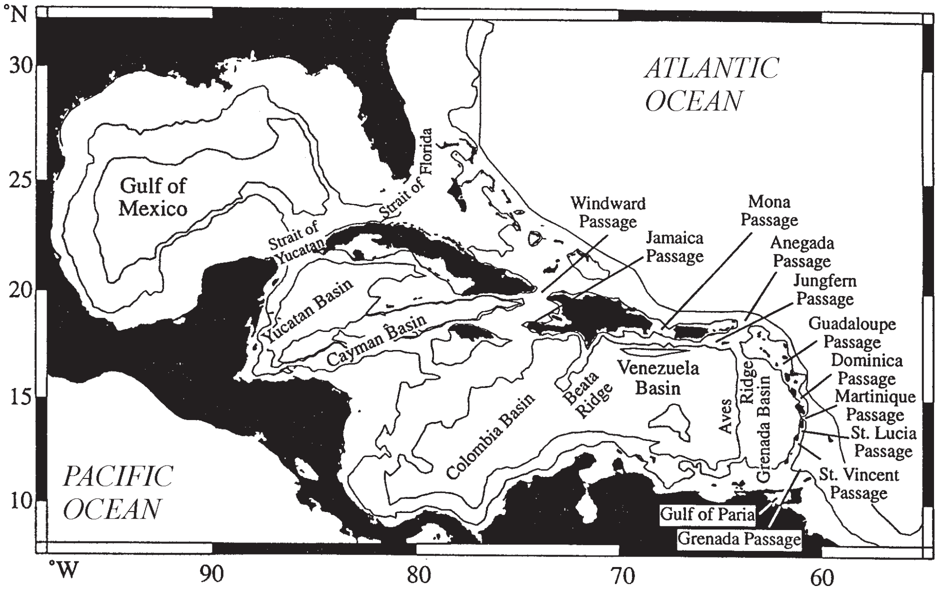

Fig. 9.4. Caribbean Sea. Bathymetry. Contours represent depths of 1000, 3000 and 5000 m. From Tomczak and Godfrey (1994).

Holcombe, 1985). The western basin is formed by the smaller Yucatan and Cayman basins, but with depths down to 7600 m. The Straits of Yucatan connect the Caribbean to the Gulf of Mexico. Along the southern perimeter of the Caribbean Sea is the Cariaco Trench (in reality a basin) separated from the main Caribbean by the Tortugas Sill. This results in the waters of the deeper parts of the 1800 m-deep Cariaco Trench being anoxic (Richards, 1975).

Hydrography

Because of the depths of the Caribbean Sea there has been some considerable discussion of its circulation and deep-water formation, as the sills through which water can pass from the Atlantic are all shallower than 2000 m (Fig. 9.4) except the Jungfern Passage that has a depth of 2800 m (Matthews and Holcombe, 1985). Initial observations suggested that the main influx of water into the deep Caribbean was via the Windward Passage into the western basin and the Jungfern Passage into the eastern basin (Fig. 9.5). Other possible passages for the flow of water from the Atlantic to the Caribbean included the Dominica (or Martinique) Passage (1400 m) as well as other Lesser Antilles Passages. Deep-water outflow from the Caribbean was almost exclusively northwards into the Gulf of Mexico via the Yucatan Channel. Sturges (1965) believed that the Windward Passage was the main source of inflow, and that the inflowing deep water arose from both Antarctic Intermediate Water (AAIW) and North Atlantic Deep Water (NADW). As water passes from these Passages into the body of the Caribbean proper there was an increase in the homogeneity of deep water. Sturges (1965, 1975) provided data to show that the main inflow to both basins is over the sill in the Windward Passage rather than over the sill of the Jungfern Passage. More recently, Kinder et al. (1985) have given a more detailed account of deep-water formation in the Caribbean Sea (Fig. 9.5a–c). They described the circulation below a depth of 1000 m as being of low net horizontal flux, which has to undergo vertical excursions of several hundred metres to flow throughout the Caribbean. Mean volume transport into the Caribbean is 10 Sverdrups ($10^6\ \mathrm{m^3\ s^{-1}}$) through the Windward Passage, 15 Sverdrups through the Passages of the southern Lesser Antilles and 5 Sverdrups through the remaining passages. Such a total is supported by the more recent work of Nof (2000). In summary, Kinder et al. (1985) suggested that the Windward Passage, with a controlling sill depth of 1690 m, supplied water to the Yucatan and Cayman Basins, while the Anegada–Jungfern Passages [sill depth 1815 m according to Kinder et al. (1985), but 2800 m according to Matthews and Holcombe (1985)] supplied water to the three eastern basins. On the Caribbean side of the Jungfern Sill, Stalcup et al. (1975) measured a layer of Atlantic water ~200 m-thick representing an inflow of $56\times10^3\ \mathrm{m^3\ s^{-1}}$. This layer was rapidly mixed with surrounding Caribbean water, suggesting that the

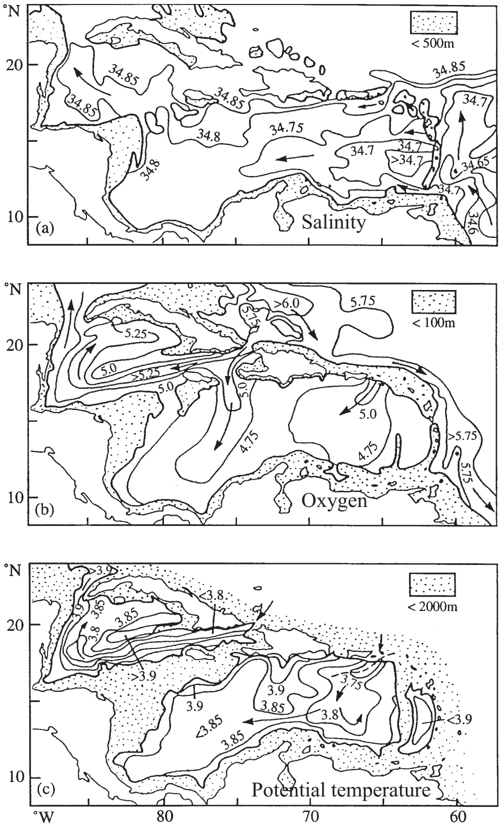

Fig. 9.5. Caribbean Sea. (a) Salinity at a depth of ~750 m; (b) oxygen concentrations ($\mathrm{ml}\,\ell^{-1}$) at ~2000 m depth; (c) bottom potential temperature. From Tomczak and Godfrey (1994).

inflow may be sporadic. This mixed water then flows westward along the slope on the southern side of Puerto Rico. Although the inflow over the Jungfern Sill is low (estimated to be $50\times10^3\,\mathrm{m^3\,s^{-1}}$, equivalent to ~0.2% of the Caribbean flow), it is sufficient to maintain temperature and oxygen levels in the Venezuela Basin (Sturges, 1975; Kinder et al., 1985). An estimated inflow of 50 Sverdrups would renew all the deep water in the Caribbean in 800 years (Sturges, 1975). Although evidence is lacking, Kinder et al. (1985) suggested that a similar maintenance of temperature and oxygen concentration occurs because of the flow over the sill in the Windward Passage.

Understanding of the deep circulation of the Caribbean is based on limited data and modelling. Roemmich (1981) suggested a slow cyclonic circulation of a few $\mathrm{cm\,s^{-1}}$ in the Venezuela Basin as well as in the Grenada Basin. Real data from the Grenada Basin (Kinder et al., 1985) suggest a slow cyclonic circulation of variable flow with episodes $>10\,\mathrm{cm\,s^{-1}}$ (Fig. 9.5b). Modelling of the data suggested that, in a two-layer model, topography exerted an influence steering any inflowing water along the northern boundary of the basin to the west, as found off the slope south of Puerto Rico. Kinder et al. (1985), however, urged caution in the interpretation of their model results, suggesting that more data are required to validate the model.

Most of the deep water in the Caribbean has a temperature of 3.8 to 4ºC and a salinity of 34.9 (Fig. 9.5a,c) (Sturges, 1965). At intermediate depths below the thermocline the temperature is ~6ºC. Oxygen values average $5.24\,\mathrm{ml}\,\ell^{-1}$ in the western basins and $4.69\,\mathrm{ml}\,\ell^{-1}$ in the eastern basin. The deeper waters of the Cariaco Trench are anoxic.

Sediment distribution

Sediment distribution is best known for the Venezuela Basin (Richardson and Young, 1987). At the eastern end of the Venezuela Basin along the western slope of the Aves Ridge are hemipelagic[3] sediments dominated by deposits from the outflows of the Amazon and the Orinoco carried into the Caribbean by the Guiana Current (Bowles and Fleischer, 1985). Sediment is deposited as the current looses kinetic energy. Sediments are terriginous clays with ~25% carbonate from Foraminifera and coccoliths (Richardson and Young, 1987). In the deepest parts of the Venezuela Basin (5050 m) the sediments are dominated by alternating layers of turbidites and fine pelagic clays. As the site is below the calcium compensation depth, carbonate content is low. In the Colombia Basin sediments grade from clays in the southeast to calcareous oozes in the northwest in deeper water. Turbidites also extend from the southeast into deep water (Prell, 1978). To the west, the deep-sea bed is dominated by pelagic carbonate oozes formed from Foraminifera, coccoliths and pteropod shells.

Surface productivity and vertical flux

The highest primary productivity is found in the southeastern Caribbean Sea ($500\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$); this decreases to the north and the west (150 to $250\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$), and in the western Caribbean Sea the surface primary production is 100 to $150\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ (Couper, 1983; Richardson and Young, 1987) (see Table 9.2). There are no data for flux of particulate organic carbon to the deep Caribbean, but it is

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[3] See Glossary, p. 477.

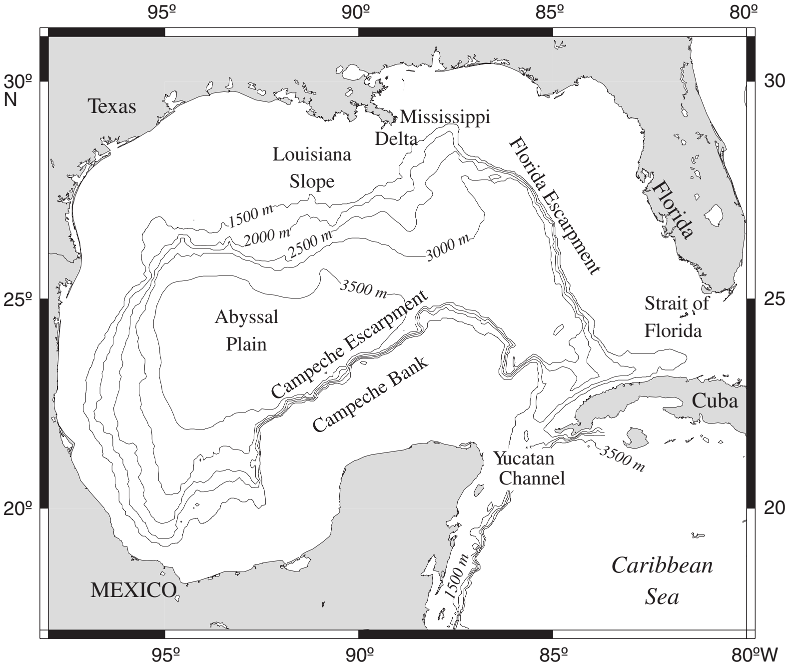

Fig. 9.6. Gulf of Mexico. Bathymetry and dominant physiographic features. Redrawn from McLellan and Nowlin (1963).

predicted that it would follow the pattern of surface primary production (Richardson and Young, 1987). The Caribbean receives considerable allochthonous material consisting of higher plant remains. The commonest inputs to the deep sea include wood, and the rhizomes and blades of *Thalassia testudinum* (Wolff, 1976, 1979; see also Chapter 11). These are brought in by turbidity flows, and are particularly abundant after hurricanes.

Gulf of Mexico

Morphology

The Gulf of Mexico consists of one large blind basin, with an extensive shelf and continental slope, and a central basin extending down to depths greater than 3400 m (Fig. 9.6). There are two connections to other seas: the Yucatan Strait (~1500 m depth) joins the Gulf of Mexico to the Caribbean Sea, and the Straits of Florida (shelf depths) join it to the Atlantic Ocean.

Hydrography

The deep-water circulation is mainly affected by the flow of water through the two straits joining the Gulf to adjacent seas. Water flows into the Gulf of Mexico from the Caribbean Sea through the deep passage of the Yucatan Sill. In the main basin of the Gulf of Mexico water temperature rises from 4.23°C [potential temperature[4] (θ) = 4.05°C] at a depth of 2000 m to 4.31°C (θ = 4.016°C) at 3000 m, and the salinity varies from 34.971 to 34.973 (McLellan and Nowlin, 1963). Water flows round the deep Gulf of Mexico as an anticyclonic gyre [called the Loop Current at the surface (Haustein and Feeney, 1985)] and in the eastern part of the Gulf mixes with surface waters and leaves the Gulf of Mexico through the Straits of Florida. Broecker et al. (1961) estimated that the deep water of the Gulf of Mexico would have a residence time of 350±100 years.

Dissolved oxygen in the deep waters of the Gulf shows lateral variability (McLellan and Nowlin, 1963). In the deeper waters in the west, oxygen levels are down to 4.2 ml ℓ^{-1} whereas in the eastern parts there is variation from 4.4 to 5.0 ml ℓ^{-1}. Oxygen does not appear to be limiting anywhere in the deep waters of the Gulf.

Sediment distribution

The dominant control on sediment distribution in the Gulf of Mexico is the discharge from the Mississippi River forming the Mississippi Fan with its

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[4] The potential temperature (symbolized as θ) is the temperature a packet of water would be at atmospheric pressure. It is always lower than the *in situ* temperature, as high pressure always increases the *in situ* temperature.

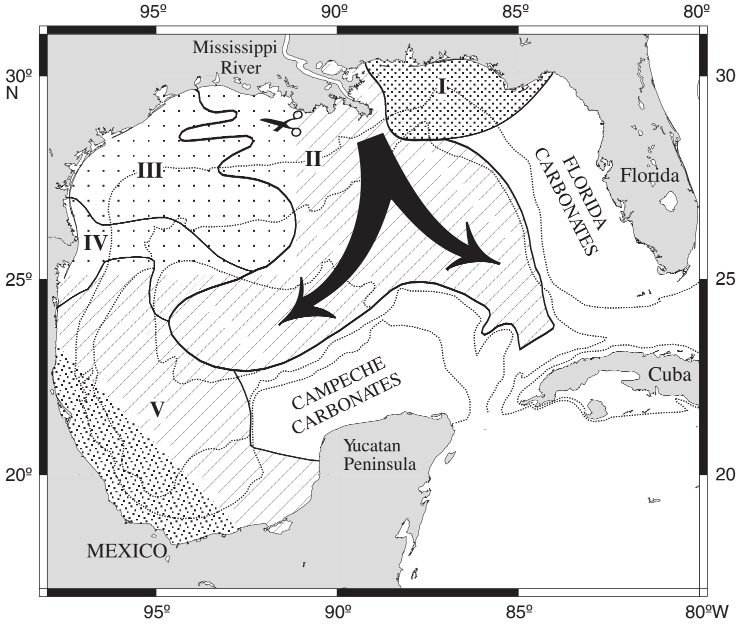

Fig. 9.7. Gulf of Mexico. Sediment distribution based on heavy-mineral composition. I, Eastern Gulf Province; II, Mississippi Province; III, Central Texas Province; IV, Rio Grande Province; V, Mexican Province. From Davies and Moore (1970).

associated levees. There is, however, input from the Rio Grande and rivers running through northeastern Mexico (Davies and Moore, 1970). Over 80% of the deep-sea bed in the Gulf is covered by sediments of Mississippi origin, and is referred to as the Mississippi province (Fig. 9.7). Dominant in the sediment are sand and silt-sized particles recognized as from the Mississippi because of their hornblende and epidote. Davies and Moore (1970) commented on the remarkable uniformity of the sediments from the Mississippi cone down into the abyssal Gulf of Mexico. It is the sediments of the Mississippi fan that contain hydrocarbon deposits supplying energy for the local chemosynthetic communities (see below, pp. 285–286).

Surface primary production and vertical flux

Surface primary production in the Gulf of Mexico has been estimated from remote sensing (Müller-Karger et al., 1991) (see Table 9.2). Primary production over deep water is synchronous throughout the Gulf, with highest values for pigment concentration ($>0.18\,\mathrm{mg\,m^{-3}}$) being found from December to February, with the lowest values ($0.06\,\mathrm{mg\,m^{-3}}$) from May to July. These data indicate a marked seasonal variation in surface production, which is likely to lead to seasonality in the flux of organic carbon to the deep-sea bed. No data, however, are available quantifying the vertical flux of phytodetrital material from the surface to the abyssal Gulf of Mexico. In coastal waters of the Gulf, aggregates average 0.5 to 3.5 mm in diameter (but up to 7.3 mm) and have a sinking rate of 10 to 89 $\mathrm{m\,d^{-1}}$ (Diercks and Asper, 1997). Organic-carbon input to the deep Gulf of Mexico remains to be calculated.

Deep seas of the Indonesian Archipelago

Morphology

The series of basins within the Indonesian archipelago form one of the most complex series of deep-sea inter-connecting basins. The seas of the Indonesian archipelago are separated from the Pacific by the island of Halmahera in the north and Papua (New Guinea) to the east, and from the Indian Ocean by Sulawesi to the west and the Lesser Sunda Islands (which include Timor) and the Outer Banda Arc to the south (Fig. 9.8). Connecting these islands are relatively shallow sills, and within the circle they form are found a series of deep basins. The largest of these are the North and South Banda Sea basins, with a depth of ~5000 m. Other basins include the Bacan (or Batjan) Basin (~4500 m), the Buru Basin (5000+ m), the Wetar and Sawu (Savu) Basins (>3000 m), the Aru Basin (3500 m) and the Weber Deep, the deepest, at >7000 m. The Timor Basin at ~3000 m is included in these

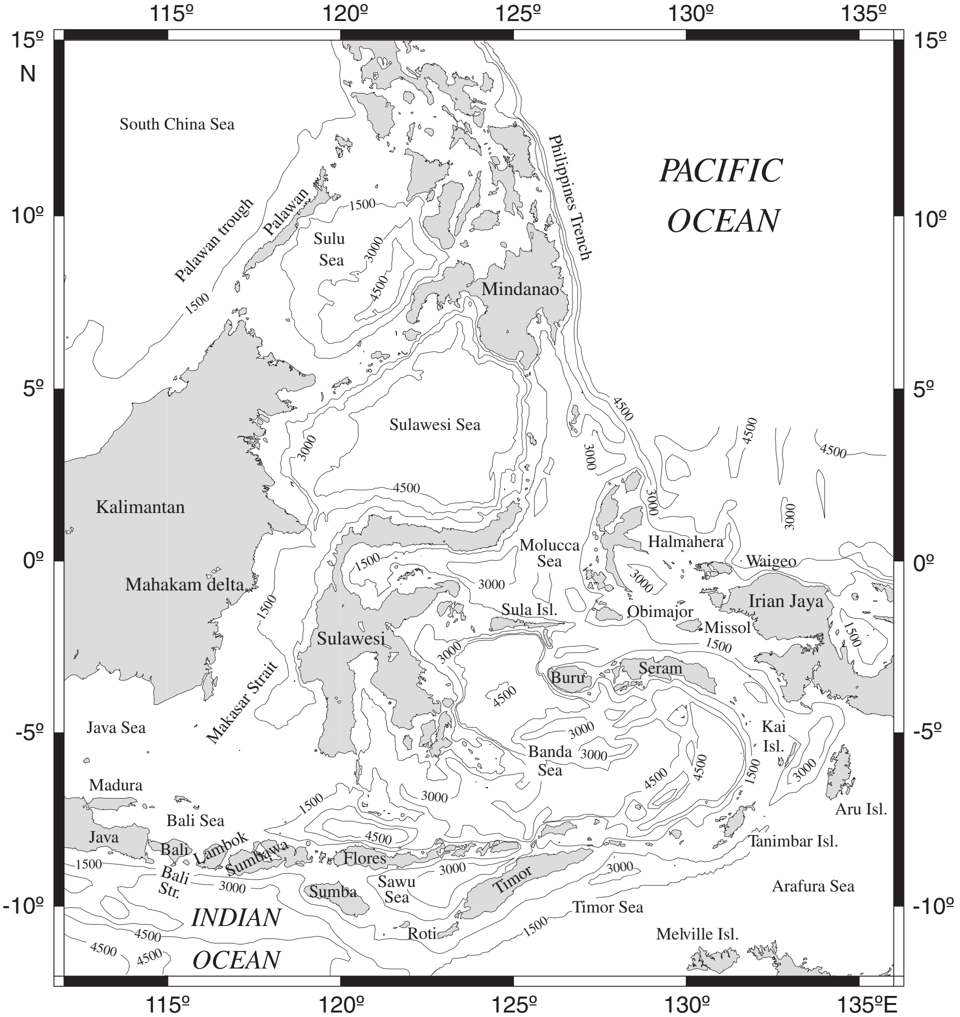

Fig. 9.8. Indonesian seas. Bathymetry. Redrawn from Tomczak and Godfrey (1994).

seas but it is strictly outside the Lesser Sunda Islands (Fig. 9.9). Also included are the Sulawesi Sea (formerly the Celebes Sea, >4500 m) and the Sulu Sea (4500 m). Below a depth of 1500 to 2000 m, depending on the sill, these deep basins are separated from the Pacific and Indian Oceans (Van Aken et al., 1988). The basins are generally, however, kept flushed and thus oxygenated by the inflow of water from the adjacent oceans, particularly from the Pacific. The exception is the Sulu Sea, which has low oxygen and high temperature at depth (Kuehl et al., 1993). The basins are of tectonic origin, and in the past low stands of the sea level have had an impact on the fauna, resulting in the so-called Wallace's Line (Fleminger, 1986).

Hydrography

The flow of water between the Indonesian islands is driven by the sea-level gradient between the Pacific and Indian Oceans (Kinkade et al., 1997). The main influx of water into these basins is over the sill of the Strait of Lifamatola (depth 1950 to 2000 m) (Fig. 9.9) to the west of Obi on the island of Halmahera (Van Aken et al., 1988). This water flows into the Buru Basin, mixing with overlying waters on the way. Intermediate waters closely resemble North Pacific Intermediate Water. Flow is also modified by the local monsoon regime. The main flow enters and sinks into the Banda Basin. Oxygen levels are lower in the Banda Basin than in the Pacific, as deep well-oxygenated water is prevented from entering the Banda Basin by the Lifamatola Sill. Only in the Savu Basin

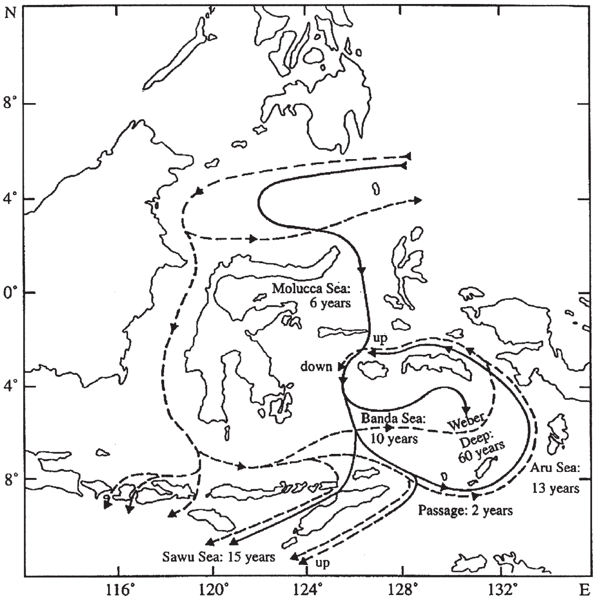

Fig. 9.9. Indonesian seas. Intermediate circulation (hatched lines) and deep circulation (solid lines), and estimated transit times of bottom water. From Tomczak and Godfrey (1994).

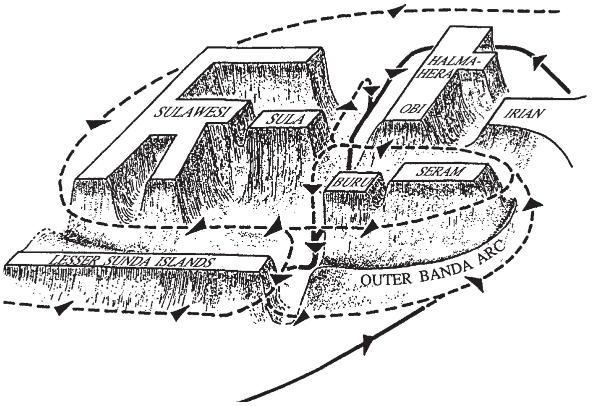

Fig. 9.10. Indonesian seas. Three-dimensional deep circulation. Hatched lines are intermediate circulation, full lines deep circulation. Redrawn from Van Bennekom et al. (1988).

and the Weber Deep does the oxygen approach a minimum in deeper waters. In the Eber Deep there is a north–south decrease in oxygen content, suggesting that this basin is ventilated from the northern end. In the Banda Sea there is also upwelling of deep water into the thermocline; this forms the Indonesian Intermediate Water mass that flows into the Indian Ocean in the lower parts of the thermocline (Emery and Meincke, 1986). Using dissolved silica as a tracer, Van Bennekom et al. (1988) have schematically determined the passage of flow through these deep basins (Fig. 9.10).

Sediments

The deep-sea bed in this region has been poorly sampled, and there are no detailed reports of the sedimentary environment. Sampling by HMS *Challenger* in this region reported 'blue mud', 'mud' or Globigerina ooze (Murray, 1895).

Surface production and vertical flux

Data of surface primary production in the Indonesian seas are limited, and there are no data for vertical flux to deep water (Kinkade et al., 1997) (see Table 9.2). Surface production is driven by the seasonally-varying monsoons and also by the (ecologically beneficial) effect of the El Niño Southern Oscilllation (ENSO). During the northwest monsoon, surface chlorophyll is similar all over the Indonesian seas, varying from an average of 0.24 mg m^{-3} in the east (Banda, Flores and Seram Seas) to 0.35 mg m^{-3} in the west (Sulawesi Sea and Makassar Strait). This corresponds with a productivity of ~1.2 g C m^{-2} d^{-1}. During the southeast monsoon biomass increases markedly in the east (2.76 mg m^{-3}) although productivity remains similar. In the west both biomass and productivity decrease during the SE monsoon (0.17 mg m^{-3} and 0.53 g C m^{-2} d^{-1}, respectively) (Kinkade et al., 1997). If this variability in surface production is translated into vertical flux (although there may be considerable recycling in the upper water column), flux to depth in the basins under the Banda, Flores and Seram Seas may be high and seasonal. In the Banda Sea organic remains of phytoplankton origin are secondary to those arising from zooplankton, particularly the remains of copepods (Van Waveren and Visscher, 1994). A second source of allochthonous material to the deep-sea bed in this region are plant remains. At the only station (St. 450) sampled by the *Galathea,* the trawl recovered branches, twigs, wood and coconuts from a depth of 4940 m (Bruun, 1957).

The Sea of Japan

Morphology

In contrast to the Sea of Okhotsk (see below, pp. 276–279), with which the Sea of Japan is connected through the shallow Soya Strait (53 m depth) and Tatarskiy Strait (15 m depth), the Sea of Japan forms an enclosed basin relatively isolated from the Pacific

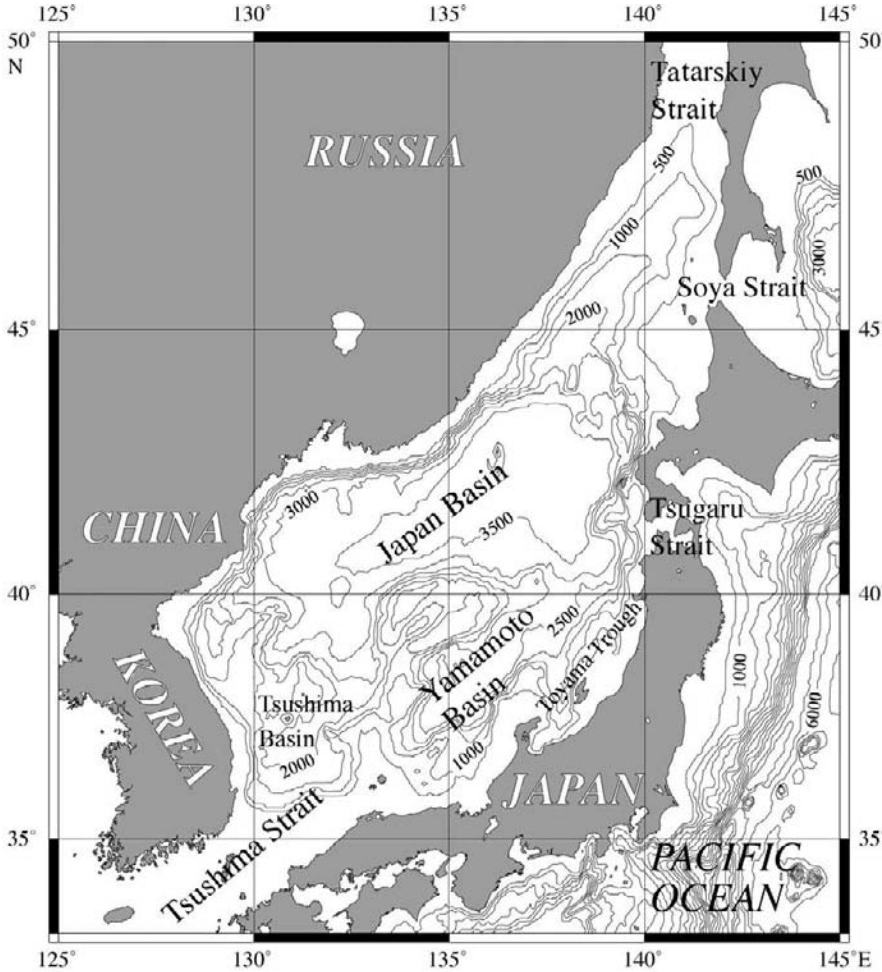

Fig. 9.11. Sea of Japan. Bathymetry. Redrawn from Zenkevitch (1963).

proper (Fig. 9.11) except for the Tsugara Strait (130 m depth) and the Tsushima Strait (130 m) (Terazaki, 1999). The input of water from the Pacific proper is only in the order of 2 Sverdrups (Nof, 2000). The Sea of Japan has shallow areas surrounding a wide single central, flat-bottomed basin, with a maximum depth of 4036 m, which occupies about 40% of the whole seafloor. Two deeps are recognized, the Japan Basin and the Yamamoto Basin, each with distinctive water-mass structures (Gamo et al., 1986).

Hydrography

Four water masses are recognized in the Sea of Japan: the Tsushima Current Water; Central Water; Intermediate Water and Deep/Bottom Waters (modified from Nishimura, 1969). Surface waters are affected by prevailing surface currents: the Tsushima Current bringing warm water in from the south, while the Liman Current brings in cold water from the north (Fig. 9.12a). The variation in surface temperature affects surface primary production, and thus the supply of particulates to the deep-sea bed (Nishimura, 1983). Winter convection forms deep cold water masses in the northwest of the Sea of Japan, which sink to the deep-sea bed and spread throughout the deep basins (Nishimura, 1969). This water forms a distinctive Bottom Water confined morphologically to the deep Sea of Japan (Uda, 1938). The mixing of this bottom water into the intermediate and upper layers is by slow eddy turbulence. Mixing of the bottom water with intermediate water gives Sea of Japan Deep Water (Fig. 9.12b). The deep and bottom water occupy the Sea of Japan from 300 m to the bed at >3000 m. In the southern part of the Sea of Japan winter cooling gives

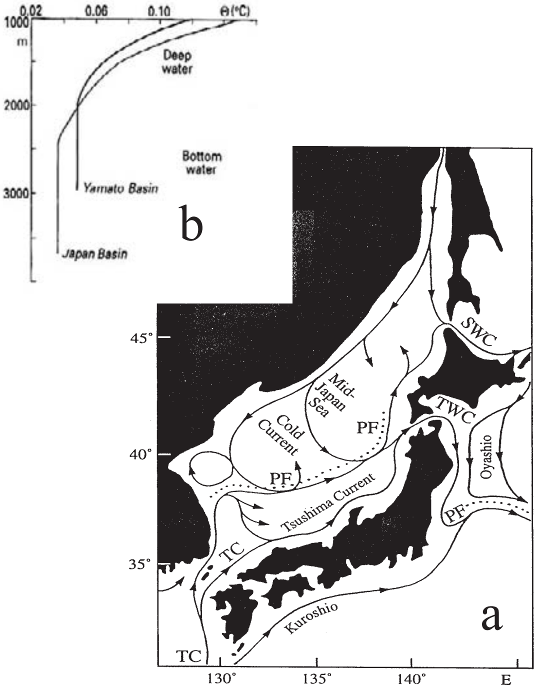

Fig. 9.12. Sea of Japan. (a) Surface circulation. Abbreviations: SWC, Soya Warm Current; TWC, Tsugara Warm Current; TC, Tsushima Current; PF, Polar Front. (b) Potential temperature (θ) in the deep water. Redrawn from Tomczak and Godfrey (1994).

rise to convectional mixing, water from which sinks to between ~100 and ~300 m, giving rise to Japan Sea Intermediate Water (Miyazaki, 1952). The deep waters of the Sea of Japan remain well aerated (Zenkevitch, 1963), although this has not always been in the case in the past (Terazaki, 1999). Bottom temperatures (θ) range between 0.03 and 0.12°C (Fig. 9.12b) and the salinity is 34.08 to 34.14, both being lower than the Sea of Okhotsk and adjacent Pacific (Zenkevitch, 1963; Terazaki, 1999). Nishimura (1969) has given cross-sectional representations, and physical properties, of the water masses in the Sea of Japan.

Sediments

Sediments in the deeper parts of the Sea of Japan are mainly silt of varying grade, and diatomaceous ooze is entirely absent. The deepest beds of the Sea of Japan are covered with ooze (Zenkevitch, 1963).

Surface production and vertical flux

Surface production is low, patchy and seasonal (see Table 9.2). In the northwest of the Japan Sea production is high, with a peak in March, whilst in the southeast it is low, with a peak in May (Nishimura, 1969, 1983). The mean surface primary production in winter is $0.21\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$, and in the summer $0.08\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ (Kano et al., 1984; Terazaki, 1999). There are no data for vertical flux to the deep seabed of the Sea of Japan.

The Sea of Okhotsk

Morphology

The bathymetry and surface circulation of the Sea of Okhotsk have been described by Nishimura (1983) in Volume 26 of this series. Much of the northern and western part of the sea is at shelf depths (Fig. 9.13) sloping to the central Deryugin Basin with a depth of 1700 m. The deepest part of the Sea of Okhotsk is the Kurile Basin in the southeast corner, inside the Kurile Islands (Kurilskiye Ostrova), reaching a maximum depth of 3657 m (Zenkevitch, 1963; Freeland et al., 1998). This deep basin is linked to the Pacific proper by deep channels of maximum depth 2318 m between the Kurile Islands, which are formed from a series of volcanoes resulting from the Kurile–Kamchatka subduction zone.

Hydrography

The surface circulation in the Sea of Okhotsk is formed from a series of cyclonic gyres (Fig. 9.14a) which in summer are decoupled from the deep circulation by the formation of a strong thermocline. Because of the effect of cold Siberian winds, there is considerable surface cooling in the winter months, resulting in surface freezing over much of the sea; this leads to increased water density and large-scale convective vertical mixing down to 400 m once the thermocline is broken down (Kitani, 1972). In the spring, surface salinity is greatly reduced by surface thawing and river runnoff from the spring melt. Convective mixing in the Sea of Okhotsk is limited by inflow of dense Pacific seawater into the deepest parts of the sea through the deep passages between the Kurile Islands.

The deep water masses in the Sea of Okhotsk (Nishimura, 1983, table 15.4) consist of a transient layer between 150 and 750 m with a temperature of 0 to 2.0°C and salinity of 33.2 to 33.8, and deep and bottom waters from 750 m to the bottom (temperature 1.8 to 2.5°C and salinity 34 to 34.5) (Fig. 9.14b) (Nishimura, 1983; Saidova, 1997; Freeland et al., 1998). The cold intermediate water (also called the *dicothermal water* because of its very low temperature), overlying the transient water, spreads out across the Sea of

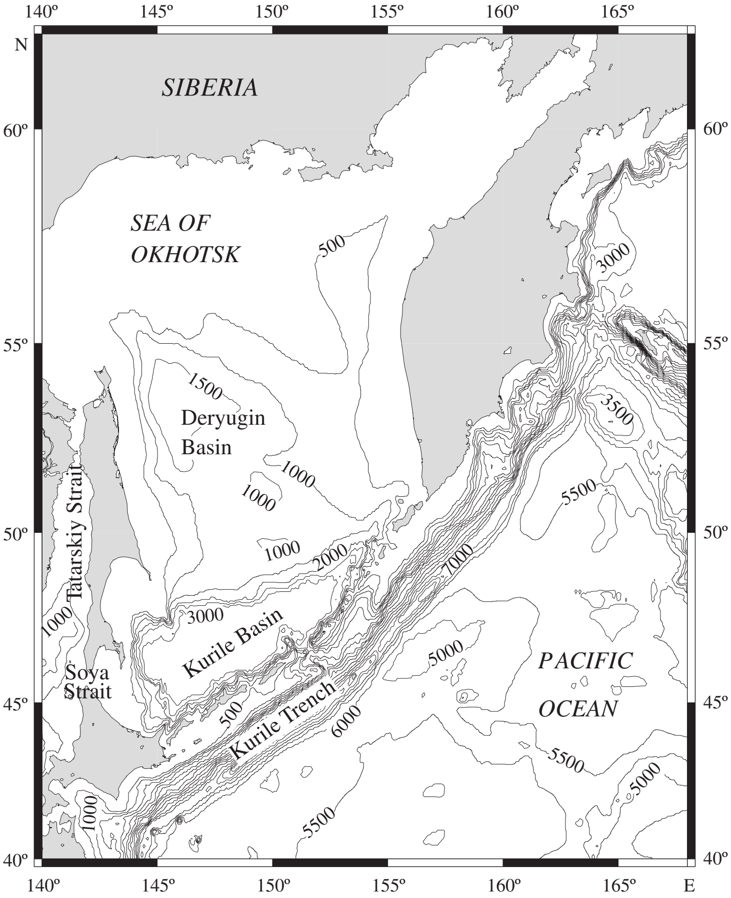

Fig. 9.13. Sea of Okhotsk. Bathymetry. Redrawn from Zenkevitch (1963).

Okhotsk and flows southeastwards through the straits of the Kurile Islands into the Pacific proper. Deep Pacific water enters over the Kurile Island ‘sill’, particularly through the Kruzenshtern Strait (Provliv Kruzenshterna), and sinks into the Kurile Basin. The deep-water circulation is cyclonic. This deep water may mix vigorously upwards with the dicothermal water to give the ‘transient water’ (Yasuoka, 1967). This influx of deep Pacific water has a profound effect on the deep benthic fauna of the Sea of Okhotsk.

Oxygen concentration decreases with depth in the Sea of Okhotsk with values of 50% of saturation in the shallowest parts of the Kurile Basin, decreasing in the deepest parts (1500 m) to only 0.7 ml ℓ^{-1} (9.2% saturation) (Zenkevitch, 1963). Saidova (1997) reported values of 2.0 to 2.3 ml ℓ^{-1} (80 to 100 μmol kg^{-1} (Freeland et al., 1998)) below depths of 1500 m in the Kurile Basin. This is probably because the deep water of the Kurile Basin is of Pacific origin.

Sediments

The deep bottom sediments of the Sea of Okhotsk form two sedimentary provinces (Zenkevitch, 1963). In the central basin coarse boulder/shingle and gravel deposits are found in the deepest parts (>1200 m) surrounded by sands at shallower depths. In the Kurile Basin the dominant sediment are clays and diatomaceous oozes. Because of the flow between the Kurile Islands, and local volcanic activity, sediments in the deeper parts of these straits are often coarse.

Surface production and vertical flux

For the Sea of Okhotsk, data both for surface production and for vertical flux are few (see Table 9.2). Much of the northern and western parts of the sea consists of shallow shelves covered with ice in winter. Mordasova (1997) reported on the results of three season’s cruises to the Sea of Okhotsk. Surface primary production is highest and very seasonal over the shelf

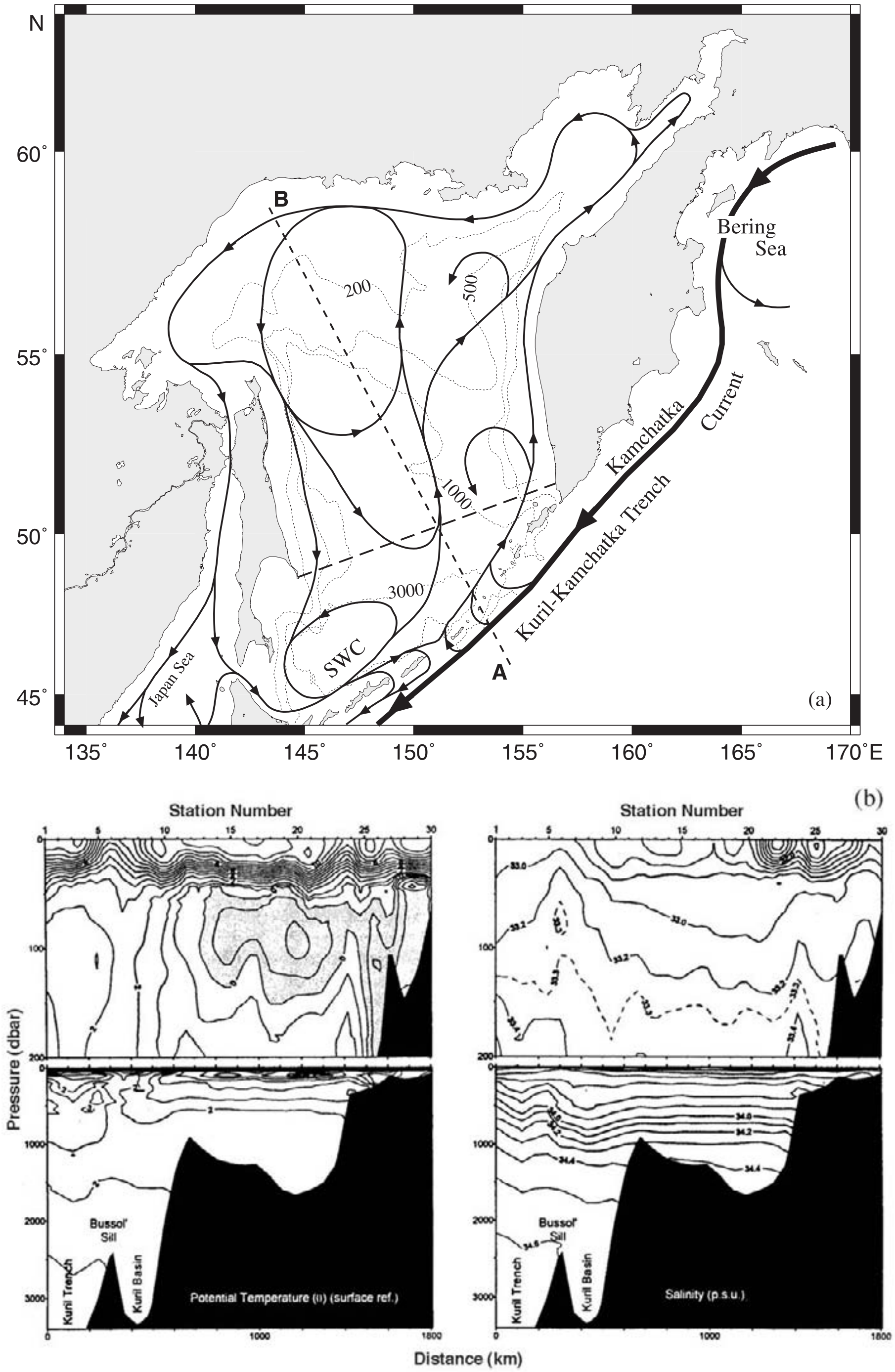

Fig. 9.14. Sea of Okhotsk. (a) Surface circulation. Redrawn from Tomczak and Godfrey (1994). (b) Distribution of potential temperature and salinity in the World Ocean Circulation Experiment (WOCE) Section P1 (A–B). Redrawn from Freeland et al. (1998).

regions beginning at the ice edge. Over the deep-water regions the chlorophyll concentrations decrease to values of 0.2 to 0.4 mg m^{-3} as a result of low nutrient availability, and the maximum chlorophyll concentration occurs at a depth of 40 m. In the southeastern corner of the Sea of Okhotsk chlorophyll levels rise to 1.0 mg m^{-3} inside the Kurile Islands, and outside the islands in the open Pacific they increase to 5.0 mg m^{-3}. Chlorophyll values above 1 mg m^{-3} were found in the Sea of Okhotsk inside the northern Kurile Islands. Such elevated values are believed to be a result of incursions of nutrient-richer Pacific waters (Mordasova, 1997). Overall, Mordosova classifies the Sea of Okhotsk as 'eutrophic', since it supports high invertebrate and fish production. No data are available for the flux of surface production to deeper waters. Any extrapolation made from surface data will be complicated by the flow of water into, and out of, the Sea of Okhotsk over the deep sills between the Kurile Islands.

THE DEEP-WATER BENTHIC FAUNA OF PERIPHERAL DEEP SEAS

Mediterranean Sea

The most recent detailed reviews of the deep-water fauna of the Mediterranean are given by Pérès (1985), Fredj and Laubier (1985) and Laubier and Emig (1993). When the Mediterranean was completely isolated from the Atlantic and Indo-Pacific during the Messinian crisis all true benthic species in the Mediterranean became extinct (Pérès, 1985). Since then, there has been colonization of deep water by species from the deep Atlantic and from shallow waters of the Atlantic via Mediterranean shallow water. No deep water species are considered Lessepsian (those species entering the Mediterraean via the Suez Canal).

Pérès (1985) identified two bathyal assemblages in the western Mediterranean:
(a) the deep-sea coral assemblage
(b) the bathyal mud assemblage

The deep-sea coral assemblage

This assemblage consists of both living and dead ahermatypic corals, which form scattered clumps but are not widespread. Their depth range is from 300 m down to a known maximum of 1000 m. The main frame corals are *Lophelia pertusa* and *Madrepora oculata* (both found commonly in the North Atlantic) and the solitary corals *Caryophyllia armata* (sic) and *Desmophyllum cristagalli*. The decline in the reef-building species is attributed to siltation resulting from deforestation on land, and the subsequent erosion and riverine transport of soil. Associated with both living and dead ahermatypic corals are the gorgonians *Isidella elongata* and species of *Muricea* and *Primnoa.* The most distinctive of the polychaetes is *Eunice floridana*, which lives on the coral. Truly bathyal species include the serpulids *Omphalopomopsis fimbriata* and *Placostegus tridentatus* and the ampharetids *Acanthicolepis cousteaui* and *Lagisca drachi*. Other polychaetes are eurybathyic and not truly bathyal. Characteristic molluscs include the chiton *Hanleya hanleyi* as well as bivalves including species of the genus *Arca, Chlamys bruei* and *Spondylus gussoni.* The dominant sea urchin in this assemblage is *Cidaris cidaris* and the main crustaceans *Pandalina profunda* and *Paromola cuvieri.*

Bathyal mud assemblage

This zone extends from 200 m down to ~2500 m, and consists of fine sediments. Compared to similar depths in the Atlantic (see Chapter 5) this zone in the Mediterranean may be considered impoverished, although by contrast with other Mediterranean biotopes this assemblage is rich in species and abundance (Pérès, 1985). Most Atlantic species at this depth are not eurybathic enough to cross the sill at Gibraltar. The lack of colonizing species, the high temperature of the deep Mediterranean (see above, p. 264), and the low downward vertical flux from relatively poor primary production at the surface, contribute to the impoverishment of this zone. Picard (1965) and Pérès (1985) have given extensive faunal lists of the species characteristic of this zone. Polychaetes and benthic crustaceans are particularly common but most major groups are represented. The origin of this bathyal fauna is still the subject of debate, but one group of organisms (the mud-loving or pelophilous species) have extended down to depth from relatively shallow areas, particularly the outer or lower part of the shelf. From 200 m down, the temperature remains fairly constant; Young et al. (1997) have shown that the embryos and larvae of shallow species are able to tolerate the pressures at bathyal depths, and may have penetrated through a vertically homogeneous water column.

Pérès (1985) divided the bathyal mud zone into three subzones:
(i) an upper zone containing mainly eurybathic species;
(ii) a middle zone with high species diversity;
(iii) a lower subzone with decreased species diversity and containing species, such as *Plutonaster bifrons,* not found in the two shallower zones. *Plutonaster bifrons* is another species that may

have invaded by larval dispersal (Young et al., 1996).

The existence of a true abyssal fauna in the western Mediterranean has been questioned (Pérès, 1985). If one assumes that the abyssal zone begins at 3000 m (see Chapter 2), the maximum depth in the western Mediterranean is 3500 m in the Tyrrhenian Basin. Originally a true abyssal fauna was believed not to occur, but this has been challenged by Reyss (1971, 1972), Laubier (1972) and Chardy et al. (1973). Typical of abyssal species are the protobranch *Nuculoma tenuis* and the cumaceans *Diastylis jonesi, Leptostylis bacescoi* and *Procampylaspis bascescoi.* Amongst the polychaetes, the species are either found at bathyal and abyssal depths in both the Atlantic and the Mediterranean, or they are endemic to the Mediterranean at bathyal and abyssal depths. Truly abyssal Mediterranean polychaetes are species of the genus *Aricidea* and *Macellicephala.* Of remark is a species of *Macellicephaloides,* previously found only in trenches. Pérès (1985) concluded that a truly abyssal fauna occurs in the Mediterranean, particularly in the Matapan Deep (4690 m). Fredj and Laubier (1985) recorded the polychaete *Lacydonia laureci* as being the species occurring at greatest depths in the Mediterranean. At other depths there is a predominance of eurybathic species. Compared to similar depths in the Atlantic, the Mediterranean abyssal fauna is species-poor. Fredj and Laubier listed the endemic Mediterranean species found below 2000 m and listed their Atlantic congeners.

Certain taxa are noteworthy by their absence in the deep Mediterranean, although found at similar depths in the Atlantic. Typical of these are elasipod holothurians, stalked crinoids, and the crab genus *Munidopsis*; in the Mediterranean, ophiuroids rarely occur below 700 m, although they are found at all depths in the Atlantic. Fredj and Laubier concluded that the species found in the deep Mediterranean are representative of the older groups within their respective phyla, whereas the 'advanced' forms, such as *Anamathia*, *Geryon* and *Munidopsis* are much less common.

As a result of programmes funded by the European Union more data have recently become available, although in many cases such observations are localized. Of particular significance have been the studies along the slope of the Golfe du Lion and the Catalan Sea. De Bovée et al. (1990) quantified the microbiota and meiofauna at 29 stations in five canyons at depths between 672 and 2367 m in the Golfe du Lion. Microbial numbers varied from 9×10^{-3} to 3×10^{-5} colony forming units ml^{-1}, the latter being in deep water. Meiofauna was dominated by nematodes with a density range from 3.6 to 100.5 individuals cm^{-2}. Meiofaunal abundance increased rapidly with depth – in fact, more rapidly than in other oceans (see Chapters 5 and 6). Such low abundance was attributed to the low organic content of the sediment ($2.7\,mg\,C\,g^{-1}$) resulting from high degradation rates at the temperature of 13ºC near the deep-sea bed. Stora et al. (1999) have determined the abundance of macrobenthos in the Toulon Canyon and the adjacent slope (south of Toulon in the Golfe du Lion) at depths from 250 to 2000 m (Table 9.3). At the stations examined there was a strong decrease in species richness with depth particularly between 250 and 1000 m, below which there was stabilization of species numbers. Biomass also decreased with depth (except between 1500 and 2000 m) from $2.14\,g\,m^{-2}$ at 250 m to $0.05\,g\,m^{-2}$ at 2000 m (Stora et al., 1999). At most of the stations surface deposit feeders dominated, followed by subsurface deposit feeders. Carnivores were well represented at the upper stations but decreased with depth. Stora et al. (1999) divided the slope into a series of groups (Table 9.3) and identified species characteristic of bathyal deep mud or abyssal assemblages. The megabenthos of the deep western Mediterranean has been described by Sardà et al. (1994). Decapod crustacean biomass was higher in submarine canyons than outside, whilst fish abundance was highest on the lower slope.

In the Catalan Sea an active slope programme has been conducted by workers at the Institut de Ciències del Mar in Barcelona. These studies have concentrated on the distribution and diet of benthic and pelagic crustaceans, and also on the local fish assemblages and their diet. Cartes and Sardà (1992, 1993) trawled at a variety of depths between 552 and 2261 m on the Catalan slope; multivariate analysis of their data showed zonal boundaries between 1200 and 1300 m, and between 1900 and 2000 m, based on the decapod fauna. Total abundance, biomass and species richness all declined with depth. The deepest community was dominated by *Acanthephyra eximia* (pelagic), *Nematocarcinus exilis* and *Stereomastis sculpta*. Cartes and Sardà (1993) concluded that decapod zonation was determined by trophic factors, the middle slope, with highest diversity, being influenced by resuspension of particles associated with local submarine canyons. More recently, Maynou et al. (1996) have shown that

Table 9.3
Zonation of the macrobenthos on the continental slope in the Toulon Canyon region[1]

Group	Depth (m)	Site	Deep species typical of bathyal deep mud or abyssal assemblages
1	All depths		*Capitellides giardi, Cyclammina cancellata, Nuculoma tenuis, Onchnesoma steenstrupii*
2a	25–1500	East Flank	*Amphilepis norvegica, Aricia kupfferi*,
2b	250	Upper East Flank	*Diastylis cornuta, Ebalia nux*
2c	250–500	Upper slope	*Aricidea* cf *abyssalis*
3a	250–500	Upper Canyon Channel	*Harmothoe impar*
3b	250	Upper Canyon Channel	None
4	500	East Flank	*Aricidea aberrans, Calocaris macandrae*, *Eriopisa elongata*
5	500	East Flank	None
6	>500	Canyon Channel/west flank	None
7	1570	West Flank	None
8	1000	West Flank	*Brada villosa, Onuphis quadricuspis*
9	1100	Channel	*Fauveliopsis brevis*

[1] Modified from Stora et al. (1999)

within the depth range of a crustacean species distribution was non-uniform, populations being segregated into areas of high density.

In the peracarid taxon Cumacea, highest diversity was at intermediate depths on the lower slope (1235 to 1355 m); *Diastyloides serratus* and *Leucon longirostris* were the most abundant of the 32 species collected between depths of 389 and 1859 m (Cartes and Sorbe, 1997). Analysis of the population biology of cumaceans on this slope showed that species living on the upper slope (389 to 500 m) had a longer reproductive period than species inhabiting the middle and lower slope. Among the species at greater depths, recruitment was limited to late winter and spring, synchronized with phytodetrital input (Cartes and Sorbe, 1996).

The group at Barcelona has also examined the diets of a wide variety of Crustacea taken at bathyal depths in the western Mediterranean. *Munida tenuimana* and *Nematocarcinus exilis* feed on fish remains and slow-moving invertebrates. Above 1200 m, pelagic remains form a significant element of the diet of *M. tenuimana,* but below this depth scavenging of teleost fish, pelagic decapods, pteropods and Foraminifera dominates (Cartes, 1993c). Cartes (1998), reviewing food resources in deep-water crustaceans at depths between 400 and 2300 m, identified five trophic groups: macroplankton feeders, macroplankton–epibenthic feeders, epibenthic feeders, epibenthic–endobenthic feeders and deposit feeders. He concluded that there was an increase in deposit feeding with depth. Such depth-related changes in diet have been observed in polychelid lobsters (Cartes and Abelló, 1992) and the shrimp *Aristeus antennatus* (Cartes and Sardà, 1989), and also in oplophorid and pandalid shrimps (Cartes, 1993a,b).

Two distinct fish assemblages are recognized in the Catalan Sea (Stefanescu et al., 1993) occurring on the middle (between 1000 and 1425 m) and lower slope (between 1425 and 2250 m). The mid-slope group is dominated by large fish with high energy demands, whereas the deeper group consists of smaller fish, more passive and with low energy demands. In this area abundance, biomass, mean fish weight and species richness all decrease with depth.

The diet of the commonest deep-sea fish in this region, *Lepidion lepidion*, was found to include a wide range of benthic and pelagic prey (Carrassón et al., 1997). As with the Crustacea, diet changed with depth from planktonic prey above 1400 m to suprabenthos[5] at greater depths. Such variation may be ontogenetic, only adults being found below 1600 m. At the highest trophic levels there appears to be exclusion between shark species (Carrassón et al., 1992). *Centroscymnus coelolepis* is restricted to depths between 1419 and 2251 m, whereas *Galeus melanostomus* was abundant between 1000 and ~1500 m. Diets of the two species showed very little overlap, mainly as a result of the specialized diet of cephalopods taken by *C. coelolepis*.

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[5] See Glossary, p. 477.

A third shark species, *Etmopterus spinax,* has a diet similar to that of *C. coelolepis,* and may compete with the latter more than *C. coelolepis* does with *G. melastomus* (Carrassón et al., 1992).

From the deep waters of the Tyrrhenian Sea, there is evidence that the six-gilled shark (*Hexanchus*) and the seven-gilled shark (*Heptanchus*) are bottom scavengers feeding on sunken whale remains. There is evidence for fin whales in this region, as well as the blue whale (*Balaenoptera musculus*) passing through on migration. These mammals may form a significant organic input when compared to phytodetrital sedimentation (M.V. Angel, personal communication).

Benthic data for the eastern Mediterranean are more limited, possibly as a result of the oligotrophic nature of the area. Forbes (1844) suggested that life was absent below a depth of 550 m in the Aegean. More recently however, because of projects funded nationally and by the European Union, there has been more interest in this region. In a transect from the Gulf of Taranto (Italy) to the coast of Egypt, Boetius et al. (1996) have determined microbial biomass and activity in deep-water sediments. There was phytodetrital input to these sediments, but the chloroplastic pigment equivalent (CPE) in the Ionian and Levantine Seas declined from $<6\,\mu g\,cm^{-2}$ at a depth of 200 m to $0.1\,\mu g\,cm^{-2}$ at 3000 m. Surprisingly, at 4260 m in the Pliny Trench south of Crete, and in the Hellenic Trough at 4620 and 3750 m the chloroplastic pigment equivalent rose to $10\,\mu g\,cm^{-2}$. Such high values of phytodetritus were explained by lateral transport down the adjacent steep slopes. Microbial production in the trenches exceeded that of the abyssal plains by an order of magnitude, and bacterial biomass was $0.1\,mg\,C\,cm^{-2}$ in the trenches compared to $0.05\,mg\,C\,cm^{-2}$ on the abyssal plain. Boetius et al. (1996) concluded that microbial activity in deep-sea sediments is regulated by food supply. Danovaro et al. (1993) maintained that, even in such oligotrophic waters, deep-sea sediments are not totally depleted of nutrient value.

Quantitative analyses of macrofauna in deep water of this region are few. Tselepides and Eleftheriou (1992) quantified the distribution of the macrofauna from a depth of 200 m to 985 m in relation to environmental variables. As elsewhere in the Mediterranean, biomass, abundance and diversity decreased with depth, especially below 500 m. The dominant macrofauna were polychaetes, with surface deposit feeders and carnivores dominating at the shallowest and deepest sites respectively.

Chemosynthetic-based communities are also rare in the Mediterranean. Most of the known hydrothermal sites are shallow rather than deep, being confined to shelf depths. Such sites contain no vent-specific fauna (Dando et al., 1999). Cold seeps appear to occur along the Mediterranean Ridge at depths of ~1900 m, consisting of mud volcanoes (Corselli and Basso, 1996). These mud volcanoes have a rich benthic community dominated by lucinid and vesicomyid bivalves. Detailed descriptions are not available at present.

Synecology has formed part of the study of Mediterranean ecosystems and there have been a number of significant taxonomic works published by Western European and Russian scientists. Such monographs include *inter alia* the stony corals (Zibrowius, 1980), polychaetes (Laubier and Ramos, 1973), the amphipods (Bellini-Santini, 1990) and the Tanaidacea (Kudinova-Pasternak, 1982). Results from Russian works are reviewed by Vinogradova et al. (1982) and more recently by Vinogradova (1997).

Finally, it is necessary to consider whether the Mediterranean has a true deep-sea fauna, or whether the fauna represents pseudopopulations from the Atlantic. Bouchet and Taviani (1992) rehearsed the current arguments, and concluded that the larval characteristics of the fauna rather than physical barriers such as the Gibraltar Sill control the potential colonization. The high temperatures of the deep Mediterranean are believed to inhibit successful colonization of the Mediterranean deep water, and reproduction of those species that do recruit is prevented by the high temperatures. As a result the Mediterranean populations are sterile pseudopopulations that are constantly recruited from larval inflow from Atlantic populations. Bouchet and Taviani (1992) applied the same argument to the Red Sea.

Red Sea

The fauna of the deep parts of the Red Sea is depauperate as a result of the physical nature of the environment. Because a number of the deep basins have a high content of hydrogen sulphide and poor convective mixing, a situation analogous to that in the Black Sea develops, and no fauna has yet been isolated from those deeps with a strong hydrothermal influence. Within the brine/seawater interface the sulphate-reducing bacterium *Desulphovibrio* has been isolated (Trüper, 1969). The fauna that survives in deep water outside the influence of hydrothermal brines tends to be of low biomass and diversity, owing to the low surface primary productivity and vertical flux to the seabed (Karbe, 1987; Thiel et al., 1987).

The only classic expedition to the deep Red Sea was that of the Austrian vessel *Pola* between 1895 and 1898. Only certain groups of organisms were described, including the Crustacea (Balss, 1915; Michaelson, 1918, 1921) and corals (von Marenzeller, 1907), whilst a general account of the fauna was given by Fuchs (1901). Modern investigations have included Russian studies (Murina, 1971; Monin et al., 1980, 1982); the Saudi–Sudan Red Sea Joint Commission examined the deep-water fauna as a prelude to assessing the possibilities of extracting metal-rich muds from the deeps (Karbe et al., 1981).

Thiel (1987) has produced the most recent review of the fauna of the deep Red Sea. Most major groups are present, at least in low numbers, but there are no records of phoronids, pogonophorans, hemichordates or crinoids. This may be a result of inadequate sampling, as there are no physiological or ecological aspects that would preclude these groups. The deep-water fauna is, not surprisingly, closely related to the deep-water fauna of the Indian Ocean, though the sill at Bab al Mandab limits gene flow between the deep-water populations on either side. The most significant aspect Thiel noted was the rarity of a 'true' benthic deep-sea fauna in the Red Sea. Invasion of the deep waters by shallow-water fauna may be facilitated by the relatively homogeneous warm upper water column. Shallow-water species that are found at depth include the stomatopod *Kempina zanzibarica* (Manning, 1981) and the fish *Iago omanenesis, Lophiodes mutilus*, and *Muraensox cinereus* (Klausewitz, 1981, 1983; Klausewitz and Thiel, 1982).

Amongst endemic deep-sea species are the prawns *Haliporus steindachneri* and *Parapandalus adensameri*, the amphipods *Glycerina teretis*, *Pseudamaryllis nonconstricta* and *Socarnes allectus* (Andres, 1981) and the anemone *Halcurias sudanensis* (Riemann-Zürneck, 1983). The meiofauna of the deep Red Sea (507 to 1977 m) is dominated by nematodes, followed by harpacticoid copepods and polychaetes (Thiel, 1979). Generally meiofaunal abundance decreased with depth, with the exception of the deepest station. Thiel (1979) explained this higher density as being due to downslope transport of organic matter past the steeply sloping station at 1549 m, which had the lowest meiofaunal abundance.

On a more local scale, Por and Lerner-Seggev (1966) described the zonation of fauna in the Gulf of Eilat. The two deepest zones they described were a *Palaeostoma–Hyalinoecia* community (from 360 to 500 m depth) and the pteropod ooze community from 500 m to ~1500 m. Of true bathyal species, these authors recorded the bivalve *Amussium siebenrocki,* the gastropod *Murex tribulus* and the decapod crustacean *Achaeus erythraeus.* Below 500 m the fauna is depauperate, but nematodes, polychaetes, aplacophorans and gammarid amphipods are found in low numbers. Por and Lerner-Seggev (1966) suggested that this fauna would be typical of the bathyal deep sea not affected by brines.

Caribbean Sea

The most detailed analysis of the deep-water biota of the Caribbean is the study of three stations in the Venezuela Basin described in detail in *Marine Geology* (1985). The three stations consisted of one on the western flank of the Aves Ridge dominated by hemipelagic sediments, a station dominated by turbidites in the deepest part of the basin, and a site covered by calcareous pelagic ooze in the western part of the basin (see Fig. 9.4).

The biomass and community structure of the microbiota were determined by analysis of ester-linked phospholipids from sediments at each of the three stations (Baird and White, 1985). Because of the complexity of organic molecules the biomass was measured as picomoles of the phospholipid palmitic acid (16:0) g^{-1} (dry weight). The 16:0 denotes methyl branching, 10 carbon atoms from the carboxyl end of the molecule. No significant difference was found between stations, the biomass ranging from 94 to 343 picomoles 16:0 g^{-1}. These values are some 20% of those at the North Atlantic HEBBLE site (Baird and White, 1985), and 3% of those in an estuary. From these data the calculated bacterial abundance in the surficial sediments of the Venezuela Basin was between 0.75×10^8 and 1.73×10^8 cells g^{-1} (Baird and White, 1985). Procaryotic organisms dominated the microbial community, and the fatty acids observed were believed to be indicative of aerobes.

In contrast to the microbiota, the meiofauna showed significant differences between the two station (Tietjen, 1984; Woods and Tietjen, 1985). In the hemipelagic sediments the density was 13.19±1.43 S.E. individuals cm^{-2} compared to the pelagic sediments (8.12±0.95 S.E. individuals cm^{-2}) and lowest in the turbidites (4.95±8.5 S.E. individuals cm^{-2}). Woods and Tietjen (1985) related these differences to the increased organic-carbon concentration in the hemipelagic site. The meiofauna was dominated by nematodes followed by harpacticoid copepods, both groups being commonest in the top 2 cm of the sediment.

The biomass and density of the macrofauna was significantly different among the stations (Richardson et al., 1985). In hemipelagic sediments, numbers of individuals varied from 376 to 1004 m^{-2}, between 148 and 364 m^{-2} in the pelagic sediments and between 124 and 428 m^{-2} in the turbidites. At all three stations polychaetes dominated numerically, with reasonable numbers of tanaids and isopods, particularly in the hemipelagic sediments (Richardson et al., 1985). At all stations a wide variety of fauna was found, but often in very low numbers. Biomass reflected the density at each station, the hemipelagic site having values between 287 and 392 mg wet weight m^{-2}, the pelagic sediments 22 to 127 mg wet weight m^{-2} and the turbidite 41 to 261 mg wet weight m^{-2}. Biomass was dominated by polychaetes at the turbidite and hemipelagic sites, but the biomass of this group was low at the pelagic site. Mollusca and echinoderms were sub dominant at the turbidite and hemipelagic sites, whilst the sipunculids generally dominated at the pelagic-ooze site. As with the meiofauna the higher biomass at the hemipelagic site is related to increases in organic matter, as a result of both the input of terrigenous sediment and the flux from surface production. The data have been summarized by Richardson et al. (1985) and Richardson and Young (1987).

Both density and biomass of macrofauna decreased with depth into the sediment, numbers being highest in the top 4 cm but extending down to 12 cm depth at the hemipelagic site. Biomass was concentrated in the top 8 cm of the pelagic and turbidite sediments, but was still relatively high at a depth of 12 cm at the hemipelagic site (Richardson et al., 1985).

The megafauna also showed variation in both density and biomass between stations (Richardson and Young, 1987). Density of megafauna was highest at the pelagic-sediment site, although biomass, particularly that of sponges, was significantly higher at the hemipelagic site. Apart from sponges, the megafauna was dominated by anthozoans, holothurians and decapods. There was no significant difference in megafaunal densities between the three sites. Briggs (1985) has examined the feeding potential of two species of seastar and two species of holothurian from the three different sedimentary provinces in the Venezuela Basin. On the pelagic and hemipelagic sediments, the sediment composition within the gut of the echinoderms was similar to that of the top 5 mm of sediment, suggesting unselective deposit-feeding. On the turbidite, the gut contents suggested that the echinoderms fed on recently-settled faecal pellets from midwater or surface production, which indicates selective feeding. Wolff (1976, 1979) has analysed the fauna associated with plant debris in the deep Caribbean. Isopods were the commonest group, but there were significant numbers of gastropods, polychaetes and other taxa. Some species were using the plant material as food, whilst others were using it as a substratum or shelter (Wolff, 1976).

Anderson et al. (1985) described the entire fish fauna collected from below 2000 m in the Caribbean. These authors reported 35 species of demersal fish, dominated by Ophidiiformes (17 species) and the alepocephalids (7 species), and recognized the fish fauna of the Caribbean as being a depauperate component of the world's abyssal fish fauna.

Gulf of Mexico

With the exception of the cold-seep communities found along the Mediterranean Ridge, all the deep water communities of the peripheral seas considered so far have relied on input from surface production for their energy source. As a result these communities are considered allochthonous. By contrast, the Gulf of Mexico has both allochthonous and autochthonous communities. The autochthonous communities are at cold seeps on the Louisiana Slope and at the base of the Florida Escarpment, and their energy is derived from chemosynthesis driven by hydrogen sulphide and methane in sediments (see Chapter 4). The species of the two community types are quite distinct, although there are some species overlaps. The Gulf of Mexico has received much general attention, particularly in the late 19th century, when the US steamship *Albatross* sampled extensively. These cruises resulted in a series of monographic treatments of the samples and the reader is referred to Menzies et al. (1973) for a list of publications.

Deep-water allochthonous communities

Rowe and Menzel (1971) and Rowe et al. (1974) determined the biomass of macrofauna at a series of stations along the northern slope of the Gulf of Mexico, as well as five stations at abyssal depths. At the slope stations mean density was between 500 and 600 individuals m^{-2}, whereas at the abyssal stations in the eastern Gulf mean density was 19 individuals m^{-2} with a mean biomass of 31 mg m^{-2}, and in the western Gulf the corresponding figures were 112 individuals m^{-2} and 82 mg m^{-2}, respectively. These values are far less than those at corresponding depths in the Northwest Atlantic (Chapter 5; see also Rowe et al., 1974). These means are proportional to surface productivity, the offshore rate of decrease in benthic biomass being proportional to the offshore decrease in surface primary production.

More recently data have become available for the deep-water fauna from Mexican waters in the western Gulf of Mexico (Escobar-Briones and Soto, 1993; Escobar-Briones et al., 1999). Escobar-Briones and Soto (1993) have provided a list of the dominant megafauna and macrofauna below a depth of 200 m. Many of the species are found in the Atlantic also, although a number of species have subspecies endemic to the Gulf of Mexico. In a subsequent analytical paper (Escobar-Briones et al., 1999), infaunal macrobenthic density was analysed along a depth gradient from the shelf break to abyssal depths eastwards along the 24ºN parallel of latitude. Density increased at bathyal depths, the highest density (mean 2713 individuals m^{-2}) being found at 1250 m, immediately below the oxygen minimum. Density was highly variable on the abyssal plain (means from 794 to 1669 individuals m^{-2}). The main structuring factors along this portion of the slope of the Gulf of Mexico were surface production, thermal stratification and the oxygen minimum zone.

Autochthonous communities

Communities fuelled by either methane or hydrogen sulphide are found from depths of ~500 to 2200 m from the Mississippi Fan westwards along the slope to bathyal depths off Texas (Kennicutt et al., 1985; MacDonald et al., 1990a). Chemosynthetic communities are also found at the base of the Florida Escarpment, where sulphide-rich hypersaline waters seep out at a depth of ~3000 m (Paull et al., 1984).

Dominating these chemosynthetically-based communities is an undescribed species of the vestimentiferan *Lamellibrachia* (Kennicutt et al., 1988; MacDonald et al., 1989). This organism is found as dense bushes at Bush Hill and in Green Canyon, but has not been observed in the Mississippi Canyon area. Large clumps of *Lamellibrachia* sp. are particularly well established in the Green Canyon area. Where *Lamellibrachia* occurs there is often the co-occurrence of a second vestimentiferan *Seepiophilia jonesi* (MacDonald et al., 1989). *S. jonesi* tends to form irregular small clumps at the base of the larger *Lamellibrachia* ‘bushes’. In contrast to vestimentiferans found at hydrothermal vents, both these vestimentiferan species are supported by hydrogen sulphide diffusing up the inside of the worm tube to the trunk, rather than being absorbed through the tentacles. Fisher et al. (1997) have shown that *Lamellibrachia* grows very slowly (in contast to vestimentiferans at hydrothermal vents), averaging 0.77 cm y^{-1}, and recently Bergquist et al. (2000) have suggested that this species, with a life span of 170 to 250 years, is the longest-lived metazoan on earth. *Lamellibrachia* also supports an epifaunal community. The bivalve *Acesta bullisi* (MacDonald et al., 1989), a species of *Echinus* (personal observation), and a recently described sponge *Ectyomyxilla methanophila* (Maldonado and Young, 1998) all occur on the tube of *Lamellibrachia*. Other associated fauna include the crabs *Bathyplax typhla*, *Geryon* sp. and *Rochinia crassa* and the giant isopod *Bathynomus giganteus*.

The other dominant organisms in this region include the seep mussel *Bathymodiolus childressi*. The taxonomy of this genus has recently been clarified. It has been suggested that, in the Gulf of Mexico, at least three species exist, one at Bush Hill (600 m) and Alaminos Canyon (2222 m), and two at the base of the Florida escarpment (3314 m). There is possibly a fourth at the oil-drilling station Garden Banks-386 (650 m), but this may be more closely related to the genus *Idas* (Craddock et al., 1995). All the *Bathymodiolus* species are able to use methane as an energy source (Fisher et al., 1993; Nix et al., 1995), although there is some evidence that they are also able to use suspended particulate organic matter (Page et al., 1990). The fine-scale distribution of mussels suggests that aggregations of living mussels may form clusters up to 5 m diameter, separated by sediment or by clumps of dead and disarticulated mussels (MacDonald et al., 1990b). A truly remarkable environment on the Louisiana slope is the Brine Pool (MacDonald et al., 1990c), which is 22 m long, 11 m wide and some 20 m deep. The salinity is ~121, and there is a strong pycnocline between the pool and overlying seawater. It is surrounded by a ‘halo’ of *Bathymodiolus* and occasional vestimentiferan tubes. Associated invertebrates include the gastropod *Bathynerita naticoidea*, the decapods *Alvinocaris stactolitha* and a species of *Munidopsis,* and an orbinid worm *Methanoaricia dendrobranchiata* (personal observation).

On other parts of the Louisiana slope additional chemosynthetically-supported bivalves include *Calyptogena ponderosa* and *Vesicomya cordata,* found at seeps from Garden Banks off Texas to the western part of the Green Canyon site off Louisiana (Rosman et al., 1987; Kennicutt et al., 1988).

Underlying many of the sediments of the Louisiana slope are gas hydrates, or solid methane (Chapter 4; see also Brooks et al., 1986). Inhabiting this exceptional environment is a hesionid worm *Hesiocaeca methanicola* (Desbruyères and Toulmond, 1998). The physiology of this remarkable organism is still being elucidated (C.R. Fisher, personal communication).

The last seep environment in the Gulf of Mexico is at the base of the Florida Escarpment (Paull et al., 1984). This seep is at a depth of approximately 3000 m, and the associated chemosynthetic community is driven by sulphide-rich water seeping out of the bedrock. The fauna consists of patches of vestimentiferan tubeworms (*Escarpia laminata*) and mussel beds with associated limpets, holothurians, ophiuroids and anemones. Cary et al. (1989) have shown that the chemosynthesis is driven by two sources of hydrogen sulphide. The first is geothermal from groundwater leaching, and the second is microbial sulphide produced *in situ.* There is also methane seepage. *Escarpia laminata* relies on sulphide oxidation, whilst *Bathymodiolus* relies on methane oxidation.

In contrast to the other peripheral seas where the benthic biomass at the deep-sea bed is determined by the vertical flux from overlying waters and hence surface production, the benthic biomass in certain parts of the Gulf of Mexico is higher than would be predicted by surface production owing to energy availability for chemosynthetic production.

Seas of the Indonesian Archipelago

No cruises to the Indonesian archipelago have been dedicated to examining the deep-sea metazoan fauna. Ecology of shallow water has been dealt with extensively by Tomascik et al. (1997). Both the *Challenger* and *Galathea* sampled in this region. In the Banda Sea at Station 195, depth 2850 m, *Challenger* recovered 26 metazoan species, whilst in the Sulawesi Sea (then known as the Celebes Sea) 21 species were recovered at Station 198 in 4300 m of water (Murray, 1895). The *Galathea* sampled a single station (Station 450, 4940 to 4970 m) in the Sulawesi Sea, and recovered five individuals of the rare brotulid fish *Typhlonus nasus* (Nielsen, 1966). Since that time additional knowledge of the deep-water fauna of this region has been scanty. There is limited information from the few deeper stations of the *Siboga* and *Snellius* cruises and some information from the *Naga* cruises. For a list of the monographs resulting from the *Siboga* cruise the reader is referred to Menzies et al. (1973), although only a few observations were from deep water. Fujita and Ohta (1988) reported the association of the ophiuroid *Asteronyx loveni* with the gorgonian *Radicipes* sp. from a depth of ~960 m in the Flores Sea. More recently the KARUBAR French–Indonesian expedition (Crosnier et al., 1997) has provided some reports on the deep-water fauna (Norman et al., 1997).

There has been some recent interest in the protozoan fauna in the deep sea of this region. Miao and Thunell (1993) zoned the Sulu Sea according to the dominant Foraminifera. Number and species diversity decreased with depth, and four faunal assemblages were recognized. At depths of <1400 m, the *Uvigerina* assemblage was found. From 1400 m to 2000 m is found the *Pyrgo murrhina* assemblage. Below 2200 m are two assemblages dominated by *Oridorsalis umbonatus.* This zonation is driven by the organic-carbon content and oxygen penetration into the sediments. Rathburn and Corliss (1994) showed that Foraminifera had even finer microhabitat preferences than those described by Miao and Thunell, with different species occupying different levels within the sediment.

Although not in the deep sea, there has been an intriguing suggestion recently (Barber et al., 2000) that there may be the marine equivalent of Wallace's line through the shallow water of the Indonesian seas. It would be of great interest to see if this faunal boundary extended into deep water.

Sea of Japan

Previous reviews of the fauna of the Sea of Japan (Zenkevitch, 1963; Nishimura, 1966, 1968, 1969, 1983) have suggested that the deeper parts do not have a true deep-sea fauna, but rather have a fauna composed of cold-adapted eurybathic species with affinities to Arctic forms (Nishimura, 1969). The bottom-living fauna of the Sea of Japan decreases markedly in biomass with depth. Zenkevitch (1963) recorded only five macrofaunal species from below 3000 m and only 25 species between 2000 and 3000 m (Terazaki, 1999). Down to 2000 m the fauna is dominated by the echinoderms, *Ctenodiscus crispatus, Luidiaster tuberculatus* and *Thaumatometra tenuis,* the cnidarians *Caryophyllia clavus, Lafoeina maxima* and *Primnoa resdaeformis pacifica,* and the polychaetes *Harmothoe impar, Jasmineria pacifica* and *Nephthys longisetosa,* as well as decapods and molluscs, particularly the Buccinidae. Nishimura (1966) referred to this community as the 'taraba community III'. He believed that the 'taraba community III' extended from about 300 m to 1500 m, below which the community petered out. Below 2000 m the qualitatively and quantitatively poor fauna included a variety of polychaetes, the brittle star *Ophiura leptoctenia*, and the molluscs *Axinus* sp. and *Pecten randolfi,* as well as a number of peracarid crustaceans (Zenkevitch, 1963). The main characteristic of this faunal group is its apparent evolutionary youth since, owing to the young geological age of the Sea of Japan, it has not had time to acquire an endemic character of its own. Zenkevitch (1963) considered the polychaetes *Harmothoe derjugini* and *Tharyx pacifica*, the echinoderm *Pedicellaster orientalis* and the decapod *Chionoecetes angulatus bathyalis* as the only true endemic forms in the Sea of Japan. Nishimura (1966) was more conservative, suggesting that only the deep-sea polychaete *H. derjugini* is truly endemic. All other species found in the deep waters of the Sea of Japan are eurybathyic forms also found in the cold waters of the Pacific and Bering Sea. A number of boreal forms have also invaded the Sea of Japan. Vinogradov (cited in Zenkevitch, 1963) identified the low temperature and salinity of the Sea of Japan rather than its recent history as causes of the low diversity. Nishimura referred to the deep fauna as a *pseudo-abyssal fauna* and supported Vinogradov in suggesting that the unique cold temperatures and high salinity account for the penetration and success of a cold-adapted secondary deep-sea fauna, and the failures of archaic deep-sea faunas to colonize the deep waters, especially after periods of anoxia (Terazaki, 1999).

The deep-water fish of the Sea of Japan are also characteristically cold-water species from the families Cottidae, Liparidae, Lumpenidae, Pleuronectidae and Zoarcidae (Nishimura, 1968, 1983). Some 20 species have been recognized (Zenkevitch, 1963); Nishimura (1968) listed 8 deep-water zoarcids, 12 deep-water cottids and 16 deepwater species of Liparidae. The poverty of invertebrate species is reflected in the lack of diversity of the fish fauna. Of particular interest to Nishimura (1968) was the poverty of macrourids in the Sea of Japan compared to deep waters on the Pacific side of Japan. Approximately 50 species of macrourids are known from off southern Japan in deep water, whereas in the Sea of Japan there were only one or two species, about which there was some taxonomic uncertainty. The same feature is seen in the Myctophidae where some 33 species are seen on the Pacific side of Japan and only two within the Sea of Japan (Nishimura, 1968). These two species were also believed to be recruited by larval transport from the East China Sea.

Sea of Okhotsk

Benthic biomass in the Sea of Okhotsk is patchy. The biomass and species composition is particularly affected by the low oxygen concentration. Zenkevitch (1963) identified two zones of deep-sea benthic fauna in the Kurile Basin. The deepest part of the basin is dominated by a zone of bottom feeders including the polychaete families Capitellidae and Maldanidae, the holothurian family Molpadidae, the echinoid *Brisaster* and the asteroid *Ctenodiscus.* Mean biomass in this zone is ~102 $\mathrm{g\,m^{-2}}$. The main part of the Kurile Basin is dominated by immobile filter feeders including the pennatulids *Pavonaria* and *Umbellula*, crinoids, the ascidian *Culeolus*, sabellid worms and the pogonophoran *Lamellisabella zachsi.* In this zone the biomass is at its lowest at ~30.5 $\mathrm{g\,m^{-2}}$. The low benthic biomass may be related to the particularly low surface primary production in the central part of the Sea of Okhotsk. Much of this fauna has close links with those at similar depths in the Pacific. A particular feature, noted by Zenkevitch (1963) is the high incidence of gigantism amongst deep fauna in the Sea of Okhotsk, the barnacle *Balanus evermanni,* the holothurian *Psychropotes raripes* and the polychaete *Potamilla symbiotica* all displaying gigantism.

The benthic foraminiferal communities of the Sea of Okhotsk have been described in detail (Saidova, 1997). In the Kurile deeps these communities are dominated by *Globobulimina auriculata, Trochammina abyssorum* living in the deepest parts on sediments with an organic content reaching 2%, and *Bolivina pseudodecussata, Elphidium batialis* and *Miliolinella recenta* living at depth, but on sediments with <1.5% organic carbon.

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Chapter 10

LARGE-SCALE SPATIAL AND TEMPORAL PATTERNS OF DEEP-SEA BENTHIC SPECIES DIVERSITY

Carol T. STUART, Michael A. REX and Ron J. ETTER

INTRODUCTION

The discovery of high species diversity in the deep-sea benthos by Hessler and Sanders (1967) required fundamental changes in the understanding of marine biodiversity. Sanders (1968) synthesized patterns of diversity among coastal and deep-sea communities, and proposed the stability–time hypothesis as a new unifying explanation. This very influential idea is the principal paradigm that shaped the course of modern deep-sea ecology, and represents the logical starting point for a consideration of deep-sea biodiversity. Two key assumptions of the theory are that the deep-sea environment is ecologically stable, allowing a high level of coexistence through competitive niche partitioning, and that this condition has persisted over a geological time span sufficient for extensive evolutionary diversification. Much of contemporary deep-sea research has been directed at evaluating these assumptions, and identifying the scales at which ecological factors and historical processes operate to control diversity.

The assumption of environmental stability in the deep sea has been greatly modified by recent exploration. Species diversity and composition have been shown to vary locally (Grassle and Maciolek, 1992), regionally (Cosson-Sarradin et al., 1998) and globally (Rex et al., 1993, 2001; Wilson, 1998), suggesting changes in the environmental factors determining community structure at all spatial scales. The benthic landscape, far from being monotonous as once assumed, is revealed to be a topographically complex patchwork of distinctive habitats (MacDonald et al., 1988; Van Dover, 1990; Mellor and Paull, 1994). Population fluctuations and reproductive cycles in the deep benthos are linked to seasonal changes in surface production, mediated through surface–benthic coupling (Gage and Tyler, 1991; Young and Eckelbarger, 1994). Catastrophic submarine landslides (Rothwell et al., 1998) and ash from volcanic eruptions (Hess and Kuhnt, 1996) can obliterate huge areas of the seafloor. Current-driven “benthic storms” that resuspend sediments are regular features of some deep regions (Gage, 1997). The deep sea is a complicated, dynamic environment, and one that functions as an integral part of the global biosphere.

New advances in paleoceanography are changing the assumption of a long history of stability or even continuous occupancy of the deep sea. The deep sea experienced a global mass-extinction event as recently as the Paleocene (Kennett and Stott, 1991), and developed large-scale gradients of diversity as the planet cooled during the Cenozoic (Thomas and Gooday, 1996). Much of the vast deep-sea environment may be relatively new compared to terrestrial and shallow-water ecosystems, and may have changed substantially during the last 50-million-year “ice-house” era. During the Pliocene and Pleistocene, the deep-sea environment is now known to have fluctuated dramatically in temperature, in nutrient input, and in the position and intensity of the deep thermohaline circulation, with the waxing and waning of polar ice sheets (Raymo et al., 1998). These oscillations are reflected in microfossil communities recovered in seabed cores (Cronin and Raymo, 1997).

In this chapter, we review the basic features of large-scale geographic patterns of diversity documented during the last thirty years of exploration, and the changes of environment and community structure through geological time that are emerging from paleoceanographic studies of the last decade. They

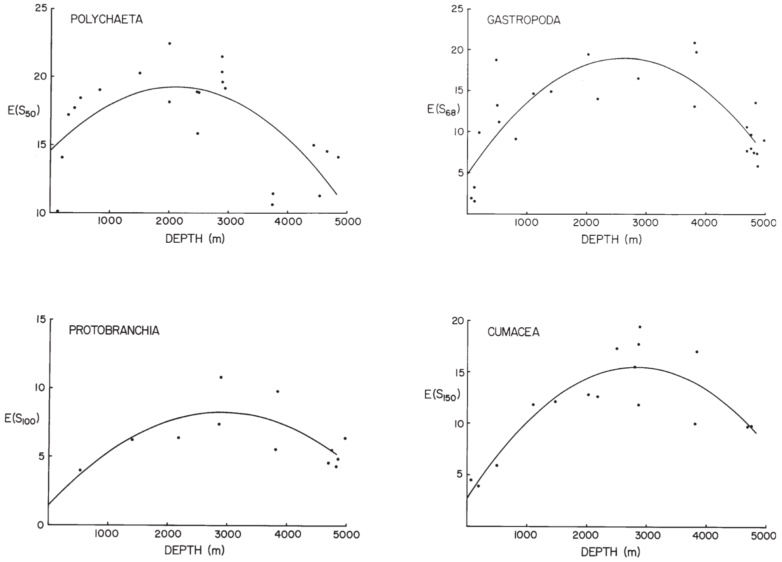

Fig. 10.1. Patterns of species diversity with depth for the macrofauna collected by epibenthic sleds in the western North Atlantic. Diversity is measured using Hurlbert's (1971) expected number of species $E(S_n)$. All groups show a unimodal diversity–depth pattern, with maximum diversity at intermediate depths. Reprinted with permission from Rex (1983) in: *The Sea,* Vol. 8, G.T. Rowe (Editor), pp. 453–472. Copyright 1983, John Wiley and Sons, Inc.

provide only an incomplete picture of biogeography in the deep sea, one that will undoubtedly improve and change with further exploration. However, it is already a view that puts deep-sea diversity and the notion of spatio-temporal stability in a more relative context. A central and enduring tenet of Sanders' (1968) stability–time hypothesis is that community structure is shaped by two interrelated forces: the historical evolutionary development of biotas, and the contemporary ecological milieu. We discuss how both phenomena may affect large-scale patterns of diversity in the deep-sea benthos.

CONTEMPORARY SPATIAL PATTERNS

Bathymetric gradients

Patterns of diversity

Bathymetric gradients of species diversity are the best-known geographic patterns of community structure in the deep-sea benthos. Depth gradients are the marine counterparts to elevational gradients in terrestrial environments. They are especially informative because they parallel steep environmental gradients over a relatively short geographic span. Such basic features as temperature, hydrostatic pressure, nutrient input, light intensity, sediment type and current dynamics vary with depth (Gage and Tyler, 1991). Abundance and biomass decrease exponentially with depth from the upper slope to the abyss because of the decrease in nutrient input from overhead production (Rowe, 1983; Thistle et al., 1985; Rowe and Pariente, 1992; Paterson et al., 1994). Deep-sea animals show genetic (Chase et al., 1998) and phenotypic (Rex and Etter, 1998; Rex et al., 1999) clines with depth, and appear to be adapted biochemically to specific depth regimes (Hochachka and Somero, 1984). In consequence, there is a rapid depth-correlated turnover in species composition (Carney et al., 1983). The trophic make-up of major taxa changes with depth as well (Rex, 1977; Jumars and Fauchald, 1977; Cosson et al., 1997). Species diversity also changes along depth-related environmental gradients.

The stability–time hypothesis was based, in part, on the observation that species diversity of bivalves and polychaetes (combined) increased along a gradient of decreasing annual temperature variation down the continental slope in the western North Atlantic (Sanders, 1968). When the analysis was later extended to other taxa and greater depths, bathymetric gradients of diversity in the western North Atlantic appeared to be unimodal (Rex, 1973, 1981). Diversity increased to intermediate depths as Sanders (1968) had shown, but then decreased toward the abyss. Examples of this are shown in Fig. 10.1 for four macrofaunal groups:

the bivalves, gastropods, cumaceans and polychaetes. The depth for peak diversity estimated from the regression curves varies among taxa from around 2000 to 3000 meters. A similar pattern was found in the megafauna (Rex, 1981, 1983).

Allen and Sanders (1996), using a larger database, reported on depth patterns of bivalve diversity in the western North Atlantic. Bivalves are abundant in the deep sea, but have comparatively low species diversity (Fig. 10.1). For example, thirty epibenthic sled samples taken in the western North Atlantic yielded nearly 38 000 individuals, but only 36 species. The deep-sea bivalve fauna has been exceptionally well characterized, in that diversity appears to have reached an asymptote with continued sampling (Allen and Sanders, 1996), and, therefore, is probably a reasonable approximation to the actual regional species pool. The analysis by Allen and Sanders (1996) also indicated a unimodal pattern of diversity, with peak diversity at lower bathyal depths.

It is important to note that these studies are based on data from qualitative sampling gear – epibenthic sleds (Hessler and Sanders, 1967) and anchor dredges (Sanders et al., 1965). Thus, diversity was measured over relatively large spatial scales; epibenthic sleds, for example, are towed for about a kilometer and sample on the order of 1000 m^2 of the bottom. These sampling methods obscure the spatial dispersion of individual species. Collecting devices that sample on large scales could traverse and combine together smaller patches with distinctive faunas. If small-scale patch structure varies with depth, the shape of diversity–depth gradients would reflect this. Therefore, unimodal trends, like those shown in Fig. 10.1, could be an artifact of changes in dispersion patterns on smaller scales.

Jumars (1976) first drew the attention of deep-sea biologists to the problem of scale – later recognized as the central problem in ecology (Levin, 1992). The development of the box corer by Hessler and Jumars (1974) was a major advance in the understanding of scale in the deep-sea benthos. The box corer collects a relatively undisturbed 0.25 m^2 area of sediment with the animals still in position, making it possible to compare diversity on small scales that are more relevant to the minute organisms that inhabit deep-sea sediments. It also provides an effective way to explore patterns of community structure among subcores of a single box corer (centimeter scales), and among core samples spaced different distances apart (meters, kilometers and so on) in a spatial array. Diversity can be measured as actual species densities (number of species per unit area) rather than estimated by artificially normalizing large samples. The number of coexisting species can be correlated directly with animal abundance and with sediment characteristics from the same core samples. Deployment of box corers greatly increased understanding of spatial dispersion on small scales (Jumars and Eckman, 1983; Gage and Tyler, 1991). It also made it possible to study bathymetric patterns of diversity by using sampling scales that capture microhabitat patchiness.

The Atlantic Continental Slope and Rise Study off the east coast of the United States was the most intensive box-corer sampling study ever undertaken (Blake et al., 1985, 1987; Maciolek et al., 1987a,b). Sampling was carried out in three geographic regions: south of New England, east of New Jersey, and off the Carolinas. The two more northerly regions showed similar unimodal patterns of diversity and shared much of the same fauna (Etter and Grassle, 1992; Rex et al., 1997). The combined data for these two regions representing the whole macrofaunal community are plotted in Fig. 10.2a. Diversity peaks at around 1500 meters, roughly 1000 meters shallower, on average, than for separate groups collected by qualitative sampling near the same geographic area (Fig. 10.1). Hence, the general unimodal diversity–depth pattern seems to hold, but maximum diversity is shifted to shallower depths. No sampling was carried out below mid-bathyal depths.

Why peak diversity should appear somewhat shallower in the box-corer study remains unclear. The two sets of diversity curves (Figs. 10.1 and 10.2a) are not directly comparable. The data from qualitative sampling gears (Fig. 10.1) are for only a subset of deep-sea benthic taxa, whereas the box-corer data represent the entire benthic community. The sizes to which samples are normalized differ between the two types of samples. The shape of the fitted curve for the box-corer study (Fig. 10.2a) represents only the upper bathyal region. It is clear from Fig. 10.1 that abyssal samples can strongly affect the overall diversity–depth pattern. The most abundant and diverse group, the polychaetes, has the shallowest peak in diversity of the four groups shown in Fig. 10.1, perhaps either because their maximum diversity actually is shallower, or because the data are from anchor dredge samples, which typically collect over a smaller area than do the epibenthic sleds used to collect the other three groups.

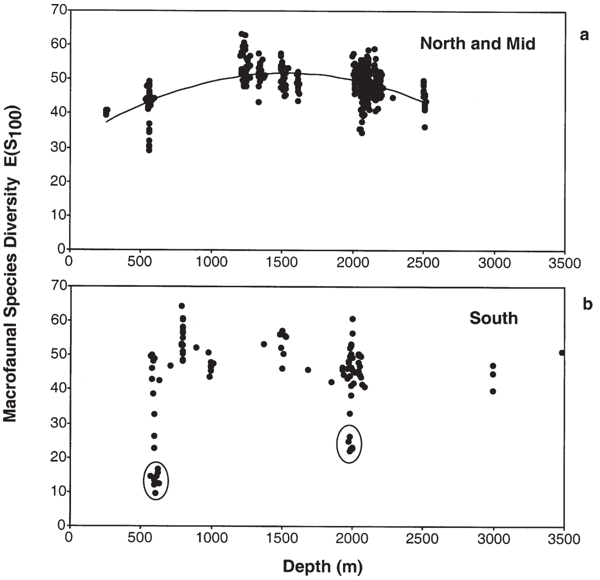

Fig. 10.2. (a) The relationship between macrofaunal diversity and depth in box-corer samples collected from south of New England and off the mid-Atlantic coast of North America by the Atlantic Continental Slope and Rise Study (Maciolek et al., 1987a,b). Estimates of diversity were normalized to 100 individuals by using Hurlbert's (1971) expected number of species. Diversity shows a unimodal trend with depth. (b) The relationship between macrofaunal diversity and depth in box-corer samples collected from the southeast Atlantic coast of North America by the Atlantic Continental Slope and Rise Study (Blake et al., 1985, 1987). Estimates of diversity were normalized to 100 individuals by using Hurlbert's (1971) expected number of species. There is no significant diversity trend with depth. Encircled clusters of samples with unusually low diversity at upper and mid-bathyal depths were taken off Cape Hatteras, where sedimentation rates of phytodetritus are high. Figure adapted from Rex et al. (1997) in: *Marine Biodiversity: Patterns and Processes*, R.F.G. Ormond, J.D. Gage and M.V. Angel (Editors), pp. 94–121. Copyright 1997, with permission from Cambridge University Press.

If polychaetes have a shallower peak than other groups, their dominance in the benthic fauna would tend to shift the peak for the fauna as a whole to shallower depths. It is also possible that larger qualitative sampling devices combine patches in a way that inflates diversity at mid-bathyal depths. The most important observation is that bathymetric patterns of diversity in the western North Atlantic have a unimodal shape irrespective of the sampling scale.

The unimodal diversity–depth trend of the western North Atlantic south of New England does not appear to be universal. Other regions are much less well known in terms of depth coverage, intensity and scale of sampling, and documentation of biogeographic patterns in different taxa. However, sufficient data exist to indicate inter-regional variation in bathymetric patterns of diversity. Unimodal patterns have been found for polychaetes in the Northeastern Atlantic (Paterson and Lambshead, 1995) and the Equatorial Atlantic (Cosson-Sarradin et al., 1998). Gastropods (Rex et al., 1997) and bivalves (Allen and Sanders, 1996) show a variety of patterns in different basins of the North and South Atlantic, even including what seems to be an inverted unimodal trend for gastropods in the eastern North Atlantic, with minimum diversity at intermediate depths (Fig. 10.3). Isopod diversity decreases with depth in the Norwegian Sea (Svavarsson et al., 1993). Amphipod diversity increases with depth from the continental shelf to 1200 meters in the Atlantic south of Iceland, but shows no clear pattern over the same depth range north of Iceland in the Norwegian Sea (Weisshappel and Svavarsson, 1998). Diversity of the macrofauna in the southernmost region sampled in the Atlantic Continental Slope and Rise Study shows no significant pattern of diversity with depth (Fig. 10.2b), primarily because samples were taken from four distinct areas that are horizontally separated and represent very different environments supporting different levels of diversity at similar depths (Blake and Hilbig, 1994). Other examples of depth-related patterns have been reported by Gooday et al. (1998), Levin and Gage (1998), Paterson et al. (1998), Vetter and Dayton (1998), and Wilson (1998).

Even the best-studied bathymetric patterns of diversity exhibit a great deal of variation in local diversity (Figs. 10.1, 10.2a,b). Characterizing diversity patterns for the deep-sea benthos in a way that is accurate enough for meaningful interpretation clearly requires intensive sampling over a broad depth range (preferably including both bathyal and abyssal regions), consistent collecting techniques, a uniform taxonomic approach, and standardized analytical methods for estimating diversity (Rex et al., 1997).

Potential causes of diversity patterns along depth gradients

This discussion of causes focuses on the unimodal patterns observed in the western North Atlantic, because they are the best documented and have the greatest potential to generate hypotheses of general significance. One set of explanations for these patterns involves the possible role of biological interactions in mediating the effects of productivity. Productivity, in this case, refers to the rate and pattern of nutrient input to the benthos from sinking phytodetritus

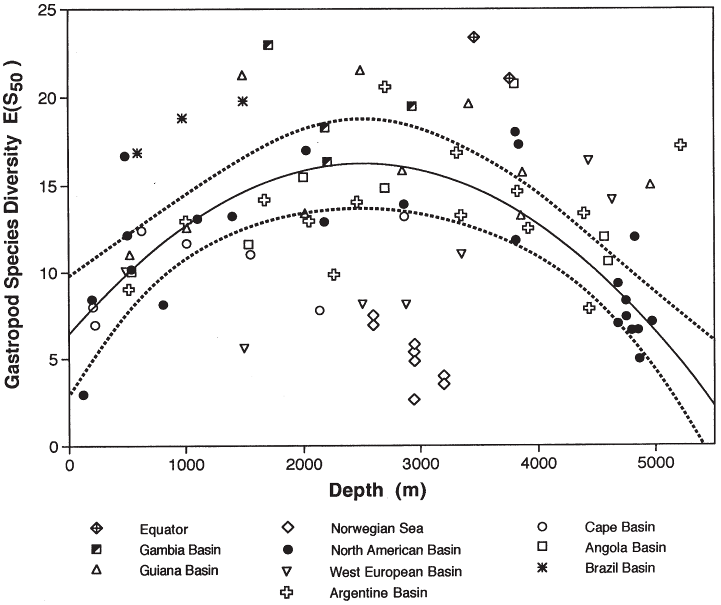

Fig. 10.3. The relationship between gastropod diversity and depth in epibenthic sled samples collected from 10 basins in the North Atlantic and the Norwegian Sea. All samples were collected by an epibenthic sled from bathyal depths (500–4000 m). The regression line and 95% confidence limits are for samples from the North American Basin. There appears to be variation in both the overall level and pattern of diversity among basins. Reprinted from Rex et al. (1997) in: *Marine Biodiversity: Patterns and Processes,* R.F.G. Ormond, J.D. Gage and M.V. Angel (Editors), pp. 94–121. Copyright 1997, with permission from Cambridge University Press.

originating from surface production. Rex (1976, 1977) proposed that both competition (Sanders, 1968) and predation (Dayton and Hessler, 1972) operate to cause the unimodal diversity–depth pattern, and that their relative importance depends on the rate and stability of production which varies with depth. Scarce food resources in the abyss might inhibit the development of upper trophic levels, and enhance competitive exclusion among prey populations. At intermediate depths, relatively moderate and stable nutrient input supports a diverse upper trophic level, which may, in turn, exert a diversifying influence on the community. At upper bathyal depths, diversity might be depressed by seasonality of nutrient input causing fluctuations in prey populations, and limiting the ability of predators to diversify by specialization in diet. A similar association of high sedimentation rates of phytodetritus with low diversity is found in the southern region of the Atlantic Continental Slope and Rise Study (Fig. 10.2b).

A better integrated explanation, using the same basic ecological variables, was proposed by Huston (1979). According to his dynamic-equilibrium model, population growth rates determine the rate at which communities approach competitive equilibrium, where superior competitors will exclude inferior species and thereby decrease diversity. Disturbance, either biotic or abiotic, interrupts a community's approach to competitive equilibrium, reducing exclusion and promoting coexistence. Both disturbance (Thistle, 1988; Vale and Rex, 1988; Gage, 1997; Thistle and Levin, 1998) and competition (Rex et al., 1988) are known to affect deep-sea communities, but little is known about how these processes vary with depth. Because deep-sea organisms rely on nutrients sinking from surface production, population growth rates should be a function of nutrient flux, which declines exponentially with depth (Rowe and Pariente, 1992; Turley et al., 1995). Therefore, rates of competitive exclusion should decline exponentially with depth. Disturbance is more difficult to estimate because there is no simple analog that has been measured along a depth gradient, and it is unclear what constitutes a disturbance. If predation pressure can be inferred from the depth-related diversity patterns of predatory snails, megafaunal diversity, and fish diversity (Rex, 1983), then biological disturbance varies parabolically with depth. Combining these two gradients provides predictions that are consistent with the bathymetric patterns observed in the western North Atlantic.

Bathymetric patterns in diversity may also reflect gradients in sediment characteristics. Etter and Grassle (1992) suggested that the nature of the sediments should play an important role in structuring deep-sea communities, because deposit feeders rely on sediments for nutrition and comprise the overwhelming majority of species (Sanders and Hessler, 1969; Jumars and Gallagher, 1982). They argued that, if deposit feeders in the deep sea partition the sediments with respect to size, as do shallow-water relatives (Fenchel et al., 1975; Fenchel and Kofoed, 1976; Whitlatch, 1980; Self and Jumars, 1988), species diversity in part may be a function of sediment particle diversity (hereafter referred to as sediment diversity) because it provides greater diversity in food resources or greater habitat complexity. Using 558 box-corer samples collected from bathyal depths (250–3029 m) in the western North Atlantic as part of the Atlantic Continental Slope and Rise Study, Etter and Grassle (1992) found a strong positive relationship between macrofaunal diversity and grain-size diversity of the silt fraction, the particle size typically consumed by deposit feeders (Taghon et al., 1978; Whitlatch, 1980; Taghon, 1982; Self and Jumars, 1988). More importantly, when sediment diversity was held constant statistically, macrofaunal diversity did not vary with depth, suggesting that the unimodal pattern documented in the western North Atlantic may largely reflect a gradient in sediment diversity. This documented correlation does not prove whether the relationship is causal; however, unlike many other hypotheses for spatiotemporal patterns of diversity in the deep sea, the sediment-diversity hypothesis can be easily tested experimentally.

It seems likely that both nutrient flux and particle size may be important in ultimately explaining why diversity varies bathymetrically, since the nature, amount and diversity of resources should exert a powerful influence on the number of species within soft-sediment communities.

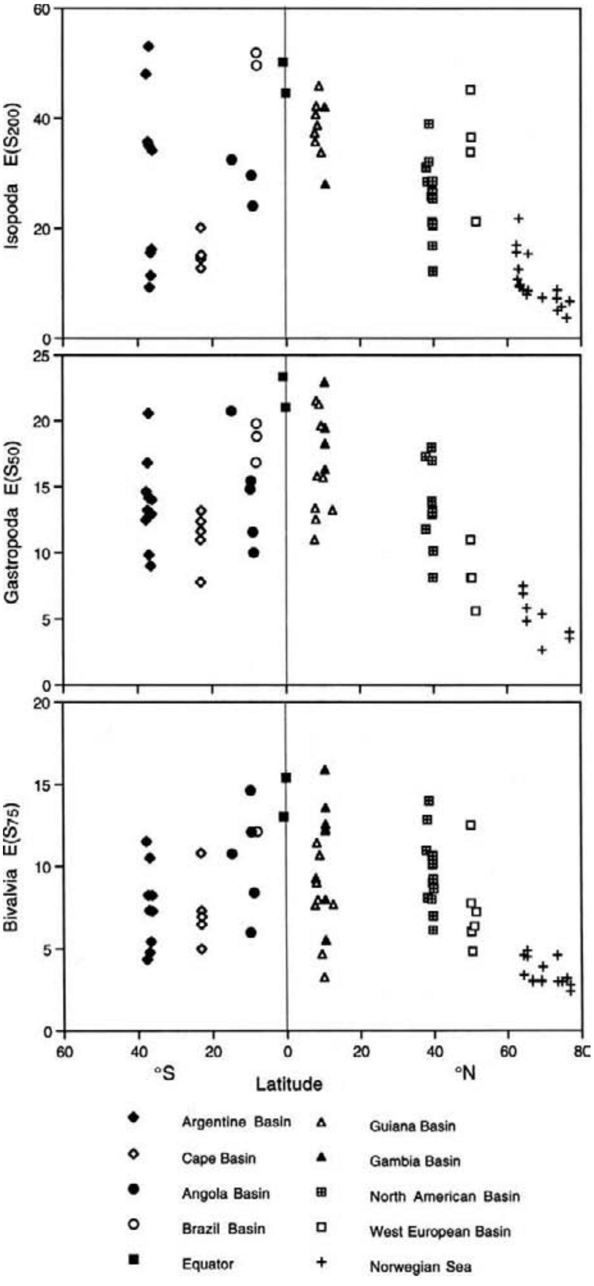

Fig. 10.4. The relationship between species diversity and latitude for epibenthic sled samples of Isopoda, Gastropoda and Bivalvia in the North and South Atlantic Ocean and the Norwegian Sea. All samples were collected by an epibenthic sled from bathyal depths (500–4000 m). Diversity is calculated as Hurlbert's (1971) expected number of species $E(S_n)$. All three groups show significant decreases in diversity in the North Atlantic and the Norwegian Sea, and interregional variation in the South Atlantic. For the statistical analysis, see Rex et al. (1993). Reprinted with permission from *Nature* (Rex et al., 1993, vol. 365, pp. 636–639). Copyright (1993) Macmillan Magazines Limited.

Latitudinal gradients

Patterns of diversity

Latitudinal species-diversity gradients are well known for marine biotas, in both pelagic (McGowan and Walker, 1993; Dodge and Marshall, 1994; Angel, 1997) and coastal (Fischer, 1960; Roy et al., 1994, 1998; Culver and Buzas, 1998) habitats. Recently, they have also been detected in the deep sea (Rex et al., 1993, 1997; Poore and Wilson, 1993; Stuart and Rex,

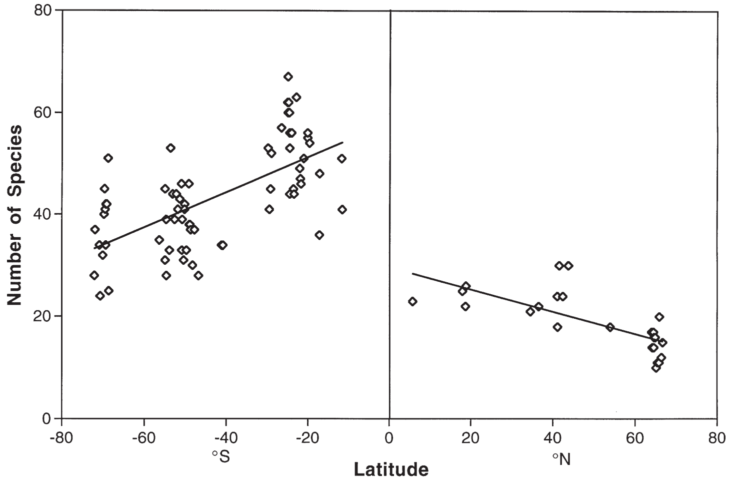

Fig. 10.5. Relationship between latitude and species richness (number of species) of deep-sea core samples of foraminiferans in the North and South Atlantic. Samples were collected from depths of 2000 to 4000 meters. Figure adapted from *Deep-Sea Research,* Vol. 47, Culver and Buzas, Global latitudinal species diversity gradient in deep-sea benthic foraminifera, pp. 259–275. Copyright (2000) with permission from Elsevier Science.

1994; Wilson, 1998; Culver and Buzas, 2000). Rex et al. (1993) showed that three macrofaunal groups, the isopods, gastropods and bivalves, exhibit poleward decreases in diversity in the North Atlantic and the Norwegian Sea (Fig. 10.4). Gray (1994) suggested that the patterns of diversity for the North Atlantic shown in Fig. 10.4 were attributable to low values in the Norwegian Sea. However, diversity still declines significantly for isopods and gastropods across the North Atlantic when the Norwegian Sea data are removed (Rex et al., 1997). Patterns for the taxa in the South Atlantic remain uncertain because it has been less well sampled (Fig. 10.4). Molluscs show a weak, but still significant, decrease in diversity toward higher latitudes. However, isopods show no significant pattern and seem to reach maximum diversity at temperate latitudes. There appears to be strong interregional variation in diversity in the South Atlantic.

Brey et al. (1994) claimed that levels of diversity for isopods, gastropods and bivalves in the Weddell Sea were similar to those reported by Rex et al. (1993) for the tropical Atlantic, implying that no latitudinal gradient existed in the South Atlantic. However, the differences in sampling and analytical methods between the two studies do not permit a controlled comparison (Rex et al., 1997). Large-scale geographic patterns of diversity for the macrofauna in the deep South Atlantic will remain unclear until consistent sampling is carried out over a larger latitudinal range.

Culver and Buzas (2000) analysed latitudinal patterns of diversity in deep-sea foraminiferans from the Weddell Sea to the Arctic Basin in the Atlantic – a much broader range than for the macrofaunal elements presented above. Foraminiferans show significant latitudinal gradients in species diversity in both hemispheres (Fig. 10.5). These are quantitative data from core samples without the problems of normalization in estimating diversity discussed below for macrofaunal groups. Thus, a major component of the deep-sea meiofauna also shows evidence of latitudinal species-diversity gradients on large scales in the Atlantic. Lambshead et al. (2000) reported an increase in nematode diversity from 13°N to 56°N in the North Atlantic and Caribbean Sea, but this appears to be a sampling artifact (Rex et al., 2001).

An underlying methodological problem in comparing latitudinal species-diversity gradients in the deep sea to those in other ecosystems is that different methods have been used to estimate species diversity. In terrestrial and shallow marine environments diversity is measured as species richness, the number of coexisting species in a unit area, typically compiled from long-term and large-scale biotic surveys. In deep-sea ecology, diversity is typically estimated by normalizing the number of species collected in samples to a common number of individuals. This normalizing approach is called rarefaction, and the expected number of species is symbolized as $E(S_n)$ (Sanders, 1968; Hurlbert, 1971). $E(S_n)$ is influenced by both the number of species and the evenness of the distribution of individuals among species. Gage and May (1993) cautioned that the deep-sea latitudinal gradients shown by Rex et al. (1993) might simply reflect shifts in the evenness of the relative abundance distribution rather than richness.

Rex et al. (2000) examined latitudinal patterns for isopods, gastropods and bivalves in the North Atlantic by using the Shannon–Wiener Information Function (H') as a diversity measure (see Magurran, 1988). H' is highly correlated with $E(S_n)$, the most commonly used expression of deep-sea diversity (see also Grassle and Maciolek, 1992). Like $E(S_n)$, H' is affected both by the number of species (S) and by the evenness (J). Evenness is uncorrelated with latitude in bivalves, and more weakly correlated than are S and H' for gastropods and isopods (Rex et al., 2000). Partial correlations between S and latitude remain significant when the effects of J are removed; but J is uncorrelated or more weakly correlated with latitude when S is held constant.

The thorough systematic revision of the gastropod family Turridae in the eastern North Atlantic by Bouchet and Warén (1980) permits latitudinal patterns to be documented for this family using simple species richness. The number of bathyal turrid species that coexist in latitudinal bands from 36ºN to 72ºN shows a significant poleward decrease in diversity (Rex et al., 2000). Thus, it seems likely that latitudinal gradients in species richness exist in the deep sea, just as in other major ecosystems. Nevertheless, it should be borne in mind that known macrofaunal data still represent only three major groups in one ocean, and that estimates of deep-sea diversity are based exclusively on scattered remote-sampling programs rather than on the intensive survey data available for more accessible environments. As with terrestrial and coastal environments, it seems reasonable to expect a variety of large-scale patterns to emerge for different taxa and in different regions of the World Ocean.

Potential causes of latitudinal gradients in species diversity

It is likely that large-scale patterns of diversity in the deep sea are shaped by both ecological and historical factors. Historical causes involving speciation and the radiation and geographic spread of taxa have only recently been investigated. Hypothetical evolutionary scenarios have been discussed by Wilson and Hessler (1987), Stuart and Rex (1994) and Allen and Sanders (1996). The most specific case study is Wilson's (1998) analysis of deep-sea isopod diversity on a Pan-Atlantic basis. Deep-sea isopods are composed of two distinct taxonomic components that have quite different evolutionary and geographic origins. Asellotes are the most diverse, and include many families that are endemic to the deep sea. They are the dominant isopod taxon in the deepest regions of the oceans. Flabelliferans are a more recent clade with no endemic deep-sea families. Their representation decreases with depth, and they show a significant decrease in diversity from 60º South to 50º North (Fig. 10.6). Wilson (1998) was able to partition diversity statistically between asellotes and flabelliferans to examine independently their contributions to overall isopod diversity.

Wilson (1998) suggested that asellotes colonized the deep sea first, possibly in the late Paleozoic or early Mesozoic, and radiated there extensively. The deep-sea flabelliferans represent a more recent invasion from coastal habitats, probably after the mid-Tertiary, which has not yet produced endemic higher taxa. Their prevalence in the South Atlantic may reflect its openness to immigration from the Indo-Pacific area. Since the North Atlantic Basin is more isolated from the World Ocean, lower isopod diversity in the North Atlantic and the poleward decline in diversity observed there could be partly a historical consequence of the recent northward spread of flabelliferans in the deep Atlantic. Future research on spatially-referenced phylogenies may help to reveal the influence of speciation and geographic spread of taxa on large-scale patterns of biodiversity in the deep sea.

Recently, much attention has been focused on the potential importance of Rapoport's Rule – the tendency for geographic ranges of species to expand at higher latitudes as an adaptive response to greater climatic variation [Rapoport (1982); see also Stevens (1989, 1992); on the other hand, see Gaston et al. (1998)]. For the deep-sea Turridae of the eastern North Atlantic discussed above, latitudinal range of species is not correlated with either latitude ($n = 12$, $r_s = 0.055$, n.s.), or the number of species ($n = 12$, $r_s = -0.050$, n.s.). One reason why Rapoport's Rule might not obtain in the deep sea is that below the permanent thermocline, which occurs at upper bathyal depths, the environment is very cold and nearly isothermal. The latitudinal gradients in physical climatic effects, like seasonal temperature variation, freezing, and precipitation, that are thought to be responsible for latitudinal gradients in the geographic ranges of terrestrial species (Stevens,

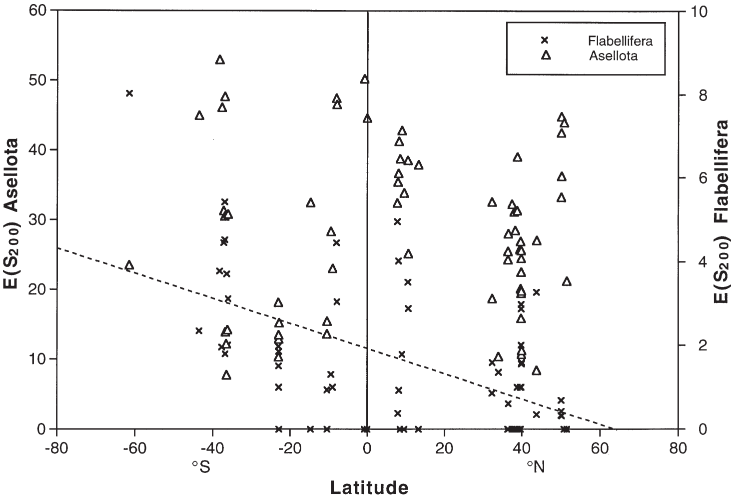

Fig. 10.6. Relationship between latitude and diversity for epibenthic samples of asellote and flabelliferan isopods from the North and South Atlantic. All samples were collected by an epibenthic sled from bathyal depths (500–4000 m). Diversity was partitioned between the two groups, based on samples rarefied to 200 individuals. Dotted line shows relationship between diversity and latitude in the Flabellifera. Diversity in the Asellota is on the left axis and in the Flabellifera on the right axis. Flabelliferan diversity decreases from south to north in the Atlantic. Figure adapted from *Deep-Sea Research II,* Vol. 45, G.D.F. Wilson, Historical influences on deep-sea isopod diversity in the Atlantic Ocean, pp. 279–301. Copyright (1998), with permission from Elsevier Science.

1989), may not apply. Rapoport's Rule also does not appear to hold for bathymetric gradients in deep-sea taxa (Etter and Rex, 1990; Pineda, 1993; Pineda and Caswell, 1998) or for latitudinal gradients in coastal marine mollusks (Roy et al., 1994, 1998).

It seems doubtful that area effects could be responsible for deep-sea latitudinal gradients in species diversity. A decrease in habitable area from the equator to the poles has often been invoked as an explanation for latitudinal gradients in diversity (Osman and Whitlatch, 1978; Rosenzweig, 1995). Latitudinal species-diversity gradients in coastal marine mollusks are not attributable to species–area effects (Roy et al., 1998). On large bathymetric scales in the deep sea, there is no relationship between diversity and area (Rex, 1981). There is also no simple obvious poleward reduction in area with latitude across the North Atlantic which might reasonably account for latitudinal species-diversity gradients, but this relationship remains to be tested in a critical precise way.

Rex (1981) and Rex et al. (1993, 1997, 2000) proposed that large-scale patterns of deep-sea species diversity, including the bathymetric gradients discussed earlier, inter-basin differences and latitudinal gradients, are related to the rate and seasonal pattern of nutrient input from overhead production. In the North Atlantic, latitudinal gradients of deep-sea diversity correspond to a poleward increase in the annual rate and seasonality of surface production in the North Atlantic [Campbell and Aarup (1992); Sathyendranath et al. (1995); Falkowski et al. (1998); see, however, Christensen (2000)]. The poleward decrease in evenness and increase in density observed in some deep-sea taxa may be induced by seasonal nutrient loading. There are numerous localized deep-sea habitats where high fluxes of organic carbon to the seabed from upwelling and lateral transport (Sanders, 1969; Levin et al., 1994; Blake and Hilbig, 1994; Gage, 1997) or proximity to oxygen-minimum zones (Levin et al., 1994) cause organic enrichment. These areas also have elevated density, high dominance and depressed diversity compared to adjacent communities at similar depths (Levin et al., 1994; Levin and Gage, 1998). As discussed earlier, depressed diversity at upper bathyal depths close to high coastal production may be related to high and variable food availability (Rex, 1981). Similar cases include sites where bottom topography concentrates sinking food resources, as in deep-sea trenches (Jumars and Hessler, 1976) and submarine canyons (Vetter and Dayton, 1998), and areas where episodic strong near-bottom currents increase food availability by exposing reactive sediments (Aller, 1997). Perhaps the most extreme examples are reducing environments, such as hydrothermal vents and cold seeps (see Chapter 4), where *in situ* production increases standing stock and decreases diversity by orders of magnitude compared to surrounding areas (Van Dover, 1990, 2000; Tunnicliffe, 1991). Levin et al. (1994) noted that organic-rich zones in the deep sea bear a striking resemblance to the frequently observed effects of moderate organic pollution in coastal marine environments: higher standing stock, fewer species and numerical dominance of a few species leading to low evenness (Pearson and Rosenberg, 1978).

We stress that patterns of species diversity on these very large scales cannot represent controlled within-habitat comparisons. For example, upper bathyal diversity gradients in the western North Atlantic are correlated with the variability of sediment particle size (Etter and Grassle, 1992) as well as animal abundance. Sites of localized organic enrichment can also experience physical disturbance from sediment resuspension by strong near-bottom currents (Aller, 1997), or occasional catastrophic sediment displacement from mass-wasting on steep slopes (Levin et al., 1994). Hydrothermal vents occur in hard substrata, in contrast to the soft sediments that characterize most deep-sea habitats, and vent communities are distinctly different in being fueled by bacterial chemosynthesis rather than by sinking phytodetritus. Species composition and the life-history characteristics of the faunas at enriched sites also differ from those in neighboring habitats. A variety of biotic and abiotic environmental causes is undoubtedly, to some extent, responsible for geographic variation in deep-sea species diversity (Rex et al., 1997; Levin et al., 2001). However, the most consistent ecological factor associated with the combination of elevated standing stock and depressed diversity in deep-sea communities is some form of pulsed nutrient loading. The relative importance of the rate of nutrient input and its variability is unclear.

TEMPORAL PATTERNS OVER GEOLOGICAL TIME

Until quite recently, knowledge of temporal variation in deep-sea communities was limited to seasonal and interannual changes in reproductive pattern and population density linked to short-term cycles of sinking phytodetritus (Gage and Tyler, 1991; Young and Eckelbarger, 1994). The extraordinary advances in paleoceanography during the 1990s are beginning to provide, for the first time, a historical dimension to life in the deep sea over geological time-scales. Exposed fossil assemblages of deep-sea organisms are rare. The new understanding comes from seabed cores taken by the Deep-Sea Drilling Project. The cores provide a continuous sedimentary record, which can be dated using accurate chronometric methods. Analyses of elemental make-up and stable-isotope ratios in microfossils and lithic materials from the cores provide climate-proxy data for reconstructing the physical oceanography of past oceans, including temperature gradients, water chemistry, the deep thermohaline circulation, surface ice volume and iceberg discharges (Shackleton et al., 1984; McManus et al., 1994; Kennett and Ingram, 1995; Dwyer et al., 1995; Adkins et al., 1997; Marchitto et al., 1998; Oppo et al., 1998; Raymo et al., 1998). Coincident climate shifts are also recorded in the skeletons of deep-sea corals (Smith et al., 1997; Adkins et al., 1998). These environmental changes can be associated with the diversity and composition of microfossil assemblages, and with the geographic distribution and morphological evolution of individual species (Cronin and Schneider, 1990).

While catastrophic biological crises of the remote past have been attributed to major changes in the deep circulation, such as Permo-Triassic mass extinction (Knoll et al., 1996; Wignall and Twitchett, 1996; Isozaki, 1997), the most precise record exists for the Cenozoic, particularly the last several million years. During this era there were glaciation cycles in the Northern Hemisphere on time scales of 10^4–10^5 years, which now seem linked to variation in the Earth's orbit (the Milankovitch cycles). The advance and retreat of polar ice sheets and the attendant changes in global climate were not gradual regular transitions. They were accompanied by briefer episodic climate changes on millennial time scales (Dansgaard–Oeschger events) during which temperature changes could be surprisingly abrupt, sometimes occurring over decades or centuries (Severinghaus et al., 1998). Many of these climate changes appear to have been global in scale (Kotilainen and Shackleton, 1995; Steig et al., 1998). The causes of these short-term fluctuations remain uncertain, but probably involved complex interactions between the atmosphere, ocean currents and ice coverage which may be intrinsic to Earth's climate, or interactions among orbital forcing parameters and internal climate factors (Driscoll and Haug, 1998; Marchitto et al., 1998; Raymo et al., 1998; Weaver et al., 1998). Shifts in the ice-age climate affected the deep-sea environment through reorganization of the thermohaline circulation and the potential for surface–benthic coupling. Their discovery requires

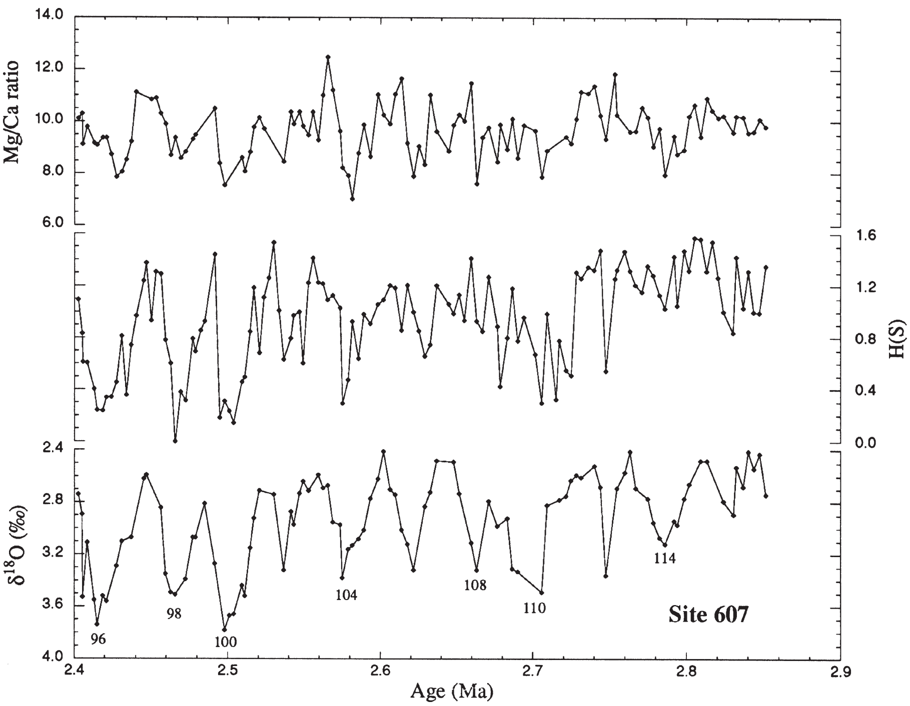

Fig. 10.7. The relationship between deep-sea ostracod species diversity and oxygen-isotope ratios ($^{18}O/^{16}O$) in benthic Foraminifera and Mg:Ca ratios in Ostracoda over time (Ma). Species richness was measured by the Shannon–Wiener index [H(S)]. Lighter isotope values indicate interglacial warm periods with low ice volume. Higher Mg:Ca ratios indicate warmer bottom-water temperatures. Ostracod diversity fluctuated with glacial–interglacial cycles during the Pliocene. Reprinted with permission from *Nature* (Cronin and Raymo, 1997, Vol. 385, pp. 624–627). Copyright (1997), Macmillan Magazines Limited.

a re-evaluation of the still widely held assumption among ecologists that the deep-sea environment has been stable over geological time.

The deep sea has not been immune from global mass-extinction events during the Cenozoic. Sharp isotopic excursions and a convergence of isotope levels between benthic and pelagic foraminiferans at the Paleocene–Eocene transition indicate a rapid increase in ocean temperature of about 20ºC and elimination of the temperature gradient through the water column (Kennett and Stott, 1991). This warming episode occurred abruptly over about three thousand years, and was temporary, lasting about 30 thousand years before cooling to near earlier levels and restoration of the vertical temperature gradient occurred. The event coincided with the extinction of 35–50% of benthic foraminiferan taxa, probably as a consequence of oxygen depletion in the deep sea following global changes in deep-water formation. The exact physical and biotic causes that led to the extinction appear to have been complex, possibly involving dissociation of methane hydrates, carbonate dissolution and changes in surface production (Thomas, 1998; Thomas et al., 1999). Kaiho (1994) has reviewed deep-water extinction events and their causes during the last 100 million years.

Two recent studies have linked paleoclimatic change to long-term changes in deep-sea biodiversity observed in seabed cores. Cronin and Raymo (1997) measured fluctuations in the diversity of benthic ostracods in the North Atlantic through eleven glacial–interglacial cycles spanning a 450 000-year interval of the late Pliocene. The glaciation cycles correspond to the Earth's 41 000-year obliquity cycle of solar insolation. Figure 10.7 shows ostracod species diversity, estimated by the Shannon–Wiener Information Function (H'), plotted against time along with Mg:Ca ratios of the ostracod shells and oxygen isotope ratios of co-occurring foraminiferan tests. The latter two variables reflect shifts in bottom temperature associated with changes in the deep thermohaline circulation, and in surface ice volume, respectively. The oscillation in species diversity coincides with orbitally-driven cycles of glaciation in a remarkably consistent way. Diversity is highest in interglacial phases and declines during glacial advances. Throughout the time sequence, H' is negatively correlated with oxygen isotope values and positively correlated with Mg:Ca ratios. Even the magnitude of the change in diversity appears to match the extent of glaciation. Severe glacial episodes signaled by unusually heavy oxygen isotope values (e.g., those at 2.42, 2.46, 2.5 and 2.7 million years) coincide with some of the lowest values of diversity. Interestingly, the variation in diversity is not a function of origination and extinction of species. Species periodically lost to the assemblage during glacial phases persist in cores taken elsewhere in the Atlantic. and evidently re-invade during interglacial phases. No new species appeared. Cronin and Raymo (1997) suggested that fluctuations in diversity do not result from changes in bottom temperature *per se* or in raw nutrients (e.g., nitrogen and phosphorus). They proposed that changes in primary production in surface waters and in the consequent flux of organic material to the deep sea that accompany the advance and retreat of ice sheets provide the most plausible explanation. The data clearly reveal that deep-sea diversity on local spatial scales is not constant on millennial time scales, and that diversity responded to cycles of Pliocene glaciation in a highly repeatable way.

Glacial episodes also must have directly affected the upper bathyal ecosystem. Studies on stable isotopes in benthic foraminifera, fossil coral-reef terraces and hydrographic models indicate five major low sea-level stands during the last 500 000 years which were more than 100 meters below present sea level (Rohling et al., 1998). The last glacial maximum, 20 000 years ago, depressed sea levels by about 120 meters. Earlier glacial maxima during the Pleistocene may have resulted in even lower levels. Such dramatically lower sea levels would have eliminated much of the productive neritic region, extended the euphotic zone to the upper continental slope and increased the impact of terrestrial and sea-surface climatic variation on the upper reaches of the deep sea. All of these factors probably acted to increase the temporal and spatial heterogeneity of the upper slope. Active formation of submarine canyons and downslope transport during the glacial era must have greatly influenced deep-sea ecosystems near continents (Emery and Uchupi, 1972; Gage and Tyler, 1991). The Late Pleistocene was also a time of massive megaturbidite[1] formation (Rothwell et al., 1998). These catastrophic sediment slumps must have drastically altered the deep seascape and obliterated natural communities over huge areas.

Thomas and Gooday (1996) have analysed changes in the diversity of foraminiferans from seabed cores over much larger scales of time and space. They compared the number of species (rarefied to 100 individuals) in cores representing much of the Cenozoic taken in the Weddell Sea off Antarctica and in the equatorial Pacific. The most interesting pattern to emerge, for the present discussion, is the divergence of diversity between polar and equatorial sites that arose in the Eocene at around 40 million years ago (Fig. 10.8). This was the beginning of a period of global cooling, when continental ice sheets developed in Antarctica; the transition from the "greenhouse world" of the Paleocene to the "icehouse world" that persists to the present. The effects of this major global change in surface climate affected the deep-sea environment as well; indeed, there is growing evidence of a strong interaction between surface climatology and the deep thermohaline circulation (e.g., MacLeod and Huber, 1996). Figure 10.8 shows the initial establishment and persistence of a latitudinal gradient in species diversity of deep-sea foraminiferans between the tropics and polar regions. Since the formation of ice cover in Antarctica in the late Eocene, polar diversity has declined and tropical diversity remained continuously higher. The low-diversity communities at high latitudes became dominated by opportunistic foraminiferan species exploiting sinking phytodetritus as a food resource. Because of this, Thomas and Gooday (1996) suggested that the seasonality in organic enrichment attending global cooling and the formation of an Antarctic ice sheet may have had an important role in creating latitudinal gradients of species diversity.

Rapidly expanding research in paleoclimatology and paleoceanography, particularly during the past decade, is revolutionizing understanding of how major ecosystems function, change and interact. While many challenges remain (Charles, 1998), it seems clear already that the deep-sea environment is linked to climate cycles, both during long phases of gradual temperature change and on surprisingly short time scales during Quaternary glaciation. Environmental changes on long and short time scales appear to affect community structure in the deep sea, though it would be premature to speculate on their general importance

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[1] See Glossary, p. 477.

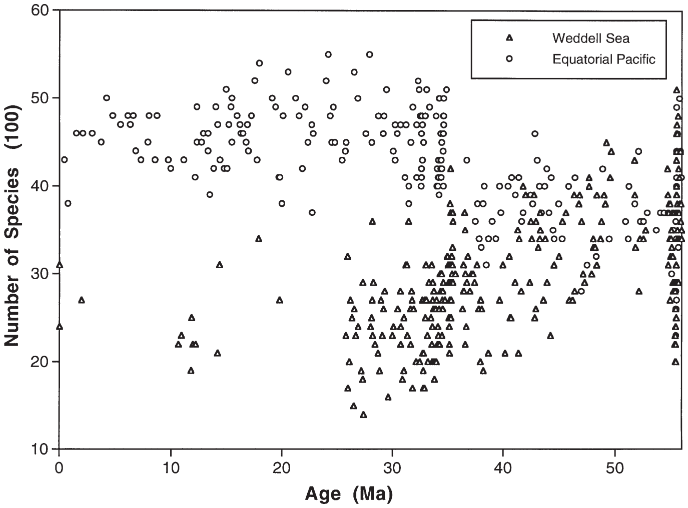

Fig. 10.8. The pattern of deep-sea foraminiferan diversity from the Weddell Sea and equatorial Pacific over geologic time from the early Eocene until the present. Estimates of diversity were calculated to the number of species per 100 individuals using Sanders' (1968) rarefaction method. The divergence in diversity between polar and equatorial regions from the late Eocene to the present shows the establishment of a latitudinal gradient in deep-sea foraminiferan diversity. Adapted from Thomas and Gooday (1996), *Geology,* Vol. 24, pp. 355–358. With permission from Geological Society of America, Inc.

relative to other marine habitats. However, the prevalent notion among ecologists of a historically unvarying environment will require re-evaluation.

In addition to its influence on ecological opportunity and community structure, Pleistocene glaciation may have been a driving force in the evolutionary development of deep-sea biodiversity. While much has been learned during the past twenty years about geographic patterns of diversity, research has only just begun on how and where the deep-sea fauna originated and diversified (Rex et al., 1997; Chase et al., 1998; Wilson, 1998). It has been particularly difficult to understand how allopatric speciation could occur, since there are no obvious geographic isolating barriers (Chase et al., 1998). In many parts of the World Ocean, oxygen-minimum zones may provide effective geographic isolating barriers on continental margins (Rogers, 2000; see, however, Cannariato et al. 1999). The effects of glaciation on sea level and shifts in major deep currents may also have provided opportunities for separation and fusion of populations. Active canyon formation during low sea-level stands might have effectively separated populations along the slope face for thousands of years. The changing intensity and shoaling of thermohaline currents could act to compress, expand and shift species ranges. These effects should be most pronounced at upper to mid-bathyal depths. Interestingly, in the western North Atlantic, mollusks show the highest degree of interpopulation variation in shell architecture and mitochondrial DNA at upper bathyal depths (Etter and Rex, 1990; Chase et al., 1998; Etter et al., 1999).

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Chapter 11

FOOD INPUTS, UTILIZATION, CARBON FLOW AND ENERGETICS

John D. GAGE

INTRODUCTION

The biota of the deep-sea bed and the immediately overlying layer of water, the *benthic boundary layer,* constitute an almost totally *heterotrophic* ecosystem (its metabolism reliant on breakdown of complex organic molecules). It is also an *allochthonous* system. Except at hydrothermal vents, and in sediment subject to methane seepage (see Chapter 4), this typically comes from organic-material flux to the deep ocean basins from contemporary primary photosynthetic production in the euphotic zone (the thin surface layer of the oceans where light penetrates). Nearer to the continental margin increasing amounts of this organic input may be derived from neritic (coastal) and terrestrial organic material, in both particulate and dissolved form.

I shall not further consider non-photosynthetic, *chemosynthetic,* production at hydrothermal vents and methane seeps. Although estimates of the contribution of these sources to global organic production are still uncertain, they are unlikely to be more than trivial and will not be further considered in this chapter (see Chapter 4 for an account of chemosynthetically fuelled communities in the deep sea). It is noted that these chemosynthetic inputs occur directly at the deep-ocean bed, and thus are not subject to the intense biological reprocessing and mineralization in the upper water column.

While food characteriztics strongly influence the species composition of the community present, the quantity and quality of food input to the seabed community is the single most important determinant of the abundance of populations in space and time, and may also influence species richness (see Chapter 10). Furthermore, because of the huge area covered by the deep ocean, the dynamics of organic food consumption and the recycling of this carbon by the allochthonous system on the deep-sea bed is thought to be of considerable importance to understanding of the global carbon cycle, whose inputs are now significantly augmented from combustion of fossil fuel.

Historical aspects

After discovery during the 19th century of life on the floor of the deep ocean world-wide, there was active discussion on how these remote populations are sustained. The reports from the exploring voyages of British navy ships *Lightning* and *Porcupine* in the Northeast Atlantic and Mediterranean in the 1860s (e.g., Jeffreys, 1869) and the famous world-encircling voyage of H.M.S. *Challenger* in 1872–1876 (Thomson, 1880; Murray, 1895) address the transfer of organic material as food to the bottom in the form of dead surface-dwelling animals. These, and later expeditions by ships of other nations, recognized the passive sinking of organic particles as the main category of food to the deep-sea ecosystem. Some of the observations made, such as the quantitative importance and seasonal nature of fast-sinking gelatinous plankton to the deep ocean floor (Moseley, 1880), presaged findings one hundred years later.

After World War II in the 1950s and 1960s there was an extensive, world-wide program of deep-sea sampling by Russian workers. This prompted discussion of nutritional sources and categorization of feeding types in deep-sea benthic organisms (Sokolova, 1959). The availability of new methods for measuring organic carbon in organisms, in sediments and in sea water then led to the first attempts to make a budget for the marine organic-carbon cycle (Riley, 1970). At the same time, new studies on the deep-sea benthos by American workers in the 1960s led to fresh discussion of the sources of nutrition for the remote community on the deep-sea floor (e.g., Menzies, 1962; Sanders and Hessler, 1969).

Three main pathways, or mechanisms, for input of the various forms of particulate organic matter as a food source for the ecosystem of the deep-sea bed have been put forward (Fournier, 1972). These are:

(1) passively sinking detrital rain;
(2) active biological transport; and
(3) the utilization of dissolved organic carbon.

An important goal in deep-sea biology has been to describe and quantify these organic inputs in relation to the global distribution of deep-sea benthic biomass (e.g., Rowe and Staresinic, 1979; Rowe, 1981). The density of this deep-sea biomass is typically one or two orders of magnitude less than in coastal benthic systems (see Chapter 10 for a detailed account of this pattern, and of the global and depth-related patterns in biomass distribution). The traditional paradigm of the deep sea became one of a 'low-activity' ecosystem because of these very low densities in microbial and animal biomass, and the low nutritive value of much of the refractory organic material typically caught in sediment traps set for short durations in the water column. This was reinforced by the recovery of remarkably well-preserved crew's packed lunches left for a year in the submersible DSV *Alvin* which was accidentally flooded and sank onto the deep-sea bed in the Northwest Atlantic in 1968 (see Chapter 5, p. 154).

The modern view of the functioning of deep-ocean ecosystem

Two linked discoveries upset the 'low-activity' ecosystem paradigm. The first was the unexpected discovery of seasonal peaks in flux of organic particles in long-term sediment traps set at great depths (Deuser and Ross, 1980). The second resulted from dramatic seabed photographs of mass accumulations of phytodetritus suddenly arriving on the abyssal sea floor (Billett et al., 1983). These discoveries encouraged a new and more dynamic view of deep-ocean processes. Furthermore, the conventional wisdom of low microbial reactivity at the deep-sea bed was challenged by discovery of rapid microbial reaction to freshly deposited phytodetritus incubated under pressure (Lochte and Turley, 1988). This showed rapid degradation of the phytodetrital material by barophilic bacteria and other prokaryote microorganisms as opposed to the increasingly pressure-inhibited activity of bacteria on material sinking down from the surface (Suess, 1988).

Other data previously had indicated rapid utilization of fresh planktonic detritus by microbes and metazoans, of dead fish by scavengers (Isaacs and Schwartzlose, 1975) and of wood blocks by specialized molluscs (Turner, 1973). These observations showed that the deep-sea bed ecosystem was able to react rapidly and vigorously to availability of new organic carbon. This was linked to unexpected findings of seasonal variability in reproduction and recruitment, and indications of relatively rapid growth rates, and seasonal growth-banding in skeletal parts, of deep-sea deposit-feeding benthic invertebrates (Tyler et al., 1982; Gage and Tyler, 1991; see also Chapter 12). All this challenged the conventional view and revealed similarities to the more familiar functioning of shallow-water benthic ecosystems.

The view of constancy in small-particle input has now given way to one where much of the deep ocean is subject to pulsed intermittency in volume and quality of organic flux (Conte et al., 1998). This view has resulted from improved resolution of the nature of small-particle flux, which constitutes the bulk of organic input to the deep ocean from the euphotic zone. Intermittency in events at the surface results in delivery of a large portion of the most nutritious material to the benthic community within relatively short periods, albeit with sometimes marked spatial variability. Important implications for deep-sea biology of this spatial and temporal variability in organic-material input have yet to be clarified. But it seems likely that such episodic, but high-quality, detrital flux, represents a most important nutritional source for the deep-sea bed community.

The idea of a very attenuated link between the upper ocean and the deep-sea bed communities, where for all intents and purposes the upper ocean could be regarded as a closed ecosystem with no important carbon sink except respiration, is now of limited value in quantifying global organic carbon-flux. Instead the complex community dynamics of the upper-ocean ecosystem may be seen as involving major and highly variable losses to the deep ocean, particularly after phytoplankton blooms. The openness of the whole system leads to benthic–pelagic coupling that may be dynamic and highly variable, just as it is on the continental shelf.

Furthermore, the recent advent of improved instrumentation for use on the seabed has allowed one to appreciate the importance of flow-related dynamics of resuspension and lateral transport of this organic

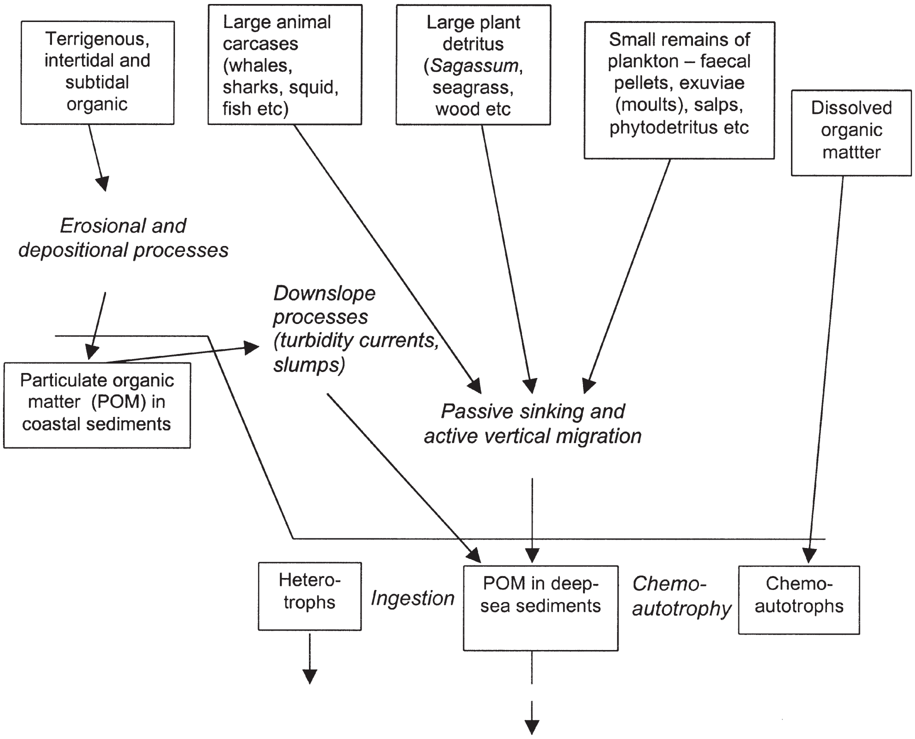

Fig. 11.1. Categories of food inputs to the deep-sea bed ecosystem.

flux on the deep-sea bed. These *advective* processes mainly take place in the layer of water immediately above the bottom that is mixed by turbulent shear with the bottom, the *benthic boundary layer* (benthic boundary layer). In physical terms there are sub-layers or gradients in many parameters, including flow, potential temperature and particulate and chemical concentrations (see Chapter 2). The importance of these in determining the nature and biological response to organic input to the deep-sea processes (which are particularly intense on the continental margin) have previously been under-appreciated. Taking these into account on the slope, supply and demand, which previously seemed enigmatically unbalanced from measurement of input from vertically sinking particle flux, now seem roughly in equilibrium.

However, such processes operate on the ecological time scale. Overwhelming fluxes of organic carbon may occur from episodic events over a longer time scale triggered by earthquakes, for example (Thunell et al., 1999). These may transfer large quantities of organic carbon to the deep ocean from turbidity flows and slides down the continental slope. The associated smothering effect caused by displaced sediment will certainly cause extinction of the benthic ecosystem in the immediate vicinity. While such turbidites may be conveniently preserved in the sediment biogenic structure and trace fossils as ‘ichnofabric’ (Wetzel and Uchman, 1998), there may be enhanced sedimentation of organic carbon associated with resuspended sediment from shallow depths over large adjacent areas of the deep ocean (e.g., Thunell et al., 1999). To what extent the living benthic communities are able to utilize this bonanza before it is buried is unknown.

Scope of chapter

Because of the openness of the oceanic ecosystem in terms of carbon export, it is appropriate to track from source all significant organic fluxes to the deep-sea ecosystem (Fig. 11.1). In order to understand the variability in response shown by the benthic boundary layer (BBL) ecosystem, one now needs to understand these sources better than was previously thought necessary in deep-sea biology. These sources will be described in turn, starting with active biological transport, followed by the various size categories of passive transports. The first and most important category, the living or dead organic entities conveyed passively from origins in the upper ocean to utilization at the bottom, shows wide variability in size of particle and nutritive value, as well as sources. They range from the small organic detrital particles called "detrital rain", through terrigenous and coastal plant debris, to falls of animal carcasses ranging in size from zooplankton to whales. These inputs to the deep-sea bed will be dealt with in order from small to large.

Small particles may consist of the remains of planktonic animals, including faecal pellets and moults, as well as phytoplankton. Apart from some small, light particles that are completely broken down in midwater, most sink within days or weeks; but the smallest, which may consist of very old carbon and lithogenic particles along with isolated bacteria (Bauer and Druffel, 1998) may stay suspended almost indefinitely. The final category, dissolved organic matter (DOM), is derived from particulate organic matter, and is highest in the sediment and overlying water in organically enriched areas. Arguably, this may be an important food source for certain metazoans, and certainly for heterotrophic bacteria. However, although quantitatively very large, most of the dissolved organic-carbon pool of the oceans is very old and refractory (and therefore probably of very limited value in fuelling the deep-sea ecosystem), whereas labile material is quickly utilized and kept at threshold values.

This chapter also addresses the utilization of these varied inputs in relation to modes of feeding and other responses of organisms of the deep-sea bed to these organic inputs at the differing space–time scales of these processes. These are considered in turn in the context of each category of particle. Not only feeding mechanisms are included, but also the aerobic and anaerobic utilization of organic-particle flux by the sediment community. By feeding on these particles, and breaking them down to fuel their activity, growth and reproduction, organisms of the deep-sea bed remineralize organic carbon to carbon dioxide. Quantitatively most of this recycling of carbon is mediated by micro-organisms, so this chapter also briefly reviews measurements of aerobic respiratory demand by the total sediment community of the deep-sea bed.

After summarizing these various inputs and modes of utilization of organic carbon to the benthic boundary layer community, I shall also briefly consider what is known of anabolic metabolism in deep-sea animals as a major energetic pathway. This includes both somatic and reproductive production of individuals and populations and should be considered as an integral part of understanding of the dynamics of the bottom community as driven by organic carbon. Such population processes are also important in understanding sensitivities to environmental change, including that caused by man's increasing intervention in this remote environment.

The chapter then examines the combined feeding activities and trophic interrelationships of the deep-sea bed community. It finishes by examining attempts to model the deep-sea bed food web by means of intensive comprehensive study of single, hopefully representative, sites. By such means the eventual aim is to project energy flow, using the proxy of carbon dynamics, from the local scale to the scale of the regional and global deep-sea ecosystem.

ACTIVE BIOLOGICAL TRANSPORT TO THE DEEP-SEA BENTHIC BOUNDARY

The importance of midwater biota as an important medium for the transfer of organic carbon to the deep-sea bed grew from studies after World War II on the vertical migrations of large zooplankton and nekton between the surface and the deep ocean. This work had been stimulated by military observations of vertically moving deep scattering layers, during development of acoustic devices for anti-submarine warfare. The scientific studies suggested the presence of continuous faunal linkages based on predator–prey relationships within a chain of different midwater organisms. This was first developed by Russian workers in the 1950s as a 'ladder of vertical migrations theory' (see Vinogradov and Tseitlin, 1983). Vertical diel migrations by surface and midwater plankton and micronekton (organisms intermediate between feebly swimming plankton and active swimmers such as fish, otherwise known as nekton) may actively transport material in their guts after feeding at night in the surface layers and defaecating at depths as great as 1000 m during the day (Wiebe et al., 1979; Angel, 1989; Longhurst and Harrison, 1989). Lampitt et al. (1990) estimate that less than 5% of mass particle flux may be actively transported to depth in this way.

Trophic coupling of benthopelagic fauna with midwater fauna

Vereshchaka (1995) showed on continental slopes that various invertebrates of benthopelagic habit (usually swimming or drifting in the water immediately overlying the ocean floor, but sometimes able to spend varying amounts of time on, or buried within, the seabed), particularly penaeid prawns, periodically ascend to feed on pelagic animals. Benthopelagic fish, however, are thought to be major consumers of diel migrating mesopelagic biomass (from depths of 200 to 1000 m), either captured near the bottom (e.g., Sedberry and Musick, 1978), or through vertical migration by the fish predator. For example, some benthopelagic fish, such as hake, prey on mesopelagic organisms, including smaller fish that perform diel migrations (Blaber and Bulman, 1987). On the continental margin many deep-water benthopelagic fish are thought to feed almost exclusively on mesopelagic organisms whose distributions and migrations take place on the slope (Mauchline and Gordon, 1991). Some fish, such as the orange roughy, also play an important rôle by staying at depth, aggregated around sea mounts and submerged banks, and feeding on enhanced flux of prey drifting past these features, as well as on diel migrators during their downward migration (Koslow, 1997). By this means they are important in the transfer of energy as organic carbon to the deep-sea benthos (Rosecchi et al., 1988). The deep-sea scavenging community will also fall into the category of large benthopelagic predators, because these animals, which range from actively swimming fish to highly motile swimming invertebrates, tend to remain within the benthic boundary layer. These organisms (see below) will therefore serve only to redistribute the already sparse concentrations of organic material over the seabed.

Energetic considerations

Some idea of the energetic losses associated with the links in the midwater food chain may be obtained from measurements of the dramatic decline in macroplankton and micronekton biomass with depth. Although there is an increase in mean body size of bathypelagic organisms with increasing depth (Mauchline, 1972), this is accompanied by an order-of-magnitude drop in biomass from the surface to 2000 m and a further order-of-magnitude drop to a depth of 4000 m (Angel and Baker, 1982).

SMALL PARTICLES

Small particles have long been thought to be the chief means of organic-material input to the deep-sea heterotrophic ecosystem. They are small because of the size structure of the plankton community, with its primary producers typically unicellular. The detrital rain exported to the deep ocean actually consists of a range of small particles. Passive aggregation to form marine snow, or active aggregation as faecal pellets or dead zooplankton, however, results in larger-sized particles with a faster sinking potential (McCave, 1975).

Because small-particle flux is the most important source of organic carbon to the deep ocean, large-scale patterns in the distribution of deep-sea benthic biomass, both in terms of organism size and density (Chapter 10), should relate to large-scale patterns in primary productivity at the surface. The latter, of course, should be indicative of the transfer to the bottom of the new and recycled production (see Chapter 3). Russian studies world-wide after World War II have shown that this is broadly true at the regional scale (see Belyaev, 1972). Although increasing depth is associated with rapidly decreasing benthic biomass as a consequence of midwater utilization, benthic biomass, particularly near continental margins, will also be much affected by laterally transported particles resuspended from the bottom. I shall consider this rapidly expanding area of study later in conjunction with associated processs in the benthic boundary layer.

Typically, the amount of small-particle material caught in deep-ocean sediment traps is equivalent to a mass flux of between 7 and 45 $g\,m^{-2}\,yr^{-1}$. If particles sink at rates between 20 and ~1000 $m\,day^{-1}$, these traps need to be set well above the benthic boundary layer in order to avoid collecting resuspended aggregates, the so-called rebound flux of Gardner and Walsh (1990) (see p. 329 on upwards flux of biogenic particles). This mass flux will in turn be seen broadly reflected in the pattern of organic-carbon content in the sediment, or better, in measures such as chloroplastic pigment equivalents (CPE) that directly reflect the amount of organic material derived from primary production (e.g., Pfannkuche et al., 1983). For example, in the North Atlantic north of 20°N, the organic-carbon content of the sediment increases with latitude and decreases with depth out to the abyssal plains. From 20°N to the equator the pattern is more variable, being influenced by coastal upwelling off Northwest Africa.

The biological particle cycle in midwater

Because of the dependency of the deep-sea ecosystem on surface processes, one needs to look briefly at the euphotic zone, rarely extending deeper than 200 m, from where most of the organic particles that sustain deep-sea life originate. Classically, the phytoplankton are grazed by zooplankton, which package most of their waste into faecal pellets. These, in turn, are eaten and decomposed by other organisms, including bacteria, within this surface layer. Hence, nearly all the organic matter present is constantly recycled within a surface-layer loop. Only a very small fraction, perhaps up to about 10%, escapes to be exported from the euphotic zone into deeper water by sinking as dead bodies and faecal material (Fowler and Knauer, 1986; and see Chapter 3).

Even before it reaches the deep-sea bottom far below, this organic matter provides food for various midwater animals, the mesopelagic zooplankton and nekton. Many of these organisms are the diel migrators contributing to active biological transport. These animals are able to intercept the particles, so that they may be repackaged many times before reaching the seabed. Sediment traps through the water column show that overall only a tiny proportion, about 1–3%, of the surface primary production reaches the abyssal seabed (e.g., Deuser, 1986) as a result of utilization by midwater organisms. Each particle will also carry its own little community of microbial decomposers. About three-quarters of the organic particles sinking from the euphotic zone may be decomposed and recycled within the uppermost 500 to 1000 m of the water column – that is, above the winter mixed layer, or permanent thermocline, constituting the upper boundary of the deep open ocean. The proportion of surface production arriving at the bottom increases at shallower depths, so that bathyal depths and above will receive values up to the total export flux from the euphotic zone.

As a result of the midwater consumption, the proportion of skeletal material will increase with increasing depth in the water column. This is composed of the calcium carbonate and siliceous structures of the shells of phytoplankton and chitinous exoskeletal structures of small crustaceans and other invertebrates, which are dissolved progressively with increasing depth. This means that, compared to its inorganic composition, the organic content decreases markedly and particle size becomes more variable by the time it reaches bottom (Honjo, 1982).

Episodic mass deposition from the euphotic zone

Superimposed on the scheme outlined above are episodic phenomena in the euphotic zone, ranging from the spring ‘bloom’ to short-lived mini-blooms with high spatial as well as temporal variability. The latter may only be easily detectable by optical sensors. Such short-lived events are not recorded in sediment traps, which integrate sedimentation over long enough periods (varying from 3–4 days to 1 month) to collect enough material. The largest events, by overwhelming the normal recycling processes by herbivore populations in the euphotic zone, bypass the tightly coupled processes previously thought to characterize the biogeochemistry of the euphotic zone. On the other hand, data from the Northeast Atlantic suggest that quickly expanding populations of efficient grazers such as salps may effectively prevent the further development of the oceanic phytoplankton blooms (Stienen et al., 1988).

Boyd and Newton (1999) suggested that variability in size-structure of the phytoplankton community, rather than primary production itself, is the cause of mass sinking of ungrazed algal cells. Hence the flux of particulate material to the deep ocean may depend on the development of certain algal communities rather than on total new production. By such means large quantities of material may escape remineralization during these periods to sink as highly labile, fast-sinking particles into the ocean’s interior, and eventually fuel the benthic boundary layer ecosystem.

This idea is supported from Deuser’s (1986) time-series observations, as the percentage of organic carbon in traps is highest in winter/spring when carbon utilization is least efficient during the period of highest productivity, and lowest in the autumn when the plankton community is mature and utilization is maximal. Even if not detectable as peaks in particle export, faecal pellets enriched with fresh plant cells may occur, enhancing the quality of sedimented particles as potential food (Fisher et al., 1996). It is now thought likely that such transient ‘rain’ events, rather than the slow background drizzle of refractory particles, makes up a large part of the export flux of biologically available organic carbon and easily remineralized elements, throughout the deep ocean (Conte et al., 1998).

The question how much of the total sedimentation of intermediate-size particles arrives at the deep seabed at rates significantly above the ‘background’ level still remains difficult to quantify. These events will range from events that are quickly utilized by the benthic community to those resulting in long-lived mass accumulations of detrital material on the deep ocean bed, and even depositions which, from deep sediment-core evidence, may completely overwhelm and smother the benthic community (Kemp and Baldauf, 1993).

Particle aggregation and 'marine snow'

Fine particles of sinking organic material are subject to aggregation, thus increasing their size to the range of millimetres, and consequently their rate of sinking. This discovery in the late 1970s displaced the widely held view that the deep-sea ecosystem is the recipient of a continuous, sparse rain of very fine particles taking perhaps months or years to sink down. These aggregated, intermediate particles make up the chief constituents of the material caught in deep oceanic-sediment traps. But they are extremely difficult to collect intact, and their amorphous and highly variable shape, from which their name 'marine snow' was coined by Japanese workers, are best seen by scuba divers, or from the viewing port of a manned submersible. Because of their size, the sinking rates of this particulate matter are commonly between 100 and 1000 m day^{-1} (McCave, 1975). The aggregation into many larger particles was originally thought to be exclusively driven by biological processes or packaging, where feeding by heterotrophs will eventually repackage particles into larger faecal pellets and other egesta (Fowler and Knauer, 1986). Other processes are now recognized as important in aggregating small particles. These include physical processes, such as Brownian movement, which dominate in the interactions between the smallest particles. Differential settling and water turbulence will promote collisions between particles, which bind together and capture further smaller particles into macroscopic aggregates (McCave, 1984; Angel, 1984; Fowler and Knauer, 1986; Alldredge and Silver, 1988; Jackson, 1990; Alldredge and McGillivary, 1991). Lampitt (1996) has provided a readable, and less technical account of marine snow. Marine-snow particles are generally larger than about 100 μm, and up to many centimetres across. They sink down at rates measured between 1 and 368 m day^{-1} (Diercks and Asper, 1997), in agreement with estimates of the time interval between phytoplankton blooms and interception in traps or accumulation on the ocean floor. The agents binding marine snow are sticky mucus exudates composed of polysaccharides secreted by phytoplankton and bacteria. Because these particles may collide and stick to much smaller, more numerous particles with a lower sinking rate, they will act slowly to clear nepheloid layers of fine particles (Hill and Nowell, 1990). As the flocculent particles sink down they also scavenge other particles, such as algal cells and small faecal pellets, thus accelerating their sinking (Kranck and Milligan, 1988). This process is thought to be important in the growth of the larger snow particles (Alldredge and Gotschalk, 1989).

It is probable also that such aggregates are constantly being disaggregated or eaten. Each aggregate may form a microhabitat rich in microbial communities and nutrients. Within each aggregate, processes of decomposition and nutrient regeneration will occur at greater intensity than in the surrounding water, so that their chemical and biological characteriztics change rapidly. Sinking rate is enhanced by their increased size and mass, but this flocculent material typically is composed of detritus, carrying large numbers of tiny attached phototrophic and micro-heterotrophic organisms including bacteria, and some inorganic matter – mostly clay particles. In some areas marine snow includes the bodies of gelatinous pelagic macrozooplankton, particularly salps and the abandoned gelatinous 'houses' of larvaceans whose mucous composition particularly improves particle adhesion (Angel, 1984; Smetacek, 1985; Alldredge and Silver, 1988; Alldredge and Gotschalk, 1989; Lampitt et al., 1993; Pfannkuche and Lochte, 1993). Salps, because of their high rate of growth, may create dense swarms at the ocean surface at middle latitudes (Wiebe et al., 1979; Iseki, 1981; Matsueda et al., 1986; Bathmann, 1988; Morris et al., 1988). Off California, larvacaean 'houses' alone have been estimated seasonally to provide a huge proportion of the larger-sized particles below the euphotic zone (Silver et al., 1998).

'Marine snow' as habitat for microbial activity

Marine-snow particles might be thought to be an important site for microbial degradation and a habitat for microzooplankton. Paradoxically, Fowler and Knauer (1986) and Karl et al. (1988) found they are rather poor habitats for microbial growth at depth. This is probably because surface-living bacteria are carried down with these particles into deeper water (Lochte and Turley, 1988). Pressure-related effects much diminish their role in organic degradation, so that below depths of 1000 to 2000 m they become unimportant (Turley, 1993). Probably, free-living bacteria are more active in particle degradation, breaking them into fine non-sinking particles at the expense of fast-sinking ones (Cho and Azam, 1988). Overall, such small particles of intermediate size, whether representing macro-aggregates or faecal pellets, constitute the majority of the flux of organic material to the deep-sea floor (McCave, 1975).

Very fine particles

There are, of course, smaller organic particles, (<1 micron to tens of microns) at the ocean surface, consisting of fine organic detritus, nanoflagellates and free-living bacteria, whose activity may be important in determining organic-carbon flux into deep water (Cho and Azam, 1988). These fine particles stay in suspension or sink very slowly and consist mainly of refractory compounds. Stable isotope ($\delta^{13}C$) and radiocarbon (^{14}C) ageing of deep particulate suspended carbon (particulate organic carbon$_{susp}$) shows it to be older, as well in far higher concentrations, near the margin than in the adjacent oceanic gyres in the Atlantic and Pacific, where it becomes diluted with particles of more recent origin at the surface (Bauer and Druffel, 1998). Bauer and Druffel show that, particularly in ocean margins, the pool of particulate suspended carbon, like that of dissolved organic carbon (DOM) (see p. 359), far exceeds that constituted by sinking particulate carbon.

Faecal pellets

While marine-snow aggregates typically dominate particle flux in some temperate areas such as the Northeast Atlantic, at high latitudes faecal pellets characteristically make up the dominant flux of fast-sinking particles to the deep sea. The size and shape of these pellets depend on the source organism (reviewed by Fowler and Knauer, 1986). Copepod pellets may sink at rates up to 153 m day^{-1} (J.T. Turner, 1977). Those produced by salps are like those of temperate latitudes and are recorded as loose, amorphous aggregates resembling macroflocs, although Hamer and Robison (1992) tracked the descent of faecal pellets from doliolids, salps and pteropods, using an ROV, at speeds of 2100 m per day. Such particles may be quantitatively significant in many areas (e.g., Iseki, 1981; Bathmann et al., 1987; Pfannkuche et al., 1988).

The compact, streamlined, densely packed pellets produced by small crustaceans such as copepods and euphausiids should also sink very quickly, explaining the response observed within days at 1430 m depth in the Norwegian Sea (Graf, 1989). Many faecal pellets are enclosed by a chitinous peritrophic membrane that is important in determining their degradatory ‘half life’ and whether they reach the deep-sea bed intact (Lampitt et al., 1990). The composition of faecal pellets is diverse. Most contain phytoplankton cells along with gut bacteria that are claimed to be of greater importance in their degradation than microbes colonizing from the water (Gowing and Silver, 1983). Inorganic components, mainly calcium carbonate and silicate, ballast the particles, and increase rate of sinking. Overall, the nutritive value of faecal pellets on arrival is higher than that of fine particles because their faster sinking means they are less degraded by colonizing microbes. Particularly at high latitudes it seems likely that such intermediate particles comprise the dominant source of food for the deep-sea benthic deposit-feeding community.

Moults and dead zooplankton

Crustacean moults and dead intact organisms may comprise the dominant component in conditions of large particle flux, such as during seasonal blooms of zooplankton. The mass deposition to the seabed of the bodies of macroplanktonic species such as salps, larvaceans and jellyfish also has been noted by several workers (e.g., Cacchione et al., 1978; Wiebe et al., 1979; Stockton and DeLaca, 1982). Observations by remote-operated vehicles show that these may sink many hundreds of metres per day (Hamer and Robison, 1992). Although it is unlikely that these falls attract specialized scavengers to the same extent as other carcasses, they might form part of the diet of some of the less specialized scavengers such as smaller lysianassid amphipods and brittle stars. In the Southern Ocean a ‘dead body rain’ composed of euphausiids appears, from stomach contents of brittle stars, to make up their main diet (Sokolova, 1994).

Pattern and quantification of particle flux

Measurements of particle flux from sediment traps illustrate how small a proportion, roughly 1 to 14%, of total organic-carbon production in the euphotic zone sinks into the interior of the ocean. The bulk composition of particles is far from uniform, the proportion of organic carbon varying by up to an order of magnitude, especially in the polar ocean. This accompanies changes in organic composition, such as chlorophyll and amino acids, showing a concomitant seasonal change which can be related to whether particles are mainly from phytoplankton or zooplankton material (e.g., Lundgreen and Duinker, 1998).

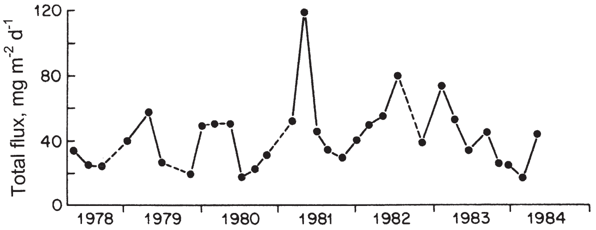

Fig. 11.2. Six-year time series of particle flux into the deep sea. Each point represents the flux into the trap, which was moored 1000 metres above the bottom in a depth of 3200 m depth in the Sargasso Sea. The connecting lines may have no meaning in representing flux between the 2-month servicing periods. The pecked lines represent gaps in sample coverage. From Deuser (1986).

Large-scale patterns in particle flux

Strong latitudinal trends in particle flux are surprisingly absent, despite the considerable annual variability in bulk flux and global spatial pattern in surface productivity which has now been well described. At lower latitudes, there appears to be a linear relationship between organic flux and surface primary production when the latter is at lower levels, but at higher values of surface production organic flux levels out to a constant value. Furthermore, there appears to be no latitudinal trend in organic-carbon flux at depth. Lampitt and Antia (1997) concluded that there is a positive relationship between surface primary production and particle flux into the deep ocean up to certain modest levels of surface production; above this level the flux remains constant. In abyssal areas, such as the central North Pacific (K.L. Smith, 1992), remote from downslope advective inputs, particle flux is probably predominantly controlled by the structure and dynamics of the upper water column, and the biogeochemical processes and plankton ecology of the surface layer.

Seasonal variability

The idea of a slow and uniform rain of small particles into the deep ocean which could be addressed by a single, ‘snapshot’ measurement has given way to a view of rapid coupling of fluxes between surface and deep-ocean waters. Time-series observations over several years using sediment traps that sample at monthly, or bimonthly, intervals have shown clearly that particle flux into the deep ocean at depths below 2000 m varies in response to the annual cycle in primary production (Fig. 11.2). This can result in rapid transfer of material to depth (Deuser et al., 1981; Asper et al., 1992). With the increased amount of research from the 1960s and 1970s on particle flux there are now available sufficient data sets to look for large-scale patterns. The range in variability available is wide (reviewed by Lampitt and Antia, 1997), with polar areas having both the most variable and the highest and lowest values. The data show a global pattern of annual variability, expressed as a flux stability index, which increases (becomes more stable) with depth, and is highest in the tropics, and lowest (least stable) in the Antarctic.

Longhurst (1995) and Longhurst et al. (1995) have mapped regional-scale differences in the biogeochemical processes and the plankton ecology of the upper ocean. Patterns appear only to be associated with differences in variability in particle flux. There is no significant relationship between the extent of variability in the flux and its annual mass, and only a weak relationship between variability and net export flux from the surface. Perhaps surprisingly, Lampitt and Antia (1997) have shown that even the most variable sites outside polar seas export only about twice as much to depth as the most stable ones in oligotrophic, low-latitude gyres such as the Sargasso Sea (although interpretation of polar exports to depth are much more uncertain).

Episodic particle flux and mass phytodetrital accumulation on the deep-sea bed in the North Atlantic

Phytodetrital mass accumulations on the deep-sea bed have perhaps provided the most dramatic evidence for episodic export of particles from surface production. These were first revealed by seabed photographs taken from a towed bottom sledge and from a time-lapse photographic system, Bathysnap (Fig. 11.3). These photographs showed mass sedimentation of organic detritus of phytoplankonic origin to the ocean floor in the Porcupine Seabight following the spring bloom in the Northeast Atlantic (Billett et al., 1983; Lampitt, 1985). Effective sampling of this flocculent material has been possible using a multiple corer (Barnett et al., 1984) developed by the Scottish Marine Biological Association (SMBA) – now the Scottish Association for Marine Science. This device utilizes hydraulic damping to allow the core tube to enter

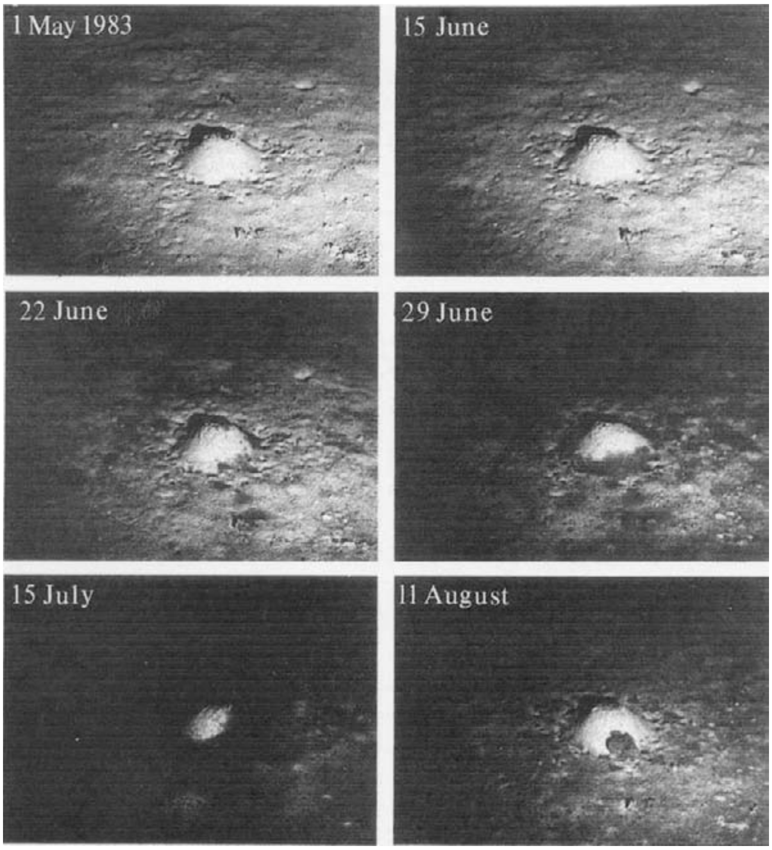

Fig. 11.3. Time-lapse sequence of deposition of phytodetritus on the deep seabed from 1 May (a) to 10 August (f) in the Porcupine Sea Bight at 4025 m depth in 1983. From Gage and Tyler (1991).

the sediment slowly without disturbing this light, superficial layer (Fig. 11.4). The material initially formed a green-coloured continuous phytodetrital carpet, *c.* 1 cm thick, subject to periodic resuspension and redeposition. In the bathyal Porcupine Seabight (Northeast Atlantic) the material becomes degraded, or incorporated into the sediment, within 4 to 8 weeks during the summer following deposition (Rice et al., 1986; Lochte and Turley, 1988).

Phytodetrital mass deposition was also detected on the adjacent abyssal plain at the German BIOTRANS site (Thiel et al., 1988/89; Pfannkuche, 1992, 1993), and on the Porcupine Abyssal Plain at the PAP site (at 47ºN) of British work (Rice et al., 1994). In the North Atlantic the spring increase in particle flux may start as early as January at 34ºN, and in March at 48ºN (Honjo and Manganini, 1993). However, seabed monitoring further south at 31ºN in the Northeast Atlantic on the Madeira Abyssal Plain detected no deposition. Rice et al. (1994) thought this to be associated with the shallower (<150 m thick) extent of winter mixing than that only 16º further north on the Porcupine Abyssal Plain (Rice et al., 1994). However, Christiansen and Thiel (1992) collected small amounts of phytodetrital floc in core samples from the station at 31ºN, and observed floc in depressions and around mounds on the Madeira Abyssal Plain at 34ºN. Processes and ecology in the water column may more likely explain such regional-scale differences described by Rice et al. (1994). But whatever the explanation such differences are accompanied by considerable differences in the structure and biomass of the benthic community, while deep-water particle flux at the present level of resolution (measured using sediment traps) appears similar.

Temporal pattern in deposition

During the intensive work on oceanic biogeochemical fluxes (Joint Global Ocean Flux Study, JGOFS), studies by British ships tracked the progressively increasing coverage by phytodetritus from south to north

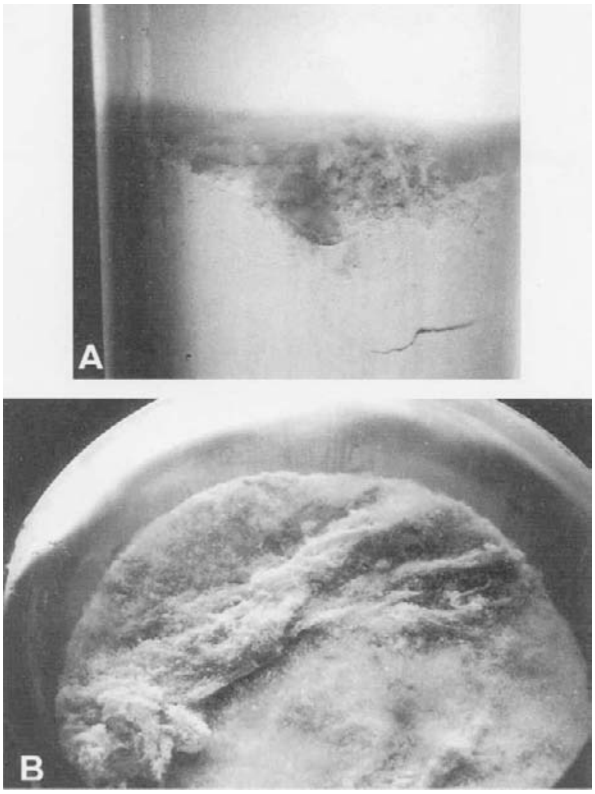

Fig. 11.4. Multiple corer sample of phytodetritus. A: Photograph taken through the side of the plastic core tube showing a sample from the abyssal seabed in the Northeast Atlantic with a layer of phytodetritus lying on the surface. A large gelatinous aggregate is visible in the front, which has been partially dragged into the sediment by the wall of the core tube. B: Surface of another core showing gelatinous membranes with incorporated phytodetritus. From Thiel et al. (1988/89).

along the 20ºW longitude meridian in the Northeast Atlantic. The main mass-deposition events closely follow spring/early summer blooms in phytoplankton at temperate latitudes, whereas they occur later (July/August) further north at about 60ºN. However, variability in this pattern from year to year may also occur; during the BENGAL program (see Chapter 5, Table 5.1, p. 114), an intensive study of benthic processes on the Porcupine Abyssal Plain (Northeast Atlantic) which took place in the late 1990s, a high mass flux to sediment traps 10 metres above the bottom was recorded in September 1996. During the following year such fresh material was absent, even in July when from earlier observations the peak in deposition is supposed to occur (Witbaard et al., 2000). At high latitudes, sedimentation following the spring bloom and later deposition of faecal pellets has been recorded (e.g., Wefer and Honjo, 1985; Graf, 1989). Pulses of sinking of organic particles of predominately zooplankton origin may occur later, following the earlier post-bloom sedimentation, whose composition reflects food-web interactions in the water column. This sedimentation, dominated by the remains of mid-water heterotrophs, may be larger and lag 1–2 months after the peak in primary production (Bathmann et al., 1990). Differences in the composition and dispersion pattern of the dominant heterotrophs, such as calanoid copepods or euphausiids, through differences in feeding pattern and vertical migration, lead to marked regional differences in quality and quantity of sinking material. This in turn modifies the seasonal signal ultimately derived from the euphotic zone by the deep-sea bed.

Mass deposition in the Pacific

Gelatinous detrital aggregates also occur in the Pacific off California, creating localized patches on the abyssal sea floor (K.L. Smith et al., 1998). Dramatic mass phytodetrital accumulations, unexpectedly, have also been documented from the equatorial central Pacific, where in places they form a continuous cover at least 5 mm thick with individual aggregates >1 cm in diameter (C.R. Smith et al., 1996). This occurred in November/December, and must have resulted from strong advective processes in the upper water column associated with the subtropical convergence, as there is no link to known variability in surface productivity at the site. Elsewhere at low latitudes high pigment levels suggesting mass pigment deposition has been reported from the tropical Southwestern Pacific off Australia (Alongi, 1987). These observations indicate that such pulsed delivery may affect a very wide latitudinal range, including areas thought to be lacking highly seasonal cycles in primary production. From Ocean Drilling Project cores taken in the eastern tropical Pacific, monospecific diatom mats sinking from the surface are thought to have occurred in the past over a large area. Their non-destruction by bioturbation provides evidence that deposition was sufficiently massive to smother the seabed and suffocate the benthic fauna (Kemp and Baldauf, 1993).

Composition of detrital aggregates on the sea bed

Analysis of phytodetritus collected from the sea bed in the Northeast Atlantic show it to consist of the remains of a variety of planktonic organisms embedded in a gelatinous and membranous matrix (Billett et al.,

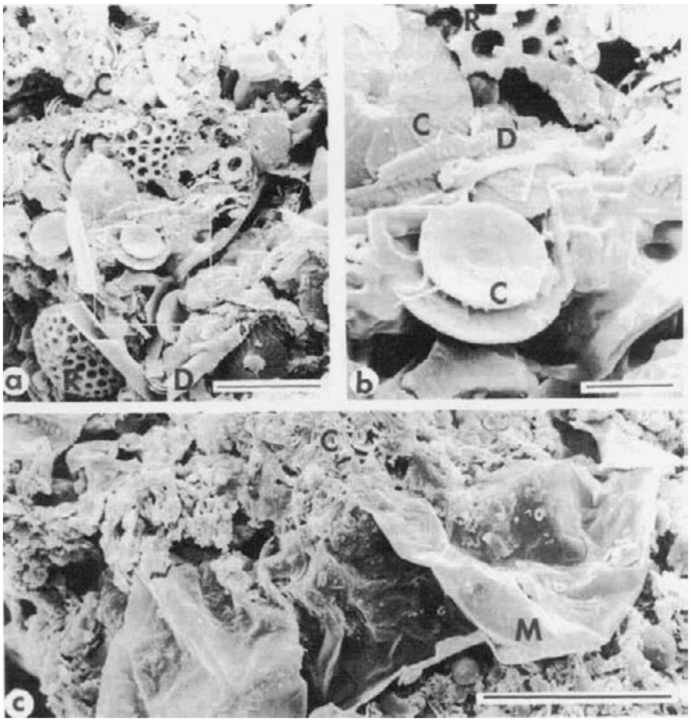

Fig. 11.5. Scanning electron microscope (SEM) images of fresh "green" phytodetritus collected in September from the abyssal Northeast Atlantic at the German BIOTRANS site, showing the skeletal hard parts of Radiolaria (R), diatoms (D) and coccolithophores (C). A: low-power image (scale bar = 10 μm); B: high-power image of middle part of A (scale bar = 3 μm); C: another part of the preparation showing membranous sheets (M) and masses of coccolithophore debris (C) (scale bar = 40 μm). From Thiel et al. (1988/89).

1983; Lochte and Turley, 1988; Thiel et al., 1988/89; Riemann, 1989). Samples of phytodetritus collected from the seafloor (Fig. 11.5) show the composition of algal species to be similar to that of the phytoplankton community at the surface. Composition changes from dominance by diatoms in spring to dinoflagellates in summer (Billett et al., 1983; Rice et al., 1986; Riemann, 1989; Thiel et al., 1988/89). The appearance of this material is variable, but the organic-carbon content is somewhat low depending on the state of degradation of individual samples; usually phytodetrital samples collected later in the summer are more degraded than those taken earlier. However, the presence of relatively undegraded algal cells and and viable Cyanobacteria reflect its rapid transit to the bottom (Lochte and Turley, 1988). A comprehensive comparison of chemical and biochemical parameters in the surface layer of sediment before deposition in March and that (consisting mostly of phytodetritus) of samples taken later in July/August when phytodetritus was present on the sediment is provided by Thiel et al. (1988/89). Although bacteria were abundant, numbers are lower by volume than in the sediment. This supports the interpretation of ongoing colonization of the material by barophilic bacteria, while those associated with it from the surface were inactive or dead. The latter interpretation is supported by the number of bacteria found by Thiel et al. (1988/89) in a state of degradation. Concentrations of biochemical compounds, proteins, carbohydrates, chloroplastic pigments and total adenylates, and bacteria appear to be considerably higher in sediment surface samples when phytodetritus was present than in equivalent samples in early spring prior to phytodetritus deposition. Pigment analyses, and the high content of particulate organic carbon, indicated that the material was relatively undegraded. Chloropigments, such as chlorophyll and phaeopigments, provide convenient biomarkers for other labile and biochemically important components such as poly-unsaturated fatty acids (e.g., Boon and Duineveld, 1996). The ratio between chorophyll-a and phaeophorbides has been used as an indicator of phytopigment freshness by Witbaard et al. (2000), phaeophorbide-a being produced exclusively by herbivore grazing.

Pfannkuche and Lochte (1993) used Cyanobacteria as a convenient tracer for tracking, in the faeces of salps, the rapid transport to the abyssal seabed of surface-derived phytoplankton during a mass swarming of salps in the Northeast Atlantic. On the seabed of the European continental rise, adjacent to the Porcupine Abyssal Plain off southern Ireland, gelatinous detritus was deposited in August. This material had a high chloropigment and nucleic acid content which could be identified as likely to be mainly from coccolithophorids, blooms of which are common features of peak surface productivity at the continental margin off northern Europe.

Beaulieu and K.L. Smith (1998) found the phytodetrital material in the abyssal Northeast Pacific to change seasonally. Chain-forming diatoms dominate just before the maximum in sinking flux, and are followed a month later by dominance by phaeodarians, an important group of sarcodine protozoans formerly included in the "Radiolaria". Both contain evidence of mucous material from zooplankton, with composition similar to that in sediment traps set above in the water column. These data indicate that phytodetritus can change dramatically in composition over a short period. Furthermore, K.L. Smith et al. (1998) found the chemical composition of detrital aggregates sampled from the bottom at this site in the abyssal Northeast Pacific to be similar to that collected in sediment traps 60 metres above the bottom.

Perhaps the characteristic of most importance, however, is the reactive state of the phytodetritus. The content of chloropigments provides a convenient indicator of this quality. Kinetic studies on detritus from the seafloor of the central equatorial Pacific Ocean show that reactivity is strongly age-dependent. The most reactive component includes chlorophyll-a, which is strongly correlated with phytodetritus (C.R. Smith et al., 1996). This component accounts for the vast bulk of on-going degradation, but only a small minority of the total inventory at any one time (Stephens et al., 1997). This suggests that other labile material escapes rapid degradation near the sediment–water interface, to degrade much more slowly in deeper layers. However, the role of benthic organisms and oxygen gradients in this remains unclear.

Causes of mass deposition on the deep-sea bed

A range of oceanographic/climatic phenomena may be responsible for pulsed particle flux (e.g., Thunell and Pilskaln, 1994). A phytodetrital floc occurring off California at a depth of 4100 m consisted of individual aggregates disappearing within hours to weeks (K.L. Smith et al., 1994), and with composition differing over short periods (Beaulieu and K.L. Smith, 1998).

Where they occur, mass accumulations of phytodetritus clearly are the result of blooms of phytoplankton, especially diatoms (Kemp and Baldauf, 1993), which deplete available nutrients so that they die and sink, and, because of their high concentration and sticky mucus production, become aggregated as rapidly sinking floc. It is still unclear to what extent the strong seasonality in particle flux detected in sediment traps (Wefer, 1989; Nair et al., 1989; K.L. Smith et al., 1992) results in mass accumulation on the bottom. Clearly, for such material to appear in quantity it has overwhelmed the usual ability of the benthic biota to consume and recycle it.

In conclusion, although the timing of their first appearance can be linked to major flux events resulting from surface phytoplankton blooms, the occurrence of mass accumulation does not necessarily mirror the time-integrated bulk peaks measured in sediment traps. Clearly a sharper temporal, and possibly spatial, resolution of bloom events in the euphotic zone, and the quality as well as quantity of export particles, will be necessary to understand bentho-pelagic coupling as manifested in mass accumulation on the deep-ocean floor. Furthermore, where mass accumulations occur one still needs to understand better the rate at which particles sink to the bottom, the associated biodegradatory processses and the nutritive value and subsequent utilization of particles by the benthos.

Interannual and mesoscale spatial variability in particle flux

I have already referred earlier (p. 323) to apparent interannual differences in mass flux of fresh detritus trapped just above the seabed in the Northeast Atlantic (Witbaard et al., 2000). Several other data sets have now identified year-to-year differences in this seasonal pattern. In the open ocean, these may result in qualitative and quantitative differences in delivery of fresh phytoplankton and heterotroph grazers, such as planktonic foraminifers, to the bottom. This may result from surface-water temperature and weather-driven variability in timing of the spring bloom, depth of the oceanic mixed layer, and the extent of surface stratification (Deuser, 1986; Thunell and Honjo, 1987; Vangriesheim and Khripounoff, 1990; Brock and McClain, 1992; Michaels et al., 1994; Townsend et al., 1994). Other possible causes are variability in the intensity of monsoon-driven upwelling (Haake et al., 1993; Rixen et al., 1996), or the El Niño Southern Ocean Oscillation (Karl et al., 1996), and in upwelling (Baldwin et al., 1998).

Such variability means that the export flux to the deep-sea bed will need to be measured over many years in order to obtain an accurate integrated estimate which can be related to the life spans of larger seabed biota. Furthermore, studies during the North Atlantic JGOFS experiments in 1989 uncovered unexpected mesoscale spatial variability. A massive sedimentation of particulate material was observed in autumn at one site, but was not registered in a trap just 100 km away (Honjo and Manganini, 1993; Newton et al., 1994). This difference is probably related to the eddy field at the time affecting the distribution of algal blooms in the surface waters (Newton et al., 1994). However, significant variability in particle flux at 100 metres above the bottom was also measured in sediment traps spaced from less than one metre to several kilometres apart in the abyssal Pacific off California (Crassous and Khripounoff, 1994).

PARTICLE DYNAMICS AT THE DEEP-SEA BENTHIC BOUNDARY

I shall here consider physical processes of redistribution of particles at and near the bottom within the benthic boundary layer. Other processes, mediated by larger burrowing animals, also occur, which contribute towards the biogenic mixing of sediments and, usually vertical, particle transport known as bioturbation. But this phenomenon, although important in its own right, will not be considered in this chapter, except where relevant later (p. 343) to the utilization of organic particles by the benthic biota.

Dynamics of fine particles

Realization of the redistribution of sediment by currents on the deep-sea bed dates from large-scale profiling of the sediment column by means of cores and acoustic profiling. In many areas large-scale sedimentary features, such as sediment drifts and ridges, have been mapped, which are thought to result from persistent thermohaline-driven current activity, particularly when constrained by major bottom topography such as the continental slope and rise. At smaller spatial scales the signature of bottom flow may be recognized in side-scan acoustic imagery and bottom photographs as bedforms ranging from dynamic ripples to huge, slowly migrating mud waves. One needs to examine such phenomena briefly in order to assess the importance of such transport in providing and redistributing food to the benthic boundary layer community.

To understand the dynamics of such large-scale particle redistribution, sedimentologists measure the cloudiness (transparency) of the water with a nephelometer. This measures transmission (attenuation) and the scattering of light by suspended particles. The result depends on both the concentration and size of particles, and on dissolved material in the water that reduces its transparency. The finest suspended particles are made up principally of clay-sized fine mineral particles forming fine sediment clouds (Thorpe and White, 1988). Such sediment clouds are thought to be be derived from resuspension by abyssal benthic storms that send bottom material high up into the water column to form nepheloid layers. More usually these sediment clouds remain close to the bed, forming a benthic nepheloid layer, or BNL (McCave, 1986). As a consequence such fine particles show up as increasing, rather than decreasing, in density nearer the bottom (see below). Nepheloids may form persistent layers hundreds of metres thick. Intermediate nepheloid layers may also occur through plume injection into the adjacent water column driven by breaking internal tidal waves on the continental slope (e.g., Dickson and McCave, 1986; Gilbert and Garrett, 1989; Ivey and Nokes, 1989; Thorpe et al., 1990). Even in deeper water on the continental rise nephelometry records have shown transient resuspension events (Beaulieu and Baldwin, 1998). These may be associated with energetic internal waves (Vangriesheim and Khripounoff, 1990) or driven by vorticity in flow in the upper water column which is propagated to the bottom to cause 'benthic storms' (Gardner et al., 1985). At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site on the Nova Scotia Rise the topmost layer of bottom sediment is periodically resuspended and redeposited by benthic storms that recur over a time-scale of weeks (see Chapter 2).

Intermediate and benthic nepheloids made up of these fine particles are likened to atmospheric clouds and mist. They appear to be conservative features in the deep ocean that can be traced far out over the abyssal plain, facilitated by isopycnal (lateral) eddy diffusion which is much greater than vertical

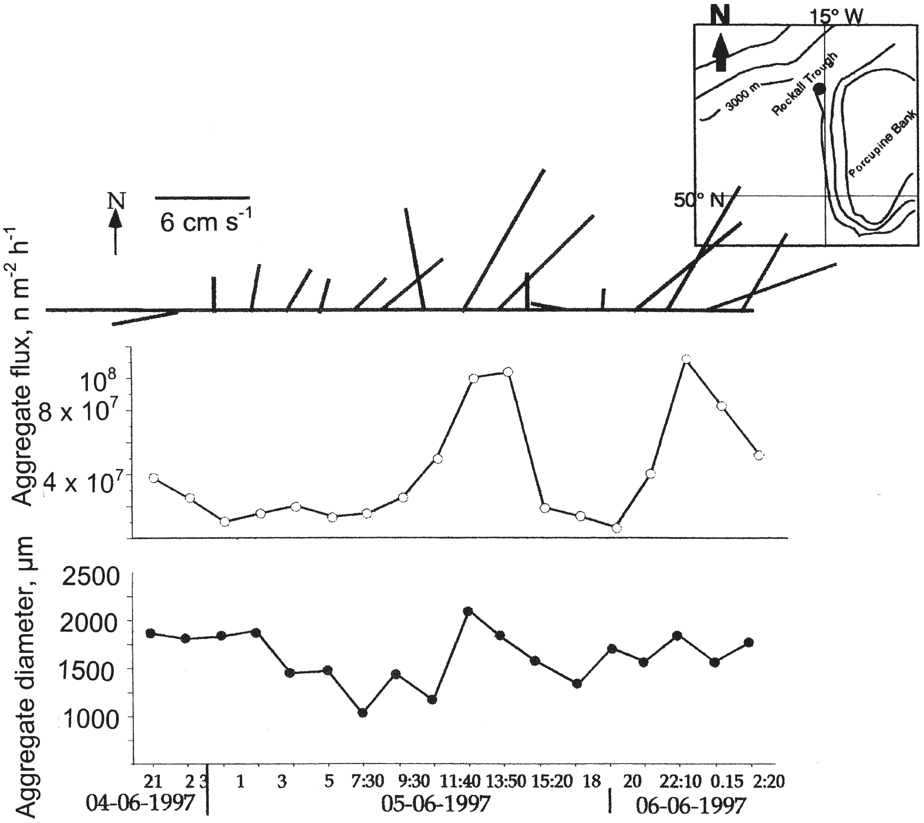

Fig. 11.6. Record from the Dutch benthic lander BoBo I of flow direction (upper), aggregate flux [*n* = number of aggregates] (middle) and median aggregate diameter (lower), measured during a 48-hr deployment in the southern Rockall Trough (Northeast Atlantic) at 2285 m depth. From Thomsen (1999).

eddy motions (Bauer and Druffel, 1998). Within and beyond the decadal time scale volcanic disturbances occasionally may also be an important source of lithogenic fine particles, especially in oceanic trenches.

Stokes Law calculations suggest that the finest particles, unless incorporated into mid-water biological packaging, would take decades or even centuries to settle passively to the sea floor. These calculations ignore their complex shape and vertical eddy diffusion, and hence may be gross underestimates. This also ignores scavenging by aggregates from the benthic boundary layer (Thomsen and McCave, 2000). However, the great age of organic carbon constituents (Bauer and Druffel, 1998) suggests that it may not be very important in the feeding of the deposit-feeding benthos – unless these particles become associated with faster-sinking material with a relatively high reactive organic content, such as marine snow particles containing photosynthetic pigment. I shall touch on this later in the context of the dynamics of particles on the continental margin.

Particle dynamics within the benthic boundary layer: intermediate particles

Largely because of the difficulty in making measurements, the importance of bottom currents in transporting the larger, aggregated particles sinking from the surface is still emerging. Most advection occurs on the slope. Improved instrumentation at the benthic boundary layer in the ocean basins (Fig. 11.6) now suggests that advective processes involving particle transport within the benthic boundary layer are of importance in the variability, on both the local and regional scale, in input of particulate organic carbon to the seabed, and hence the nutrition of the benthic boundary layer community. As more data emerge, it is becoming clearer that the lateral, current-driven advection of particle flux within the benthic boundary layer may supply the missing carbon necessary to balance the supply-side deficit measured from concurrent seabed respirometry and sediment traps in the nutrition of the deep-sea community (e.g., K.L. Smith, 1987). Such processes of redistribution must be taken into account in mapping carbon fluxes on the deep-sea floor.

Resuspension

Processes of resuspension, which provide the material transported by advection, had been inferred from some of the earliest sediment-trap data where the volume of material suddenly increased in traps set below 100 metres above the bottom after decreasing steadily downwards through the water. This process is now recognized as playing an important role in particle dynamics in the deep sea (Gardner and Richardson, 1992). Chemical analyses of material caught in a trap set by Honjo (1978) at 114 metres above the bottom at a depth of 5367 m in the Sargasso Sea showed that 60% of the total mass flux was resuspended material, mostly faecal pellets, containing 80% red clay. This material is categorized as the rebound flux (pp. 329–330) component of deep sediment traps (Walsh, 1992). For resuspension to occur after its initial deposition on the seabed, friction velocity (U^*) must exceed the critical erosion velocity of the deep-sea benthic boundary layer, the area of turbulent flow resulting from friction at the bed. This critical value (0.4 to 1.2, equivalent to between 7 and 20 cm s^{-1} at 1 m above bottom) is much lower for flocculent aggregates making up mass depositions than for the sediment layer below (Lampitt, 1985; Auffret et al., 1994; Thomsen and van Weering, 1998). It may therefore be important in the context of carbon dynamics to distinguish between rebound flux of organic aggregates from that of erosion of sediment particles below which contribute to benthic nepheloid layers (Walsh et al., 1988). There are still few data where aggregate deposition has been recorded by optical instruments or time-lapse photographs along with concurrent measurements of near-bed flow. Where this has been undertaken over long periods (e.g., Lampitt, 1985; Beaulieu and Baldwin, 1998), it is found that resuspension by periods of strong flow may occur along with rapid disaggregation, caused by biological processes (e.g., Gooday and Turley, 1990). Simultaneous measurements of downward particle flux, along with instrumentation to measure suspended particles, such as a nephelometer or transmissometer, have as yet been undertaken at only few sites. At K.L. Smith's time-series site, Station 'M', on the continental rise off California, records show not only local resuspension of recently deposited detritus, but also near-bed turbidity thought to be suspended particles advected from more energetic benthic environments on the adjacent margin (Beaulieu and Baldwin, 1998). Advection may explain discrepancies up to a factor of three in estimates of sea-bed respiratory demand and organic supply measured in sediment traps in the overlying water column (Jahnke and Jackson, 1987; Jahnke et al., 1990; K.L. Smith, 1987, 1992; K.L. Smith et al., 1992). Similar measurements by French workers, using an array of similar instruments mounted on the Module Autonome Pluridisciplinaire, or MAP, in the abyssal Northeast Atlantic, have observed that rapid disaggregation caused by biological utilization renders the particles more easily resuspended (Auffret et al., 1994). This, and deployments of this and similar bottom instrumentation, suggests that, like mass deposition of organic aggregates, resuspension may occur anywhere in the deep sea. Lateral transport of detritus of potential value as food to benthic biota may actually occur only during relatively narrow time periods. Such currents usually maintain particles close to the sea floor. Passage of a bottom current eddy may result in greater resuspension (see above) with both fine particles and aggregates taken higher into the water.

Resuspension of phytodetritus

The first observations of a mass accumulation of phytodetritus on the deep-sea bed were made on the gently sloping, bathyal area in the Northeast Atlantic, the Porcupine Seabight (Billett et al., 1983). Even moderate bed flow was sufficient to cause relocation of this phytodetritus by resuspension as it is much lighter than the underlying sediment (Lampitt, 1985). Bottom-camera evidence indicates that similar processes occur on the continental slope in the Northwest Atlantic (Hecker, 1990). There is now good evidence that advective redistribution of small particles can relocate reactive organic detrital material over considerable distances outwards onto the continental rise from the margin (Baldwin et al., 1998; Beaulieu and Baldwin, 1998). Hydrodynamic processes within the benthic boundary layer on the slope have been the subject of an important recent study in the European Ocean Margin Exchanges program (OMEX – see Chapter 5, Table 5.1, p. 114, on the Celtic Sea margin off southern Ireland in the Northeast Atlantic). This work has shown that hydrodynamic processes, in relation to bed structure

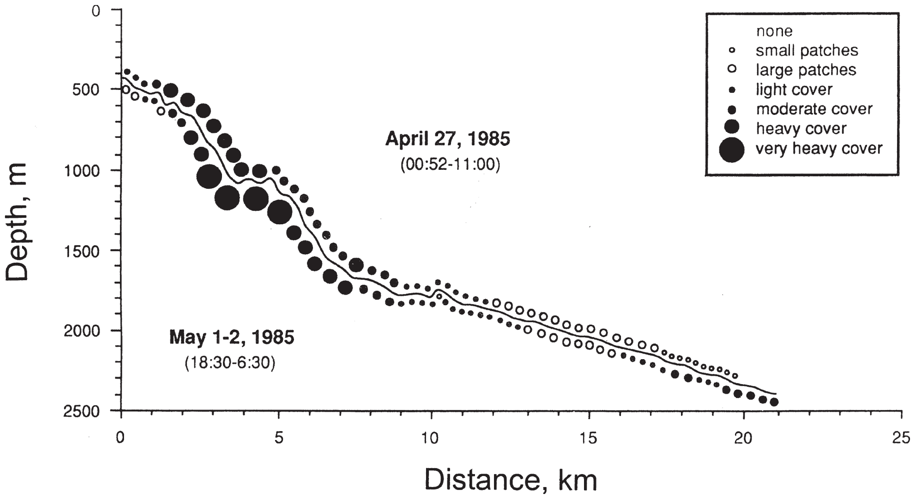

Fig. 11.7. Depth-related distribution of detrital material observed from camera-sled photographs taken in the spring of 1985 on the continental slope south of George's Bank, New England. From Hecker (1990).

and relatively high benthos activity, mobilize and aggregate intermediate-sized organic particles within the benthic boundary layer (Thomsen, 1999).

The conclusion must be that because of flow-driven advection, prolonged thick, mass detrital accumulations, as observed in the abyss, probably are transient. It is possible that they only occur where the current regime allows material to settle out and perhaps be concentrated in semi-enclosed bathyal areas. Examples include the Porcupine Seabight (Billett et al., 1983), and further north in the northern Rockall Trough just south of the Wyville Thomson Ridge, where even thicker floculant accumulations at the bottom have been observed (Dr. Brian Bett, Southampton Oceanography Centre, personal communication). On the continental slope, Hecker (1990) suggested that the thick carpet of detritus observed at mid-slope from camera-sled photographs might have been transported from the slope above. She observed that a downward shift in the maximum occurred within a few days, while at the same time more material appeared at the base of the slope (Fig. 11.7).

Upward flux

Resuspension of bottom sediment, known as 'rebound' flux, has long been known to affect sediment traps moored near the bottom. However, a research focus on resuspension of biogenic particles by turbulent events, such as benthic storms and breaking internal waves, as an upward material flux of organic material is more recent, dating from Simoneit et al. (1986). This phenomenon has been studied in the abyssal Pacific and Atlantic (K.L. Smith et al., 1989; Grimalt et al., 1990) using inverted sediment traps. The evidence is for a substantial upward flux of buoyant particles. It may total up to about two-thirds of concurrently measured downward flux, from which it is qualitatively different. Particles in inverted traps include much crustacean debris, lipid-rich eggs, and larvae, whereas algal material predominates in traps catching sinking particles (Grimalt et al., 1990). Not all the particles intercepted by inverted traps will have originated from the ocean bed (Angel, 1990). Eggs of some mid-water crustaceans will sink into deep water to hatch and these migrate vertically later. Some deep-sea benthic invertebrates, and some fish, contribute towards an upward flux. This is either because their eggs and planktotrophic larvae occur, or can be inferred to occur, near the surface (e.g., Bouchet and Warén, 1979; Rex and Warén, 1982; Tyler and Gage, 1984), or because they have been shown to be buoyant (Young and Cameron, 1987). Upward flux may control the biogeochemical cycling of some lipids in the deep ocean interior, the formation of buoyant material in abyssal waters selecting for certain lipids which are recycled back to the upper ocean, whereas other lipid components continue sinking to the bottom (Grimalt et al., 1990).

The phenomenon of upward flux underlines the importance of not relying on data from a single method, such as conventional, upwards-looking sediment traps, in order to measure organic input to the deep-sea ecosystem. Biogenic upward flux may be an important

Fig. 11.8. The seabed on the upper continental slope at 700 m depth off western Scotland. Large populations of suspension-feeding cerianthids (burrowing anthozoans related to sea anemones) with their tentacle crowns bent over facing into the current, along with interface-feeding small brittle stars, *Ophiocten gracilis,* are visible on the sandy mud bed, which also shows the sinuous locomotory furrows made of a sea urchin, *Spatangus rashi.* The string attached to the compass arm indicates a southward current. The field of view covers about 1.5 m across by about 2 m depth.

means for organic inputs to be integrated over a longer time frame where highly pulsed mass accumulations occur. To what extent such pulsed input is associated with seasonal reproduction to produce significant upwards fluxes later in the year, followed by re-input of organic material as biomass through mass settlement by larvae remains conjectoral. But there is now evidence for at least one example of biologically driven transport of this nature. This is provided by the seasonally breeding small brittle star, *Ophiocten gracilis.* This species forms dense populations on the upper continental slope (Fig. 11.8) in the Northeast Atlantic, and has a planktotrophic ophiopluteus larva that is very abundant in the oceanic surface plankton in summer (Geiger, 1963; Semenova et al., 1964; Tyler and Gage, 1982). These metamorphose to postlarvae in midwater, and are caught in large numbers in the bathypelagic zooplankton (Tyler and Gage, 1982). They may occur as a significant fraction of biomass in sediment traps set hundreds of metres above the bottom on the slope, and even occur on the adjacent abyssal plain (Sumida et al., 2000). Larvae may be transported by advective processes from the slope mentioned previously, this providing an example of significant biological export from the continental slope out to the abyss that is not associated with any benthic process.

Particle dynamics on the continental margin

Downslope processes may transport large quantities of material downslope. The most frequently occurring processes probably are internal tidal currents, particularly those focused down canyons. The present-day importance of much more dynamic events, such as sediment slumps and slides, and turbidity flows, for which submarine canyons may act as conduits (Heezen et al., 1955; Shepard and Dill, 1966), is more uncertain. However, Griggs et al. (1969) provided good evidence from postglacial structure in sediment cores, along with enhanced benthic biomass, from the adjacent continental rise and within the axis of the

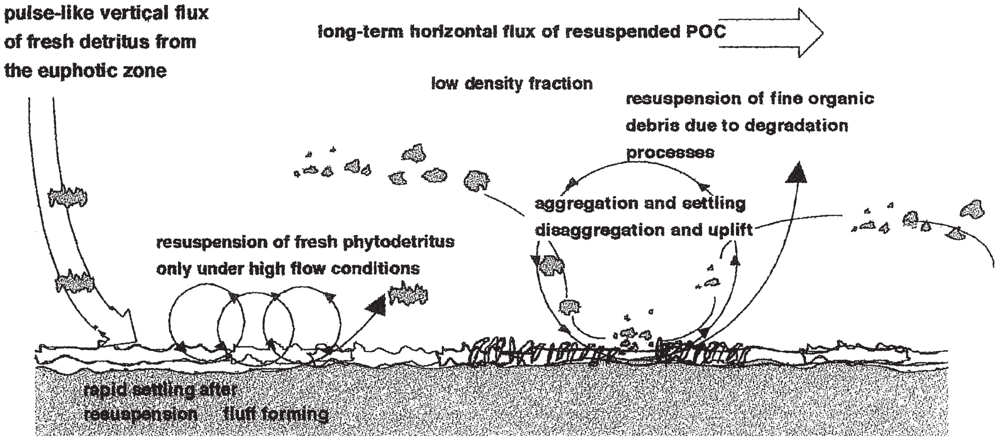

Fig. 11.9. Schema of hydrodynamic processes acting at different time scales controlling carbon input to the benthos on continental margins. From Thomsen (1999).

Cascadia Channel off Oregon that such processes are of ongoing significance to benthic consumers. Although these events occur over relatively long time-scales, when they occur enhanced organic-rich, small-particle flux resulting from turbidity flows may be experienced over large areas of the deep ocean adjacent to the canyons (Thunell et al., 1999). It remains unclear whether benthic fauna may benefit from persistence of organic-rich material in the sediment, or whether the enhanced benthic standing crop results from more frequent, but less dynamic, downslope processes such as topographically focused currents carrying supended particles.

The complex processes involved in a net transport down- and along-slope in the Northeast Atlantic have been addressed by measuring near-bed aggregate flux and its biologically mediated modification. New measurements have been made using a water sampling and particle camera system on the seabed, BIOPROBE (Thomsen et al., 1994). This has measured high densities of large, mainly organic suspended aggregates in the 0.1–5 mm size range at the Celtic Sea and Iberian margin in the Northeast Atlantic and in the Greenland Sea (Thomsen and Ritzrau, 1996; Thomsen and van Weering, 1998; Thomsen and Gust, 2000). Thomsen and McCave (2000) have shown that these aggregates originate, not from surface primary production, but from processes within the benthic boundary layer. Analysis of the particles shows up to 4.3% of the particulate organic carbon transported within the benthic boundary layer may be in the form of bacterial organic carbon attached to mineral as well as organic particles (Thomsen and Ritzrau, 1996; Ritzrau and Thomsen, 1997; Ritzrau et al., 1997; Thomsen and van Weering, 1998), with 35 to 65% of bacteria being attached to aggregates. Ritzrau (1996) has suggested that such aggregate-transported bacteria benefit from enhanced availability of nutrients, as a consequence of enhanced nutrient-flux properties resulting from the increased Reynolds number of the aggregates (Hill et al., 1992; Lazier and Mann, 1989). Phytodetritus, however, behaved differently, the particles showing settling velocities depending on the age of the material, but which were higher than those for particulate organic carbon. This results in hydrodynamic sorting of these fractions, with a short residence time in the benthic boundary layer for phytodetritus and a long one for particulate organic carbon (Fig. 11.9).

Experiments using an erosion chamber show that the aggregates may be resuspended from the sediment at critical shear velocities (U^*_{cr}) of 0.4 to 0.9 cm s^{-1}, values much lower than those for cohesive sediments (U^*_{cr} of 1.0 to 1.6 cm s^{-1}) and even for phytodetrital floc ($U^*_{\mathrm{cr}} = 0.9$ to 1.2 cm s^{-1}). The aggregates, which are not sampled by any usual sampling technique, thus provide the basis for a continuous resuspension loop of aggregation, settling and disaggregation that transports material laterally over long distances (Thomsen and Gust, 2000). The process involves scavenging of the finest, permanently suspended particles (see below). Thomsen (1999) has suggested that benthic organisms at continental margins more or less permanently live in a "marine snow flurry" consisting of resuspended benthic boundary layer aggregates.

RESPONSE AND UTILIZATION OF ORGANIC SMALL-PARTICLE FLUX BY THE DEEP-SEA BENTHIC BOUNDARY LAYER COMMUNITY

The benthic boundary layer community as a whole includes the bacterioplankton and zooplankton residing in the immediately overlying water, the near-bottom or benthopelagic fauna, and the community more intimately associated with the sediment and hard substrata, collectively known as the benthos. The total benthopelagic community would also include the larger, swimming organisms such as scavenging crustaceans and fish. This scavenging community will be addressed later (pp. 354–358) in dealing with large packages of passively sinking organic material. Apart from the small percentage living as predators or opportunist scavengers, such as some benthic crustaceans, brittle stars and sea stars, the remaining parts of the community are consumers of the detrital small-particle flux, whether sinking or laterally advected, and hence important in remineralization of particulate organic carbon. However, in view of the emerging view that much of the flux of new production from the surface arrives as episodic detrital pulses, the extent to which the community depends on such intermittent (possibly very infrequent), but probably highly nutritious, detrital food rather than on low-level 'background' fall-out is an important question. The subject has stimulated a relatively large research effort which will be referred to in the following pages, but a considerable amount of work is as yet unpublished.

Scaling of response

The manner in which detrital particles are dealt with by the benthic boundary layer community as food, and the consequences of benthic utilization on sediment mixing and particle transportation within the sediment, as well as on benthic population processes, is closely scaled to body size. For bacteria and micro-organisms the individual particles themselves provide habitat, and the population's response may cycle entirely on a single flake of marine snow, or faecal pellet. Such a population-level response will also apply to the smallest meiofaunal metazoans whose individual life spans occupy only a few weeks at most. Here increases in population densities will be the main response to seasonally pulsed flux in particles. Moreover, the strategy of utilizing particles for such small animals will be markedly different to that employed by larger metazoans. This results from the ability of meiofauna (and the young postlarval stages of macrofauna) to perceive detritus as individual particles so that they are able to select those of the narrow size range associated with most bacteria and organic particles (Self and Jumars, 1988). They will hence be macrophages specializing probably on the most nutritious particles, and their activity is restricted to the superficial layer of sediment.

In contrast, larger organisms perceive sediment as a bulk substratum that will, because of its usually low food value, require a range of specialized adaptations in order to maximize the return from foraging effort. Some of these mechanisms have important consequences in rapid relocation of fresh organic material deep within the sediment. Furthermore such larger metazoans have individual growth rates that may encompass several annual cycles in organic flux to the bottom. Hence, populations tend, as far is known, to be interannually stable, although with seasonally varying age structure reflecting any periodicity in reproduction and recruitment (Gage, 1994). This is not to say that densities of megafauna will necessarily be spatially homogeneous on the bottom. Indeed optimal foraging of motile species may involve mass shifts of populations, like the constantly moving herds of buffalo of the prairie. There may even be temporal shifts in community composition, as has been detected in the Northeast Atlantic on the Porcupine Abyssal Plain. These different activities will be considered below; but first one needs to consider data on the response of micro-organisms, which is, because of their tiny size, detected and measured in terms of its effects, such as solute flux or degradation of material substrates.

Response and utilization by micro-organisms, protists and smaller metazoan size classes

Microbial degradation

Data on rates of microbial degradation of organic inputs at the deep-sea bed date from the 1970s from experiments with labile material, such as bread or flesh, held just above the abyssal seabed. While some experiments indicated rapid rates of degradation, with some material being consumed or decayed within 10 weeks (Seki et al., 1974), others showing markedly reduced rates (Wirsen and Jannasch, 1976). Subsequent in situ studies have clarified this discrepancy. These observations confirm that barotolerant and barophilic bacteria are found right at the sediment–water interface where microbial activity is most intense (Deming and Colwell, 1985; Wirsen and Jannasch, 1986). Furthermore, large differences in microbial activity at this interface are found between oligotrophic and eutrophic sites in the abyss (Sibuet et al., 1993). These results contrast sharply with the results from the *Alvin* sandwiches, referred to earlier, which indicated inhibition of microbial activity at great depths unless accompanied by metazoan activity. Some explanation has come from data showing activity of pressure-adapted (barophilic) heterotrophic bacteria in or at the deep seabed is different from that associated with particles sinking down from the surface, whose activity and biomass become minimal below about 2000 m (Suess, 1988). Moreover, the activity of barophiles of the deep-sea bed adapted to low temperatures seems to vary in response to the quality, as well as quantity, of detrital material available (Patching and Eardly, 1997).

Response by meiofauna and Foraminifera

Little is known of the feeding characteriztics of metazoans belonging to the meiofauna. Yet this size class, consisting of both metazoans as well as larger protozoans, includes the most numerous members of the benthic fauna, and plays an important role in energy flow in the benthic system (Gooday et al., 1992; Tietjen, 1992). Meiofauna such as nematodes are thought to be important microbial grazers, probably themselves forming an important food source for deposit feeders. That these organisms do not depend directly on fresh particulate organic matter, but rather on grazing smaller organisms is supported by stable isotope studies (Iken et al., 2001). Stable isotope studies on komokiaceans (non-shelled foraminiferans with soft tests) also show strongly depleted values of δ^{13}N compared to particulate organic matter, indicating their main food also is not organic matter derived from phytoplankton. However, Iken et al. found some species with agglutinated tests and those forming 'mudballs' seem to depend more on phytoplankton-derived organic matter, while miliolids are known to ingest fresh phytodetritus (Gooday, 1988).

Sediment-community responses measured in terms of bulk biochemical parameters

French work in the 1980s in the BIOGAS program attempted to relate the organic composition of particle flux, measured in sediment traps at different stations in the Bay of Biscay (Northeast Atlantic), to that measured in the sediment (Khripounoff et al., 1985). The measurements showed an order-of-magnitude drop in the organic concentration in the superficial sediment compared to that trapped, but lacked seasonal coverage. The biochemical composition of this material was dominated by refractory humic-type compounds of high molecular weight which result from bacterial transformations, followed by labile proteins (17.4%), lipids (14%), refractory proteins (9.2%), and lastly labile sugars (3%). An index of selective nutritional utilization was derived as a coefficient of utilization based on the concentration in the trapped particles in relation to that in the sediment. This indicates that the sediment community utilize first the lipids, then the easily dissolved proteins and amino acids. The study concluded that refractory material accounted for about half of organic-matter mineralization in the energetics of the abyssal ecosystem, but did not take into account seasonality in particle flux or in the reactivity of the system.

Seasonal coverage was part of another approach by German workers employing bulk biochemical measurements as indicators of sediment community activity. Measurements of total adenylates [adenosine triphosphate (ATP), adenosine diphosphate (ADP) and adenosine monophosphate (AMP), reflecting the amount of plasma within cells] and phospholipid (reflecting the amount of biologically active surface membranes) provide proxies for the total biomass of benthic organisms in the small size class (bacteria, fungi, flagellate protozoans and small metazoan meiofauna). As indicators of activity, particulate ATP (found in mitochondria) and electron-transport-system activity (ETSA), and later in the study potential activity of hydrolytic enzymes, were measured. Results using these parameters in a long-term program at the German BIOTRANS site at 47ºN, 20ºW in the abyssal Northeast Atlantic, where organic flux is measured as total chloroplastic pigment equivalents (CPE) in the sediment, has shown a sensitive response to changes in organic flux (Pfannkuche, 1992, 1993).

Role of benthopelagic bacteria and metazoan plankton in carbon utilization and remineralization in the benthic boundary layer

There have been few attempts to address the organic utilization and metabolism of the bacterioplankton (bacteria not attached to detrital particles) and zooplankton of the benthic boundary layer. This is despite indications that the benthic bounday layer has the potential to respond rapidly to food pulses, and shows a high ingestion rate by zooplankton, suggesting that this community could have significant effects on carbon dynamics in the deep ocean (Wishner and Gowing, 1987). Although only a tiny fraction of the biomass at the surface of the ocean, biomass at 10 metres above the bottom, in response to the relatively enriched conditions in the benthic boundary layer, is nevertheless significantly greater than that at and above 100 metres above the bottom in the deep ocean interior (Wishner, 1980). Vereshchaka (1995) has provided a useful classification of the benthopelagic fauna in terms of their relationship with the bed. Some organims, such as peracarid crustaceans, may be regarded as benthopelagic by virtue of an ability to swim up into the water above. These animals may be an important part of the diet of larger benthopelagic and motile megafauna such as decapod crustaceans (Cartes, 1998). Studies of gut contents of benthopelagic zooplankton indicate that they feed on detrital particles and associated bacteria (Gowing and Wishner, 1986).

Studies of the rates of mineralization of organic carbon, which have included the small benthopelagic zooplankton (mainly copepods) along with bacterioplankton, have been conducted in the bathyal and abyssal Pacific. These studies indicate that respiratory demand by metazoan plankton and bacterioplankton together, disregarding the amount utilized in growth and reproduction, account in autumn for about 11% of the total estimated input of organic carbon to the benthic boundary layer (K.L. Smith et al., 1987). This study indicated that bacterioplankton respiration is more than an order of magnitude higher than that of the benthopelagic zooplankton, and this was confirmed in a more comprehensive study of all components of the benthic boundary layer community in the central North Pacific (K.L. Smith, 1992). As the most important consumer group of the benthopelagic community, oxygen consumption by bacterioplankton is nevertheless only about one-seventh that of the combined consumer groups represented in the sediment community. But nevertheless when compared to data for organic-carbon flux estimated for various other consumer groups in the benthic boundary layer (see K.L. Smith, 1992) the benthopelagic plankton is sufficiently important to merit inclusion in any attempt to model carbon and energy flow in the deep sea.

Carbon utilization and remineralization by the sediment community: measurement of oxygen consumption

Measurements *in situ* of solute flux across the sediment interface have provided the chief means of estimating rates of seabed mineralization as a measure of organic-carbon demand by the sediment, unenriched by addition of any further organic material. Virtually all of the organic input escaping burial is reduced by oxygen, the secondary oxidants NO_3^-, MnO_2, Fe_2O_3, and SO_4^{2-} occurring deep in the sediment and oxidizing only a small fraction of particle rain to the sediment (Bender and Heggie, 1984; Heggie et al., 1987). Some of the alternative pathways may operate at certain sites, such as upwelling zones on the continental slope. An example of this was provided by Jorissen et al. (1998) who found flourishing populations of foraminiferans living deep in reducing conditions in the sediment in the upwelling area on the upper continental slope off Cap Blanc, Northwest Africa. These foraminiferans were probably trophically dependent on anaerobic and sulphate- and nitrate-reducing bacteria. But such conditions are relatively exceptional, and never occur to the same extent as in the coastal zone. Therefore sediment community oxygen consumption (SCOC) probably provides a good overall measure of organic-matter mineralization.

Methods for measuring sediment community oxygen consumption (SCOC): Respiratory oxygen uptake has been traditionally measured in a sealed, stirred chamber, enclosing a small area of sediment. There is a need to take into account pressure adaptation and the effect of disturbance when measuring uptake from a core of sediment retrieved from the bottom. Sediment disturbance is important when a reactive flocculent layer of fresh detrital material is present, in which Pfannkuche (1993) found up to 80% of micobial respiratory activity to be concentrated. It is best avoided by a soft landing, with a controlled, slow emplacement of the chamber, which prevents any ‘bow wave’ effect that would blow superficial material sideways. If the activity of such flocculent material is not included, then artificially low values of sediment community oxygen consumption may be measured. Ideally the chamber is mounted on an autonomous vehicle, or benthic lander, in order to measure rates *in situ* (e.g., K.L. Smith, 1978; Hall et al., 1989). (Measurements of sediment community oxygen consumption from cores recovered from the bottom and incubated on shipboard tend to give higher values at greater depths than those measured *in situ*; see Glud et al., 1994; Duineveld et al., 1997). Details of the range of types of benthic chambers and the delivery system, or benthic lander, in present use are reviewed by Tengberg et al. (1995). Although varying in detail, the different systems consist of an inverted box or cylinder that is pushed into an area of sediment rarely exceeding 0.1 m^2 and usually much less. Another approach employs oxygen electrodes to provide microprofiles of dissolved oxygen in pore water, the gradient in cohesive sediment providing the basis for an estimate of diffusive flux and the depth distribution of oxygen consumption rates. Values measured by Glud et al. (1994) using a benthic chamber were 1.2 to 4.2 times the diffusive uptake measured by microprofiling at the same stations, the difference being correlated with the abundance of macrofauna in the sediment. However, when relating values to real seabed fluxes, effects of uneven stirring and bottom water oxygen concentration, should be taken into account (Archer and Devol, 1992). Another source of variability may occur at the local scale (Rowe et al., 1994). This can be addressed by mounting more than one chamber on the lander, and by recovering the chamber sediment to investigate the presence of larger organisms and other parameters (e.g., K.L. Smith and White, 1982; Pfannkuche and Lochte, 1990). At a slightly larger spatial scale this may be done by replication of deployments, or by using a manned submersible (see below). A new approach to this problem uses an autonomous tracked vehicle which is able to move, repeating measurements, over the abyssal bottom. This 'crawler' vehicle has already measured spatial and temporal variability over several months and sites at a depth of 4100 m off California (K.L. Smith et al., 1997).

Spatial patterns in oxygen consumption of the sediment community: In broad terms (integrating any seasonal variability in response to variability in detrital flux), the available data on oxygen demand of the sediment community indicate that it decreases with depth (Fig. 11.10). It falls from about 25 ml $O_2\,m^{-2}\,d^{-1}$ at 1000 m to about 1 ml $O_2\,m^{-2}\,d^{-1}$ at 5000 m. There seem to be three important factors influencing this pattern: 1) declining organic supply with increasing depth; 2) reduced temperature; and 3) pressure-inhibition of microbial activity.

Because benthic respiration must be supported predominantly by particle rain from the euphotic zone, basin-wide patterns in measured sediment community oxygen consumption broadly reflect the distribution of particle flux into the deep ocean (see pp. 317–326). As would be expected, measured rates show a positive relationship to surface productivity (Jahnke and Jackson, 1992). These authors estimated, from extrapolation of existing data for the Pacific and Atlantic Oceans alone, that seabed remineralization of the downward flux of organic matter to carbon dioxide accounts for 1–2% of global oceanic primary production, 4–10% of global new production (the excess escaping the recycling at the ocean's surface), and 33 to 40% of all remineralization of organic matter below a depth of 1000 m.

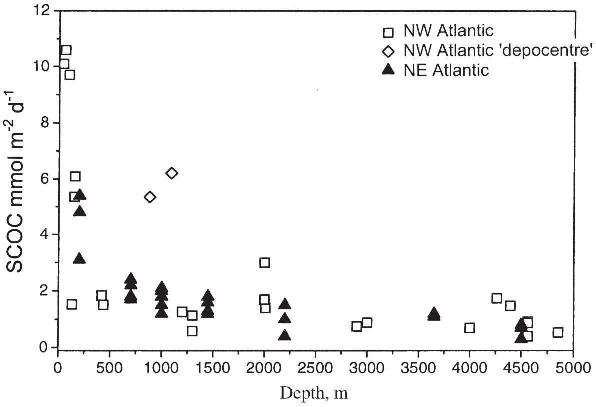

Fig. 11.10. Comparisons of rates of sediment community oxygen consumption (sediment community oxygen consumption) measured during the OMEX study in the Northeast Atlantic and the continental slope in the Northwest Atlantic. The two values (open diamonds) from the organic-carbon 'depocentre' on the Northwest Atlantic slope are the only ones to depart from the negative exponential trend. Data from various sources. From Duineveld et al. (1997).

Temporal patterns in sediment community oxygen consumption – response of microbial and other small size classes of the sediment community to mass phytodetrital accumulation: On the pattern of benthic respiration described above can be superimposed variability in direct response to seasonally varying input of organic matter. Clearly the response of the biota of the deep-sea bed to pulsed delivery of food is highly scaled to body size, with the smaller size classes being most reactive in terms of increasing biomass. This is, of course, closely associated with activity/mass ratio in the rate of population turnover of organisms. This is important in understanding the adaptations to cope with such variability.

Variability in the oxygen demand of the sediment community has been measured *in situ* by means of deployments made at different times of the year. Because of the different sources of variability mentioned above (pp. 334–335), seasonal changes need to be large to provide an unequivocal pattern. Nevertheless, a varying rate in oxygen demand, driven by the seasonal changes in organic flux to the bottom, has been detected at the abyssal station, Station ‘M’ off California (K.L. Smith and Baldwin, 1984b), the oxygen consumption of the sediment community being higher in early summer than in late autumn and winter. Later time-series data from the Californian margin out to the central North Pacific (K.L. Smith, 1987, 1992; K.L. Smith et al., 1994), have confirmed a pattern of variation in oxygen consumption consisting of up to fourfold seasonal increase associated with the peak in particle flux. However, demonstration of direct coupling to seasonally varying particulate flux from the surface has proved more elusive elsewhere. In the abyssal Northeast Atlantic at the German BIOTRANS site a seasonal increase in sediment community oxygen consumption (measured *in situ* using a benthic lander) was observed, with a doubling in consumption in July and August compared to April (Pfannkuche, 1992). But no such seasonality was detected in either the Porcupine Abyssal Plain at the BENGAL site (Witbaard et al., 2000), the bathyal Porcupine Seabight (Lampitt et al., 1995), or nearby on the Goban Spur (Lohse et al., 1998), or in the deep Sargasso Sea, southeast of Bermuda (Sayles et al., 1994), despite large variability in particle flux measured at the three sites. However, pore-water profiling of retrieved cores showed a seasonal pattern even if this was absent in concurrent *in situ* measurements of oxygen consumption by the sediment community (Witbaard et al., 2000). Although the reason for this is still unclear, and may be artifactual, the lack of the seasonal signal observed elsewhere has been related to low nutritional quality in particles (Sayles et al., 1994).

Several other studies have explicitly addressed the response of the small size classes of the deep-sea benthic community to phytodetrital mass accumulations (reviewed by Gooday and Turley, 1990). In the studies mentioned earlier at the German BIOTRANS site, measurements of various biochemical parameters and of sediment community oxygen consumption were taken at different times of the year, along with concurrent measurement of chlorophyll-a and of chloroplastic pigment equivalents (which include phaeopigments), both being a measure of reactive phytodetrital material. The close relationships between them indicate a highly geared response of the abyssal benthic community to sedimentation events, with transient increase in metabolic activity followed by increase in the biomass of small size groups (Pfannkuche, 1992, 1993). Year-to-year changes in detrital flux also might be reflected in the response by this size-class. Pfannkuche et al. (1999) found that the unusual pattern of early sedimentation peaks in March, followed by smaller, transient ones from June to August, at the BIOTRANS site in 1992 was reflected in various sediment parameters. The coupling was so close that it could be said that interannual variability in production in the surface water is closely mirrored in deep-sea benthic processes (Fig. 11.11).

Using the same approach, similarly tightly geared coupling of organic flux to the community in the small size class was detected on the adjacent continental margin off southern Ireland. Here, twin sharp peaks in deposition of chloroplastic pigment and response of transiently increased enzymic activity and biomass in the small size-class could be detected on the upper slope, one in mid-spring and the other in late summer (Pfannkuche and Soltwedel, 1998). This contrasts with the flatter summer-time deposition and response peak observed on the continental rise and abyssal plain.

Furthermore, Graf (1989), using incubation on shipboard of recompressed sediment cores taken in the bathyal Norwegian Sea, was able to measure higher rates in oxygen consumption in cores taken just after a detrital pulse to the seabed than in those taken before it occurred.

In the Pacific, Drazen et al. (1998) reported that protozoan densities and biomass increased significantly over a 4-week period following phytodetrital input, showing that these organisms can respond to organic-matter inputs within a time scale as short as weeks. These data help to explain the seasonal variability measured above. For example, although microbial biomass in phytodetritus was similar to that in superficial sediment, whether overlain by phytodetritus or not, there were many more dividing cells and larger mean cell volumes within the floc. Lochte and Turley (1988) and Thiel et al. (1988/89) found more bacteria in the sediment below the phytodetritus, and a subsurface peak at depths between 4 and 6 cm, probably resulting from the rapid incorporation of the labile organics into the sediment by macrofauna such as deposit-feeding sipunculans (see below). Another approach has addressed benthopelagic coupling by tracking biotransformation of radio-labelled dissolved organic substrates *in situ* in enclosed areas of sediment; in this case, at a depth of 2000 m in the Northeast Atlantic, rates of uptake, presumably microbial, measured in

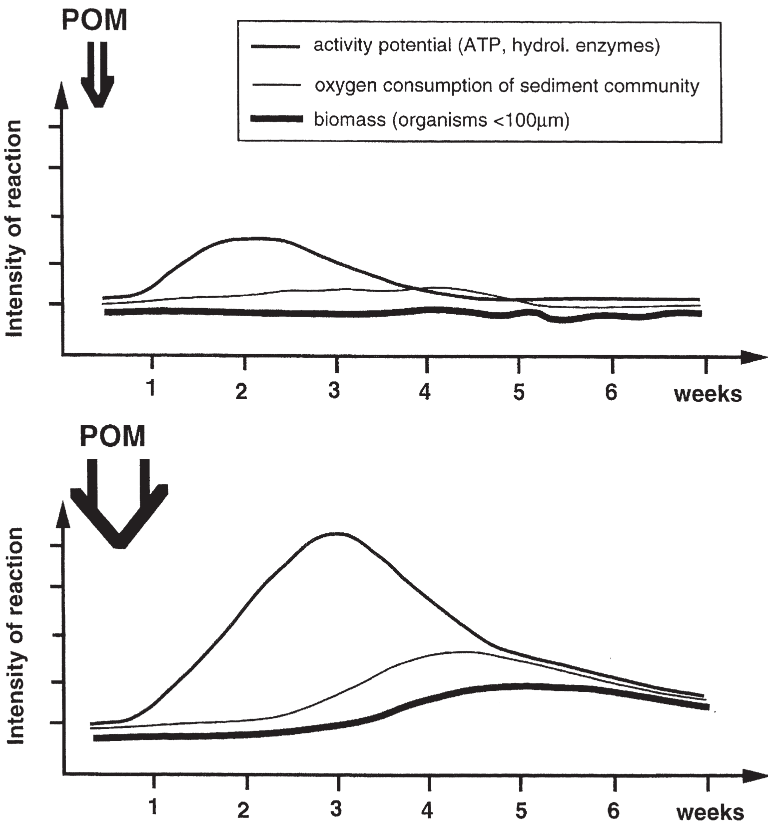

Fig. 11.11. Model of reaction of sediment community to mass sedimentation events. Upper panel: reaction to moderate event in early spring; lower panel: reaction to larger, later event. The amplitude of the response depends on the amount of flux of labile material. From Pfannkuche et al. (1999).

June were somewhat higher than those in August (Cahet et al., 1990).

K.L. Smith et al. (1998) were able, using the deep-diving manned submersible *Alvin*, to sample diffuse areas and patches of phytodetrital floc of different size and texture for *in situ* incubation using a core tube respirometer. They found that oxygen consumption of diffuse floc was similar to that in background sediment, but that discrete patches and those enriched with Radiolaria had significantly higher rates. Time-lapse camera monitoring showed distinct detrital aggregates covered up to 4.9% of the sea floor at their abyssal Station ‘M’ off California. These contributed substantially to the supply of organic carbon to the sediment community while apparently producing a minimal impact on sediment community oxygen consumption (0.34% of total annual SCOC at Station ‘M’).

Overall, it must be concluded from these differing patterns that particle quality is probably the key factor in understanding temporal variability in the metabolic and other activities of organisms living in abyssal sediments (Witbaard et al., 2000).

The linings of irrigated burrows created by metazoans provide hot-spots for microbial and meiofaunal activity (Aller, 1982), while burrows and depressions filled with phytodetritus are rich in bacteria and meiofauna which might respond within days to concentrated energy sources (J.Y. Aller and Aller, 1986). Incubations of heterotrophic micro-organisms and Cyanobacteria at *in situ* conditions showed a rate of activity that would consume natural detritus lying on the sea bed within two months (Lochte and Turley, 1988; Thiel et al., 1988/89). Further work has demonstrated an important response by barophilic bacteria (Turley and Lochte, 1990a). Respiration by these organisms colonizing detrital aggregates on the sea floor is estimated to contribute as much as 80% to the seasonal increase in sediment community oxygen consumption measured *in situ* (Pfannkuche, 1993).

Response and interactions at population level to mass deposition

Scaling considerations again determine that only the smallest size classes of organisms can show a response in terms of enhanced population abundance. These may themselves develop a mini food chain. For example, samples of phytodetritus recovered from the surface of multicores from the abyssal Northeast Atlantic became colonized by a variety of prokaryote micro-organisms (Lochte and Turley, 1988; Turley and Lochte, 1990b). These in turn are consumed by benthic allogromiid, textulariid and rotaliinid foraminifers, and by nematodes, which themselves also rapidly proliferated in the phytodetritus (Gooday, 1988; Turley et al., 1988; Gooday and Lambshead, 1989). A similar sequence of events occurs following the fall-out of organic material from surface production in shallow water (Graf et al., 1983). The organic particles are colonized by zooflagellates, amoebae, ciliates, and small metazoans such as rotifers and nematodes, which feed on the proliferating bacterial and fungal microflora associated with the particles of organic debris (see Fenchel, 1978).

In the deep Northeast Atlantic at 49ºN, Gooday (1993) has described the foraminiferal colonizers of phytodetritus as dominated by three species: two rotaliids, *Alabaminella weddellensis* and *Epistominella exigua,* and the allogromiid *Tinogullmia riemanni.* Their populations are able to respond rapidly to availability of phytodetrital floc, but numbers decline in a spectacular fashion at the end of summer when the material is no longer available (Gooday and Turley, 1990). These species are much rarer further south at 31ºN where only traces of phytodetritus have been observed (Gooday, 1993). It has been demonstrated experimentally that foraminifer species recovered from abyssal cores, including *Epistominella exigua,* can ingest microalgae supplied as food in high-pressure and low-temperature incubations (Turley et al., 1993). Because these species are not abundant in the sediment, they may be specialized opportunists. Other deep-sea foraminifers, like shallow-water forms, probably feed either by uptake of dissolved organic matter, carnivory, omnivory or suspension feeding (Lipps, 1983; Gooday et al., 1992), while others feed on organic detritus associated with sediment (Goldstein and Corliss, 1994). These in turn are grazed by macrofaunal asellote isopods, scaphopod molluscs and holothurians (Langer et al., 1995; Billett et al., 1988; Svavarsson et al., 1993).

Response of organisms within the sediment

The responses summarized above occur only within the phytodetrital microenvironment and therefore represent responses by highly adapted species to an ‘opportunistic’ lifestyle. This may also be true to a certain extent with the more generalized deposit-feeding elements of the sediment fauna below, which benefit directly by grazing phytodetritus and its associated micro-community. Other animals may benefit more indirectly as a result of the organic enrichment from faeces or dissolved metabolites from other consumers.

For example, although meiofaunal abundance is proportional to organic-food availability (e.g., Vanreusel et al., 1995), metazoan meiofauna such as nematodes may react in a less spectacular fashion than foraminiferans to phytodetritus. However, a clear increase in mean size of nematodes was shown at the German BIOTRANS site from April to July, followed by a sharp decrease (Soltwedel et al., 1996). Nematodes are found deeper in sediment experiencing phytodetrital mass accumulation than where such input is much less, but this may merely result from the activity of larger macrofaunal organisms mixing labile material deep into the sediment (Lambshead et al., 1995). However, this response is not shown by the metazoan meiofauna as a whole. Cores sectioned from the North Atlantic before and after a phytodetrital pulse showed no general migration towards the sediment surface, or any significant increase in population abundance. This suggests that meiofaunal metazoans as a whole failed to exploit phytodetritus as rapidly as Foraminifera (Gooday et al., 1996). It was argued that this reflected a competitive superiority of Foraminifera over metazoan meiofauna in exploiting a recent sedimentation event. However, the twofold increases in bulk abundance of meiofauna (mainly nematodes) shown in seasonally contrasting samples from the bathyal Mediterranean (de Bovée et al., 1990) and the Northeast Atlantic along the Hebridean margin (Mitchell et al., 1997) indicate a response over a longer time scale. Similarly, in the Pacific at Station ‘M’ off California, Drazen et al. (1998) found agglutinating foraminiferans and most small metazoan taxa showed seasonal increases in density during the winter months after detrital aggregates had disappeared and about 8 months after the peak in sediment community oxygen consumption and particulate sinking flux. Other work has demonstrated a summer-time increase in the heterogeneity of nematode populations in response to springtime deposition of phytodetritus (Lambshead and Hodda, 1994; Rice and Lambshead, 1994).

Response of larger metazoans to particle flux: body-size scaling, particle selection and choice of feeding method

The majority of multicellular organisms of macrofaunal size and above inhabiting deep-sea sediments utilize sedimented detrital particles as food. I have mentioned above that dietary response is closely dependent on body-size scaling. Whereas the smallest micro-organisms and metazoans can rapidly expand their populations in response to the availability of labile particles, those of macrofaunal size and above have life-spans extending well beyond the times of plenty. It is not known whether this has proved to be an important factor in the trend towards body-size miniaturization observed in traditionally 'macrofaunal' taxa compared to shallow water. As a consequence macrofaunal taxa are of meiofaunal size in the deep-sea miniaturization (Thiel, 1975; Gage and Tyler, 1991; Rex and Etter, 1998). But little is known, for example, of the potential abilities of metazoans to select individual particles actively, despite presumably powerful evolutionary pressures on deep-sea sediment-dwelling fauna towards adaptation to cope with scarcity of food. One argument is that by reducing body size and increasing motility organisms are able to forage more efficiently for the few labile particles available (Jumars et al., 1990). These authors cite observations of relative enlargement of feeding palps in protobranch bivalves in relation to their much diminished body size, with gut contents packed with diatom remains (Allen and Sanders, 1973), perhaps suggesting an ability to evaluate individual particles before ingestion. Another advantage of size is a relatively greater gut volume compared to smaller organisms. In the deep sea, organisms seem to have relatively large gut volumes in relation to their size. Comparisons of closely related species pairs conclusively show a greater gut volume than in shallow water (e.g., Allen and Sanders, 1966). However, because rates of deposit ingestion lag behind the linear increase in gut volume in relation to body size, residence times of material within the gut will be longer in larger deposit feeders (Cammen, 1980), and will favour more complete digestion and absorption of particulate material (Jumars et al., 1990).

Simple calculations of probable individual feeding rates of surface deposit-feeding animals from the geometry of foraging radius in relation to estimates of particle flux arriving on the bottom suggest that each sediment particle will be repeatedly reingested before its final burial. For larger metazoans of macrofaunal size, or larger, the only exception to a constraint to unselective, bulk particle processing will apply to their early postlarval stages. Their small size will enable them to feed selectively on individual particles in the same way as other metazoans of meiofaunal size (Jumars et al., 1990). However, as adults their strategies for intercepting and ingesting these particles are usually separated between suspension and deposit feeders, depending on adaptations to either intercepting somewhat unselectively particles suspended in the water, or ingesting them in bulk as settled particles forming part of the sediment. In shallow water attempts to categorize particular fauna are often complicated by the flexibility in feeding habits shown by many species.

Feeding type and hydrodynamics on the continental margin: localized populations of suspension feeders

There are strong associations between the feeding types in the benthic community and hydrodynamic conditions at the continental margin. Typically, suspension-feeding organisms dominate on the upper slope, while interface feeders (able to feed on organic particles either when lying on the surface or when resuspended by currents) mainly occur in the higher-energy mid-slope zone. On the Celtic Sea continental slope off Ireland, Flach and Thomsen (1998) found a peak in density and biomass of benthic interface feeders between depths of 1000 and 1500 m where flow is most vigorous. Further north on the slope off Scotland, dense populations of macrobenthic organisms, such as the brittle star *Ophiocten gracilis* and cerianthid sea anemones (Fig. 11.9), probably subsist on particles moving over the sediment between depths of about 700 and 1000 m (Lamont and Gage, 1998). Below this zone deposit feeders dominate at both sites (Flach and Heip, 1996; Flach et al., 1998, and personal data from the Hebridean margin).

On the upper part of the continental slope, highly depth-localized bands of suspension-feeding epifaunal organsims may occur. Examples include cold-water coral banks (Frederiksen et al., 1992), dense fields of large species of demospongids (Klitgaard et al., 1996), and, at greater depth on the slope, aggregations of the hexactinellid sponge *Pheronema carpenteri* (Rice et al., 1990; Barthel et al., 1996). The demosponges, including large species of *Geodia*, *Isops phlegraei*, and *Stryphnus ponderosus*, have long been known by fishermen as "ostur" (meaning "cheese bottom") occurring along the shelf break around the Færøerne (Northeast Atlantic), where sponges may constitute more than 90% of benthic biomass, excluding fish. Other suspension feeders, such as the cold-water coral *Lophelia pertusa,* large octocorals (Alcyonaria), stylasterids (large Hydrozoa) and some brachiopods seem to occur in the same areas.

Frederiksen et al. (1992) suggested two possible mechanisms related to intensification of bottom mixing to account for the localized occurrences of coral. In the first (Fig. 11.12A), internal waves are generated by advection of stratified water across bottom contours by the barotropic tide (geostrophic velocity constant with depth). These will propagate along pathways determined by the stratification, with one towards and one away from the shelf from a zone of critical slope, determined by bottom contours (New and Pingree, 1990). Vertical mixing is enhanced where these reach the seasonal thermocline, typically generating two nutrient-rich bands, each about 10–20 km wide, on each side of the shelf. The sponges and coral are thought to benefit from increased detrital flux resulting from phytoplankton production, which is advected at rates of tens of kilometres per day.

The second mechanism (Fig. 11.12B) applies to deeper-water populations on the slope, but is independent of depth. This is an intensification of bottom mixing in relation to areas of particular bottom slope (Wunsch, 1968; Cacchione and Wunsch, 1973). Thickening of the bottom caused by this local increase in mixing intensity results in particle resuspension from the bottom. Where vertical density gradients exist, horizontal density gradients will form between the benthic mixed layer and stratified water away from the bottom, driving particle-rich water from the benthic boundary layer out into the open ocean, forming tongue-like extrusions from the slope (e.g., Dickson and McCave, 1986; Thorpe et al., 1990). Once away from the slope, reduced turbulence means that particles start dropping out, again enhancing conditions for suspension-feeding downslope. Because of contour-following currents, particles may be advected laterally as well, so that effects may be transmitted far from the original source of enrichment. More information, however, is needed on the characteristics, particularly food quality, of these particles before the importance of these processes to the organism can be assessed.

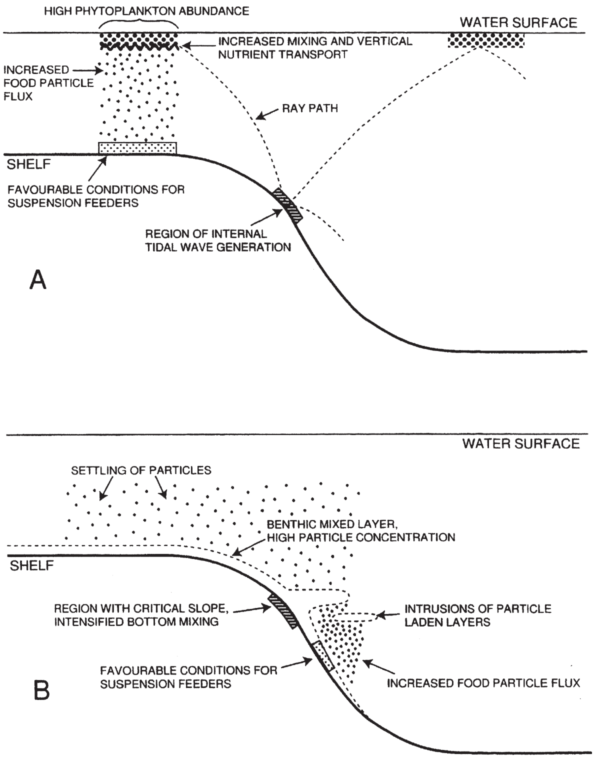

Fig. 11.12. Internal tidal mixing on the upper continental slope. A: scenario with increased particle flux at shelf edge; B: scenario for deeper mixing. See text for further details. From Klitgaard et al. (1996).

Suspension feeders markedly decrease in importance with increasing depth, reflecting increasing sparseness in number or quality of suspended particles. Furthermore, there is a well-developed trend for taxa normally associated with suspension feeding in shallow water to have evolved into carnivorous or possibly deposit-feeding life-styles in the abyssal zone. It is only in areas with enhanced current flow, such as topographic highs like seamounts, that obviously recognizable suspension feeders may again become prominent (Gage and Tyler, 1991).

Suspension-feeding methods in larger size-classes

Passive particle interception exploiting current shear is usually achieved by means of a system of meshes or fibres. These include the pseudopodial networks of large, branching komokiacean foraminiferans, the outstretched arms of ophiacanthid brittle stars and isocrinid sea lilies, the tentacles of cnidarians and bryozoans, and the branchial basket of ascidians. These

Fig. 11.13. Oblique view of the seabed on the continental slope west of the island of Lewis, Scotland, showing a field of xenophyophores (giant amoeboid protozoans), *Syringammina fragilissima,* at 900 m depth. The field of view is about 1.5 m across by 2 m deep. Photo taken by Dunstaffnage Marine Laboratory for Enterprise Oil Ltd, with permission.

organisms intercept particles, often using morphology or body orientation to enhance particle capture (e.g., Vogel, 1978), from externally driven flow as streamlines around fibres, this being the most hydrodynamically efficient way to screen the water (Rubenstein and Koehl, 1977). Active particle interception is achieved by those taxa, such as bivalve molluscs, able to pump water into a cavity equipped with complicated ciliary mechanisms using mucus which enables the animal to select particles efficiently (LaBarbera, 1984). Active suspension feeders disappear first with increasing depth as particle density diminishes, while even passive suspension feeders can only survive by efficient utilization of current flow in the benthic boundary layer (Gage and Tyler, 1991).

The tentacular structures of cnidarians associated with mucus production helps the animal entrap particles. Some have associated structures, or organelles such as nematocysts, which are able to sting and kill small zooplankton. These help to catch small living prey and by so doing provide continuity of suspension feeding with carnivory. This trend is particularly evident in the deep sea where, at least in the relatively hydrodynamically tranquil abyss, evolutionary pressure is towards maximizing opportunities for intercepting particles, which may be alive, and only limited opportunity for feeding on resuspended detrital particles. This comes from energetic considerations where active suspension feeding can only succeed where the returns repay the cost of pumping, whereas passive suspension feeders succeed where particle concentration is high, and flow conditions are predictable and fast enough. This may explain the entirely deep-sea distribution of some enigmatic organisms, called xenophyophores (Fig. 11.13), which are very large agglutinating rhizopod protozoans. Their often reticulate and folded tests may act as passive particle traps (Levin and Gooday, 1992).

It has been noted that suspension feeders dominate on the continental shelf and upper continental slope where dynamic flow regimes often prevail. The colonial, cold-water coral *Lophelia pertusa* is able to take in particles up to the size of live zooplankton (Frederiksen et al., 1992), while other large epifaunal suspension feeders, such as demospongids are limited to smaller particles from bacterial size up to a few microns (Witte et al., 1997). However, study of the gut contents of the abyssal sea anemone *Sicyonis tuberculata,* with a tentacle spread of *c.* 28 cm, indicates that this suspension feeder is able to take particles in a wide size-range, from less than 4 mm across to motile megafauna of similar size to itself (Lampitt and Paterson, 1987). This gradation by sessile suspension feeders into carnivory is characteristic of other groups in the abyss, such as benthic tunicates (Monniot and Monniot, 1978). Lampitt and Paterson (1987) also indicated that a similar microphagous and macrophagous diet applied to the deep-sea anemone *Actinoscyphia aurelia,* previously thought to be an obligate detrivore (Aldred et al., 1979). Values for δ^{13}N in stable isotope studies undertaken by Iken et al. (2001) on megafauna from the BENGAL site on the Porcupine Abyssal Plain have confirmed that sessile microphagous organisms such as the sea pen *Umbellula* sp. show varying values indicative of feeding on higher trophic levels as well. In deep-sea sponges Iken et al. (2001) found even higher δ^{13}N values in an hexactinellid sponge, but this possibly may result from symbiotic bacteria as well as small particles serving as a source of nutrition, as has been described for some shallow-water sponges (Arillo et al., 1993). Iken et al. speculated that such bacteria may be able to metabolize highly refractory material, which can then be assimilated by the sponge. Little else seems to be known of the nature or size spectra of the particles taken by deep-sea suspension feeders. However, seabed photographs commonly show the tentacle crowns of such organisms actively orientated upstream to the direction of flow. Lampitt and Paterson (1987) were able to monitor the upstream orientation of *Sicyonis tuberculata* in relation to changing flow direction and speed using the in situ time-lapse camera system Bathysnap, and from this estimated that the anemone feeds about 150 times per day on a wide range of material. The disc-shaped filter facing into the prevailing current is particularly efficient at intercepting suspended particles (Leversee, 1976; Warner, 1977). This explains why feeding is influenced by the fan shape of sessile suspension feeders, such as gorgonians. However, deep-sea gorgonians frequently also have a low, bushy structure which will be equally efficient in all directions of flow.

Importance of bacteria attached to suspended particles as food

It has been observed that erosion/deposition cycles that are characteristic of areas subjected to very strong flow stimulate the growth of sedimentary bacteria attached to lithogenic sediment particles (Yingst and Rhoads, 1980; Wainright, 1987). These particles will then be of some nutritive value to bottom biota that are able to intercept them in suspension or when redeposited. However, many suspension feeders are not abundant in the most energetic sites, perhaps because such high densities of suspended particles act to block filtering mechanisms (Thistle et al., 1985). They may, however, be more abundant at slightly less energetic sites (Gage et al., 1983), along with a higher-than-expected macrofaunal biomass (e.g., Gage, 1979). Shimeta and Jumars (1991) have reviewed the complex suite of factors affecting efficiency in capturing and ingesting particles by suspension feeders.

Interface feeders

Studies of some smaller macrofauna, such as spionid polychaetes and Foraminifera, have revealed a response where the organism, by means of a relatively simple change in behaviour, may change to feeding on suspended particles rather than on particles lying on the sediment surface. These 'interface' feeders can switch to suspension feeding, depending on flow energy, by a simple re-orientation of feeding appendages into the overlying water (Taghon et al., 1980; Dauer et al., 1981). Switching modes may be associated with markedly differing rates of particle ingestion and somatic growth (Taghon and Greene, 1992). Thomsen et al. (1995) provided experimental proof that interface feeding may be very effective in removing suspended material from near-bed flow (Fig. 11.14). Flach and Heip (1996) and Flach et al. (1998) came to the startling conclusion that interface feeders (mainly branching, arborescent agglutinating foraminiferans able to use a pseudopodial net to catch particles) may be the predominant feeding mode in smaller macrobenthos at intermediate depths on the continental slope. This, perhaps as much as any measurement of physical conditions, underlines the short temporal scales of change in flow conditions that characterize conditions in the deep-sea benthic boundary layer on the slope.

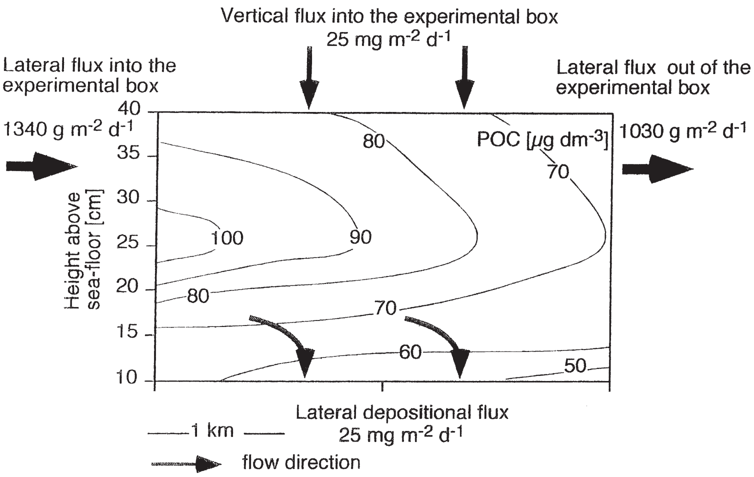

Fig. 11.14. Concentration gradient for particulate organic material in the benthic boundary layer of a mid-slope station, showing the effect of a dense population of macrofauna dominated by the interface-feeding polychaete *Myriochele* sp. in the western Barents Sea. From Thomsen (1999).

Deposit feeding in larger size classes

It has been said that many of the problems inherent in deposit feeding differ only in degree from problems of suspension feeding. It has already been seen that categorization may obscure a more flexible approach shown in many smaller infaunal invertebrates that are neither obligatory suspension or deposit feeders, termed interface feeders. Under 'normal' conditions (i.e. not those where mass accumulation of rapidly sedimented labile organic detritus occurs on the bottom) the potential food of deposit feeders seems an unpromising mixture of lithogenic and biogenic particles. These have a very low and refractory organic-carbon content, and sparse populations of micro-organisms (Jannasch and Wirsen, 1973; Sorokin, 1978; Deming and Colwell, 1982; Tabor et al., 1982). Faced with this, the foraging strategies of deposit feeders need to be efficient, and also target their activity to where maximum return on effort is obtained. Unlike coastal sediments where deeper layers may carry substantial quantities of organic matter, many more (but not all) deep-sea metazoans focus their deposit feeding on the very surface layer of sediment, where particles are most likely to be of nutritive value under conditions of low sedimentation. As a consequence, seabed photographs characteriztically show the imprint of their activity (Fig. 11.15), even at the low population densities in the deep sea. However, the extent to which megafaunal biomass decreases with increasing depth in the deep sea is less well established than similar trends in macro- and meiofauna. This is because in the abyss the megafaunal community is rarely effectively sampled in trawls (Rice et al., 1979). The usual evidence of the activity of megafaunal deposit feeders is from the variety of feeding traces and other marks associated with biogenic particle transport on the sediment surface (Heezen and Hollister, 1971; Gage and Tyler, 1991). However, Kaufmann and K.L. Smith (1997) found from time-lapse camera studies of the seabed that only a minority of megafaunal species of deposit feeders left distinct traces on the seabed, so that these traces underestimate the true scale of megafaunal deposit feeding. Furthermore, the spatial distribution of epibenthic megafaunal taxa may be highly variable (Grassle et al., 1975; Lauerman et al., 1996).

Alimentary adaptations of large deposit feeders and the role of gut bacteria

Larger size classes relying on deposit feeding require efficient methods for bulk processing of large amounts of sediment through their alimentary tract. Rates typically lie in the range of 0.4 to 120 mg ingested sediment per milligram of body weight per day (Lopez and Levinton, 1987). Chemical-reactor theory has been applied in conceptualizing deposit feeders as plug-flow reactors, where reactants continuously enter and products continuously exit with no mixing along the flow path (Penry and Jumars, 1987). There has also been a view that deposit feeders are reliant on bacteria and other microbiota for providing essential proteinaceous nutritional requirements that cannot be met by the animal itself (Phillips, 1984).

Fig. 11.15. The seabed on the middle continental slope off western Scotland at 1500 m depth. At this depth the populations of suspension and interface feeders (Fig. 11.9) have entirely given way to mostly infaunal deposit feeders; burrowing traces (as pits and mounds) are visible all over the fine muddy bed.

Although the activity and turnover of barotolerant deep-sea bacteria may be pre-eminent in overall deep-sea organic remineralization, it seems more likely that microbial food chains involving prokaryotes and other microbiota, along with small meiofauna, are important as food resources for bulk deposit feeders (Gooday, 1988). There has been a sharp divergence in viewpoint regarding how organic material in the gut is made available to the animal. High rates of barophilic microbial activity have been measured from the gut of deep-sea deposit feeders, with generation times of 2.4 hr in the hindgut of an abyssal holothurian (Deming and Colwell, 1982). However, Plante et al. (1990), in a review of digestive associations between deposit feeders and bacteria, have argued that high microbial activity in the gut is a consequence of the material in the gut, rather than being necessary to the animal in order to break down organic material. On the other hand, it has been thought that the activity of these symbiotic barophilic bacteria in breaking down refractory organics confers a powerful adaptive advantage to those bulk deposit feeders possessing them. For example, studies on the burrowing sea urchin *Echinocardium cordatum* from shallow water have shown that part of the gut functions as an anaerobic reactor with increased numbers of micro-organisms present and that microbial fermentation also occurs in gut caecae, resulting there in accumulation of organic matter. The digestive strategy of this animal appears to provide for breakdown of refractory organics and the gut also supports flourishing colonies of, possibly symbiotic, zoosporic fungi and protozoans (Thorsen, 1998, 1999). Similar adaptations may occur in deep-sea sea urchin species in order to increase the dietary availability of refractory material.

Ingested bacteria, along with diatoms, protozoans and nematodes, may provide some important biochemical components in the diet for larger deposit feeders (Phillips, 1984). This certainly seems to be the case for many sea urchins (e.g., Fong and Mann, 1980). Furthermore, study has shown that the gut of deposit feeders is an intense reaction zone, thanks to the surfactant properties and powerful battery of extracellular enzymes in the digestive fluid (Mayer et al., 1997). This results in more than 90% of ingested bacteria being removed by enzymatic action;

but work has also shown that microbial biomass does not itself constitute the major food source for detritivores (e.g., Kemp, 1987; Plante et al., 1990; Plante and Mayer, 1994). Mayer et al. (1997) have shown that similarities in the enzymatic profile between deposit- and suspension-feeding polychaetes are much greater than between deposit-feeding polychaetes and holothurians. This suggests that the biochemical nature of the food digested is different between these two important deposit-feeding taxonomic classes, even if they are considered functionally similar. Evidence from sediment distribution, enzyme and bacterial profiles along the digestive tracts of *Oneirophanta mutabilis, Pseudostichopus* sp. and *Psychropotes longicauda* in the abyssal Northeast Atlantic indicate gut tissue, rather than bacteria, as the main source of enzymes, while between-species differences in some glycosidases, such as chitobiase, suggest dietary differences (Roberts et al., 2001). These authors indicate that differences in bacterial activity observed along the guts probably reflect changes in the microbial environment which may favour different microbial communities. These differences at least offer the potential for microbial breakdown of a broader range of substrates than would otherwise be possible by the animal itself.

Particle selection

In highly specialized deposit-feeding organisms, such as bivalves, a high rate of processing may be achieved by means of prior sorting and rejection of unsuitable particles as pseudofaeces. Deep-sea protobranch bivalves have been described as possessing specialized structures performing this function (Allen, 1978). In the deep sea, as in shallow-water cohesive sediments, deposit feeders concentrate on the most nutritious, surface-most layer of the sediment where micro-organisms and the most recently deposited detritus is concentrated. Even the largest deposit-feeding organisms skim off only the very surface film of sediment. The feeding structure morphology, *in situ* observations, and analyses of stomach contents (e.g., Sibuet et al., 1984; Billett et al., 1988) support this for a range of large motile epifaunal organisms. Self and Jumars (1988) show surface deposit feeders employing radically differing food-gathering mechanisms have converged towards selection for particles of low specific gravity. These mechanisms include the ‘vacuum cleaner’ lifestyle of elasipod holothurians, the efficient radial foraging shown by the spoke feeding trace (Fig. 11.16) made by burrowed echiuran worms (Ohta, 1984; Bett and Rice, 1993), and the morphology of the feeding palps of various polychaete worms. Although some species are thought to be able to select only the most organic-rich particles (Khripounoff and Sibuet, 1980), selectivity has been found to be reduced with increasing body size (Self and Jumars, 1988). “Selection” may then merely involve feeding on the lightest of the superficial particles, which are likely to be the most nutritious.

Fig. 11.16. Spoke feeding trace made by a burrowed echiuran in the Bay of Bengal at 4010 m depth. The animal feeds using its long proboscis which is extended to progressively ‘lick’ off superficial material around the central burrow. Scale bar represents 20 cm. From Ohta (1984).

Foraging strategy and particle selection in large deposit feeders

The role in organic-matter recycling of large, motile deposit feeders has attracted much research effort in recent years. By monitoring the abyssal seabed at Station ‘M’ at a depth of 4100 m off California, K.L. Smith et al. (1993) estimated that motile deposit-feeding megafauna, mostly holothurians, traversed 88% of the 20 m^2 visible over three months. The three most abundant species, all holothurians, traversed 76.5% of this area of sea floor at this station (Kaufmann and K.L. Smith, 1997); the latter study recorded variability related to the availability of pelagically derived detrital material visible. This suggests that coverage by megafaunal deposit feeders such as holothurians is very high, with perhaps very little of the seabed not being swept by them during a year. However, the interpretation of foraging from small-scale time-lapse photographic sequences of movement of deposit feeders rests on a number of assumptions about their mode of movement. A. Smith et al. (1997) showed that simply multiplying mean speed by the swath width is too simplistic. These authors studied the elasipod holothurian, *Oneirophanta mutabilis*, in the abyssal Northeast Atlantic where it is the dominant component of the motile invertebrate megafauna. Simulations based on estimated population density and movement data from time-lapse photographs showed very different outcomes in terms of time required for 50% coverage of the sea bed, ranging from 17 years for a random-ranging strategy to 12 days for a systematic search. A simulation based on observed speeds and turning angles gives a 50% coverage in 9.6 years.

Evidence for particle selectivity comes from particle-selection studies showing deposit feeders very commonly show strong selection for particles low in specific gravity and those covered with organic coatings. This particularly applies to surface deposit feeders, but also occurs in subsurface deposit feeders (literature reviewed by Wheatcroft et al., 1990). For the deep sea, Wheatcroft (1992) has provided experimental evidence of size-selective vertical transport in the sediment which is presumably mediated by deposit feeders. There is a rapidly growing body of data directly showing particle selectivity in deep-sea deposit feeders. In epifaunal holothurians, which often make up the overridingly dominant component of the abyssal megabenthos, resource partitioning classically has been related to tentacle morphology (Roberts and Moore, 1997). Particles are selected in terms of size or organic quality (Khripounoff and Sibuet, 1980; Billett et al., 1988). However, other morphological and behavioural characteristics, such as body extension, motility and buoyancy/swimming capability of surface deposit feeders, also need to be taken into account (Billett, 1991).

Other studies have demonstrated the presence of algal cells, Cyanobacteria and chlorophyll pigments (both serving as biomarkers) from recently deposited phytodetritus and copepod faecal pellets in the guts, faeces and burrows of deposit-feeding holothurians, asteroids, echinoids, amphipods and sipunculans (Billett et al., 1988; Thiel et al., 1988/89; Graf, 1989; Billett, 1991; Pfannkuche and Lochte, 1993; Campos-Creasey et al., 1994). The observation of Billett et al. (1988) that the detrital content of the foregut of deposit-feeding holothurians closely matches the overlying phytodetritus, even when this material has a patchy distribution on the seabed, shows that the foraging behaviour of these relatively slow-moving animals is effective in feeding on patchily dispersed resources. It also indicates that this may involve active behaviour concentrating animals in such patches. The small elasipod species *Kolga hyalina* has been photographed in dense congregations, which may result from attraction to patches of detrital accumulation (Billett and Hansen, 1982). The deposit-feeding regular echinoid *Echinus affinis* also seems to be attracted preferentially to patches of phytodetritus lying on the bed (Grassle et al., 1975; Billett et al., 1983; Grassle and Morse-Porteous, 1987; Lampitt and Billett, 1984; Campos-Creasey et al., 1994).

Stable isotope analyses are now revealing new evidence for particle selection. Excess ^{234}Th activity and ^{234}Th/^{210}Pb activity ratios have been used in studies of bioturbation and particle selectivity. The isotopes are scavenged by particles settling through the water column. ^{234}Th, with a short half-life of 24.1 days is produced throughout the water column by natural decay of ^{238}U, while ^{210}Pb, with a half-life of 22.3 yrs, is supplied by *in situ* production from ^{236}Ra and atmospheric input. Their ratio thus provides a useful indication of the relative age, as well as the source, of material in the deep sea. Sediment-mixing coefficients measured using ^{234}Th are two orders of magnitude greater than those measured using ^{210}Pb (C.R. Smith et al., 1993). These authors demonstrated a negative relationship between estimates of sediment mixing and the half-lives of radiotracers used in studies of bioturbation, and ascribed this to age-dependent mixing of particles. The preference by deposit-feeding organisms responsible for bioturbation for recently deposited material has also been demonstrated in studies comparing gut contents with superficial sediment, recently deposited phytodetrital material, and material collected in sediment traps moored near the bottom in the abyssal Northeast Pacific (Lauerman et al., 1997). These authors found that values of excess ^{234}Th activity and ^{234}Th/^{210}Pb activity ratios in the guts of two motile epibenthic holothurians, *Abyssocucumis abyssorum* and *Oneirophanta mutabilis*, and in detrital aggregates from the sea floor were similar. They calculated that 91% of the gut-content material of *A. abyssorum* must have come from material similar to that in the sediment traps.

Miller et al. (2000) also found very high levels of excess ^{234}Th in two species of motile surface-deposit feeding elasipod holothurians, *Pannychia moseleyi* and *Scotoplanes globosa*, in the bathyal Santa Catalina Basin off California. The gut of *Pannychia moseleyi* also showed a 500-fold enrichment in chlorophyll-a relative to surface sediment, further indicating that these animals are indeed actively selecting for fresh organic matter, as would be expected from the age-dependent mixing model of C.R. Smith et al. (1993). A burrowing, surface-deposit feeding chirodotid holothurian, *Chirodota* sp., and a surface-deposit feeding trochid gastropod, *Bathybembix bairdii*, were less enriched in gut ^{234}Th, perhaps reflecting less selectivity, or reduced opportunity for selectivity through lower motility. In contrast, similar measurements on the Hawaiian slope from gut contents of two synallactid holothurian surface-deposit feeders, *Mesothuria carnosa* and *Paleopatides retifer,* were not enriched in ^{234}Th, but were enriched in chlorophyll-a. This, however, may show that in some situations involving frequent sediment resuspension the excess ^{234}Th activity is a poor tracer for fresh food-rich particles.

In a study of the benthic food web at the BENGAL study site in the Northeast Atlantic, stable isotope analysis has been used to investigate the trophic relationships in the total benthic fauna (Iken et al., 2001). Naturally occurring stable isotopes of both carbon and nitrogen show a stepwise enrichment between prey and consumer tissue, with ^{13}N/^{15}N activity ratios providing a more conservative estimate of enrichment among various biochemical fractions, and therefore a more reliable tracer, than δ^{13}C (the δ notation referring to the ^{12}C/^{13}C activity expressed against a standard). Analysis by these authors of δ^{13}N values and gut contents of the epibenthic, deposit-feeding holothurians *Amperima rosea, Ellipinion* sp. and *Peniagone diaphana* showed that these animals feed mainly on freshly deposited phytodetritus. Both *A. rosea* and *P. diaphana* have gelatinous, buoyant bodies and are thought to be highly motile, and furthermore seemed to have considerable quantities of phytodetritus in their gut at all times of the year, indicating very efficient foraging (Iken et al., 2001). Values for δ^{13}N measured in another, larger and less motile group of holothurians (including the species *Deima validum, Oneirophanta mutabilis* and *Psychropotes longicauda*) were higher, and this is interpreted by Iken et al. as reflecting a diet including older and more recycled organic matter than that taken by the smaller, more buoyant species above. A third group of holothurians including less motile forms such as *Pseudostichopus villosus* (a sausage-shaped epibenthic species which ploughs through the superficial sediment) and *Molpadia blakei* (a burrowing deposit feeder) have the highest values of δ^{13}N. It is in these species, which may possess enteric bacteria able to break down refractory organic material for assimilation by the holothurian, that there may also be enzymatic patterns in the gut enabling them to break down bacterial membranes.

Particle selectivity can be inferred from analysis of stomach contents of other megafauna collected at different times of the year in the BENGAL program during the late 1990s. Other work at the BENGAL site on the Porcupine Abyssal Plain (Ginger et al., 2001) suggests that *Amperima rosea* and *Ellipinion* sp. have, in less than four months, completely turned over and selectively removed phytosterols (free fatty acids) by eating freshly arriving phytodetritus and superficial sediment. That megafauna may be important in modifying the lipid content of organic matter has been shown elsewhere (Smallwood et al., 1999). These authors, working on the highly productive continental margin off Oman, provided molecular and photographic evidence that spider crabs and brittle stars play a significant role in depletion of particulate organic carbon in the sediment, these animals having a tissue lipid composition indicative of metabolic alteration of phytoplankton-derived organic material. Dense populations of epifaunal spider crabs and brittle stars photographed at the base of the oxygen minimum zone suggest that such megafauna have been responsible for these changes in the sediment. Other holothurian species at the BENGAL station, however, forage successfully on more refractory material, possibly assisted by gut bacteria (see above).

Karrh and Miller (1994) have shown, for an obligate surface-deposit feeding acorn worm in the intertidal zone, that feeding rate, measured by the rate of egestion, varies in response to food quality (measured as chlorophyll-a and protein concentration) of the sediment processed. Such behaviour may be predicted to occur also in the deep sea. Time-lapse photography has shown that motile deposit-feeding epifauna, such as echinoids and holothurians, living on the abyssal seabed in the eastern North Pacific are more active when fresh detrital material is present on the bottom than at other times (K.L. Smith et al., 1993).

Particle turnover by deposit feeders

Although large motile deposit-feeding megafauna make an important contribution to physical mixing, burial and repackaging of the sediment (Lauerman et al., 1997; Miller et al. 2000), their role in organic recycling of organic matter on the deep-sea bed is more equivocal. K.L. Smith et al. (1993) estimated carbon demand based on an assumption that motile deposit feeders take up all recently sedimented particulate organic material as they traverse the bottom. Over a 90-day period from March to June 1991 at the Station 'M' at a depth of 4100 m off California, these authors estimated that 8.7% of the available particulate organic carbon would have been taken up in the 20 m^2 area monitored photographically. In order to translate this to an estimate of how much was mineralized to carbon dioxide, K.L. Smith et al. used data on population densities, size structure and oxygen consumption for the two dominant species, the elasipod holothurians *Elpidia minutissima* and *Peniagone vitrea.* (Weight-specific oxygen consumption was estimated from data from a similar species, *Scotoplanes globosa.*) Total respiratory uptake was converted to carbon equivalent assuming a respiratory quotient of 0.85. The total value, $0.012\,g\,C\,m^{-2}$, represented 18.3% of the total particulate organic carbon ingested by these deposit-feeding megafaunal species. This concurs with the estimate of assimilation efficiency for deposit-feeding holothurians of Khripounoff and Sibuet (1980). This estimated mineralization represents only 1.6% of total flux of particulate organic carbon concurrently measured 50 metres above the bottom at Station 'M' over the three-month period. Although this low value is in agreement with the 1% estimate of Lampitt et al. (1986) for megafauna at 4000 m, they both contrast with the higher value of 7–10% of total flux of particulate organic carbon estimated by K.L. Smith (1992) for the abyssal central North Pacific.

Lauerman et al. (1997) used their stable isotope data showing rapid ingestion of settling particulate organic carbon, in conjunction with densities of the epifaunal holothurians *Abyssocucumis abyssorum* and *Oneirophanta mutabilis* (previously estimated by Lauerman et al., 1996, from towed photosled surveys), to deduce how much of the vertical flux was being processed by motile deposit-feeding megafauna during the high-flux period in summertime at Station 'M' off California. Assuming a gut passage time of six days the amount of sediment that could be ingested ($m^{-2}\,d^{-1}$) could be compared to mean downwards flux from sediment traps. Lauerman et al. (1997) were able to calculate that this population of *Abyssocucumis abyssorum* could process 0.2 to 4% of the sedimented organic material during the period of vertical flux, assuming that 91% of gut mass consisted of freshly deposited material. Miller et al. (2000) indicate that this estimate may be unreasonably low because a gut throughput time of 24 hours rather than 6 days is more likely to apply to *A. abyssorum.* This would increase the estimated ingestion rate to between 1.2 and 24% of the total flux of particulate organic carbon, a value more in line with their estimate for another species (*Pannychia moseleyi*) of comparable density.

In a study by Miller et al. (2000) in the Santa Catalina Basin off California using ^{234}Th as a tracer, the surface-deposit feeding megafauna are concluded, astonishingly, to be processing on average 39 to 52% of the daily flux to the sea floor of excess ^{234}Th activity. Based on an assimilation efficiency of about 15%, the authors suggest that this implies that *Bathybembix bairdii, Chirodota* sp. and *Pannychia moseleyi* may be respiring 4 to 11% of the vertical flux of particulate organic carbon. This estimate is in agreement with that of K.L. Smith (1992) for the megafaunal deposit-feeding fraction of the benthic community in the central North Pacific.

Miller et al. (2000) point out that, although megafaunal deposit feeders are efficient selectors of high-grade organic matter, their assimilation efficiencies for particulate organic carbon (about 15%) mean that the faeces is still relatively enriched compared to surface sediment. This provides both opportunities for further microbial decomposition and, particularly when buried by subducting bioturbating organisms, geochemical 'hot-spots' within the sediment. This contributes not only towards organic-matter preservation but also probably to greater patchiness in food resources, which may be important in promoting high local species diversity in deep-sea sediments (Snelgrove et al., 1992; Gage, 1996).

Respiratory demand by benthic metazoans

One expected consequence of the deep sea as a 'low-activity' ecosystem would be low rates of individual metabolism among metazoans. Estimating respiration of individual invertebrate animals from the deep sea is very difficult. Low rates of oxygen consumption measured from specimens recompressed after collection from bathyal depths may be affected by the drastic changes in pressure and temperature experienced during capture. Childress et al. (1990) could find no significant relationship between oxygen consumption and depth when the data were adjusted to take into account moderate metabolic dependency on temperature. Furthermore, *in situ* measurements on specimens lured into enclosures need to take into account unknown behavioural effects on respiration caused by the unnatural conditions.

Available data have been summarized by Mahaut et al. (1995), who fitted a weight-dependent relationship to all deep-sea data available in the literature. These data show, as might be expected, that weight-specific respiratory demand declines rapidly with increasing size, and that, while obvious in terms of visibility in photographs and biomass, the largest organisms, the megafauna, may account for a relatively small percentage of total organic-carbon mineralization in the benthic boundary layer community. This is in agreement with the estimates reached by K.L. Smith (1992) and K.L. Smith et al. (1993) from calculating uptake of particulate organic carbon by megafaunal deposit feeders. An integrated value covering the full size range of the deep-sea bed biota, from bacteria to megafauna, was obtained for the biomass size classes sampled from a site in the Northeast Atlantic and compared to one measured directly *in situ*. The good agreement obtained will allow investigators to estimate sediment oxygen demand from size-classified biomass. Data, when available in quantity, will provide a time- and space-integrated relationship, which will not be subject to the scaling constraints of estimates from benthic chambers or sediment pore-water profiling (see above).

Growth rates and secondary production of larger size classes

There has been, until recently, a perception that population rates, such as growth of individuals and rates of population expansion, are very slow, with rates of population turnover one or two orders of magnitude slower than in shallow water (Thiel, 1975). This view was much influenced by early observations of low rates of organic degradation (e.g., Jannasch et al., 1971) and results of a study using radiometric dating which were interpreted to show extremely low rates of shell growth in a deep-sea protobranch bivalve (Turekian et al., 1975). If this is true, then the diversion of energy into growth and reproduction could be disregarded; seabed recycling could be considered as virtually totally expressed by respiratory demand measured by sediment community oxygen consumption.

Against this viewpoint of low rates of turnover there emerged scattered observations from seabed recolonization experiments in the 1970s and 1980s that some deep-sea sediment-dwelling macrofauna, such as the protobranch *Deminucula atacellana* and the aplacophoran *Prochaetoderma yongei,* are able to grow rapidly, at least as young individuals (Grassle, 1977; Grassle and Morse-Porteous, 1987; Scheltema, 1987). However, information on the response at the population level, as somatic and reproductive production, of organisms other than bacteria to organic input is still sparse. This is because of the difficulty in undertaking the necessary monitoring of populations with the precision needed to distinguish change from background noise (Gage, 1991). Nevertheless, solid indications of rapid rates of secondary production in larger metazoans have come from a study of a sample time series in the Rockall Trough (Gage et al., 1980). One of the initially most noteworthy results was the marked increase in benthic larval and young stages in samples taken in summer after the presumed peak in organic-particle flux to the bottom (see summary in Gage, 1994). Summertime increases in populations of peracarids, such as cumaceans, have also been observed (Cartes and Sorbe, 1996). In some cases this could be linked to seasonal reproduction (Tyler et al., 1982). However, a seasonal influx of postlarvae seems to occur in other species lacking seasonal reproduction (e.g., Gage and Tyler, 1982); release of brooded young in the peracarid cumacean crustacean *Leucon profundus* peaks in late spring/early summer (Bishop and Shalla, 1994). Modelling studies applied to samples of the population changes observed among several species indicate rates equivalent to those for closely related species in coastal soft-sediment habitats (Gage, 1991, 1994, 1995). The apparent increase may then merely reflect growth, stimulated by the temporary increase in food, from a pool of non-growing or very slowly growing postlarvae which exists year-round.

Time-lapse photography has recorded rapid rates of individual growth in the barnacle *Poecilasma kaempferi* (Lampitt, 1990) and in the xenophyophore *Reticulammina labyrinthica*, the latter occurring in distinct episodes lasting 2–3 days separated by about two months (Gooday et al., 1993). Other rapid rates have emerged from use of the time-dependent change (racemization) of aspartic acid in the shell. This is used as a time marker to age the gastropod mollusc *Entemnotrochus adansonianus* (Goodfriend et al., 1995). Changes in population abundance indicate rapid growth in deep-sea Foraminifera (Gooday and Turley, 1990; Corliss and Silva, 1993). In contrast, radiometric study of a deep-sea coral *Corallium* using ^{210}Pb and other natural isotopes (Druffel et al., 1990) indicates a very slow growth rate, in line with low rates estimated for other deep-water species such as *Lophelia pertusa*

(Mikkelsen et al., 1982). It appears that, as in shallow water, a broad range in growth strategies will be found corresponding to differing lifestyles in the fauna (Gage, 1991).

Rates of secondary production

Estimates of secondary production from such data have not yet been attempted by direct methods (see Gage, 1992, for summary). However, demographic models fitted to size frequencies and skeletal growth markers offer the means to calculate production using a fitted size/mass relationship. Using models fitted to four bivalve community dominants, the ratio of annual production to biomass (P/B ratio) ranged from 0.49 to 1.65 (Gage, 1992), although their combined production (114.9 mg wet weight m^{-2} yr^{-1}) is less than half that predicted (363 mg wet weight m^{-2} yr^{-1}) from empirical relationships established from coastal studies (Brey, 1990). Total non-foraminiferal macrobenthic community production equivalent to 122 mg organic carbon based on a mean annual P/B of 0.98, was estimated by Gage (1992) for a depth of 2900 m in the Rockall Trough. This value for somatic production represents between 3 and 12% of total respiratory carbon uptake for the sediment community at this depth, suggesting that secondary production by the macrobenthos alone may be a small, but non-trivial, component of carbon consumption and turnover at the deep-sea floor.

So far the contribution of anabolic metabolism (as reproductive and somatic production) in the overall assimilation of larger deposit-feeding megafauna, which may consume a large proportion of available particulate organic carbon flux to the bottom has not been taken into account. Although it has been assumed that such rates in these animals will be very slow, recent observations of dramatic population changes among megafauna in the Northeast Atlantic (Billett et al. 2001) indicate that much faster rates may occur.

Implications of episodic food input to the benthic boundary layer community

Episodic particulate flux is of great importance because it appears to bypass a large part of the processes of recycling and biogenic repackaging of the export flux from the surface. It has been estimated that >50% of annual biogenic particle flux in the Northeast Atlantic is supplied to the bottom during the spring particle bloom (Honjo and Manganini, 1993). If this is true for large areas of the deep sea, then most of the utilizable food for deep-sea benthic organisms, including bacteria and other micro-organisms, through small meiofaunal metazoans, to macrofauna and megafauna, both motile and buried, will arrive as pulses of labile material. The tightness in the coupling between supply and demand, however, may depend on supply not outstripping demand. Smith et al. (1994) suggested that, although the North Atlantic and North Pacific both show variability in particle flux, this tends to occur as small increments in the Pacific rather than as mass deposition; in consequence, trophic coupling is more efficient in the Pacific than in the Atlantic. In the Atlantic detrital carpets accumulate over large areas, presumably as a result of supply vastly exceeding demand. However, for the rest of the time the reverse is the case, making labile particulate food for deposit feeders, and perhaps also for suspension feeders, almost vanishingly scarce. This may mean that overall efficiency in utilization (defined as the ratio of net production entering the benthic boundary layer to its assimilation) might be higher in the Pacific than the Atlantic Ocean.

Clearly these events, by imposing temporal variability on the nutrient flux to the seabed, should have a profound effect on the deep-ocean carbon dynamics. As yet, such intermittency has not been fully taken into account in models of organic-carbon diagenesis in the oceanic biogeochemical carbon cycle. Seasonally pulsed input imparts dramatic temporal variability to the solubilizing of complex organic molecules to inorganic constituents, contributing to nutrient efflux from the sediment, as well as increased rates in carbon burial (C.R. Smith, 1992; Pfannkuche, 1993). Furthermore, in view of their high quality as food, the seasonal input pulses may represent the single most important nutritional input to the community of the deep-sea bed.

Simple box models of the energetic flows in the sediment at the German BIOTRANS site before and after deposition are shown in Fig. 11.17, and a similar representation for flows in the phytodetrital layer in Fig. 11.18. Considerable heterogeneity may be imparted to the sediment because of the complexity and different size scales involved. For example, analysis of lipid content in the abyssal sediment has uncovered considerable small-scale spatial variability, very possibly related, via the feeding activity of benthic organisms, to patchiness in phytodetrital accumulation in topographic lows in the sediment (Santos et al., 1994). On the continental slope several data sets,

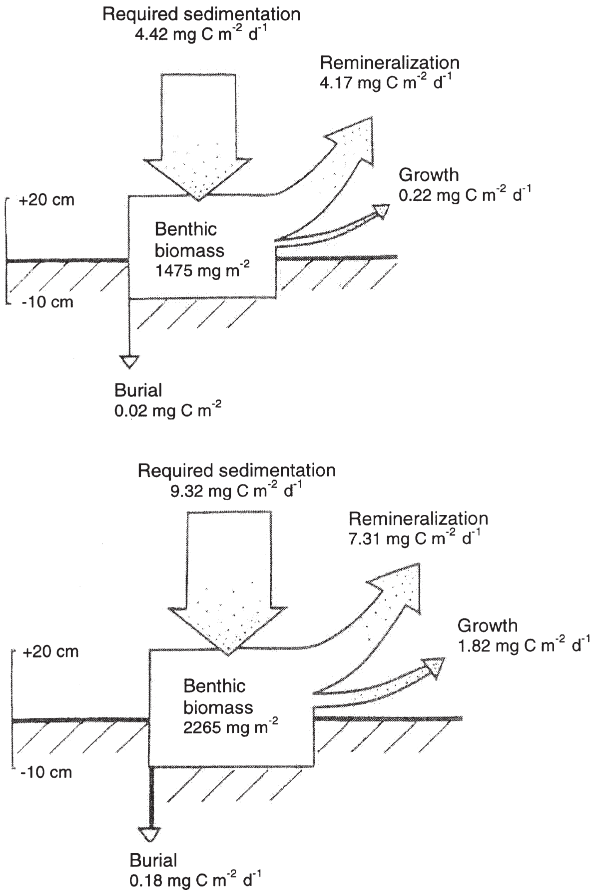

Fig. 11.17. A: Flux of particulate organic carbon (POC) through the benthic community at the German BIOTRANS site in April before the main peak in POC input; calculated from remineralization, growth and burial. B: Flux of POC through the benthic community at the BIOTRANS site in July/August after the main peak in POC, calculated from remineralization, growth and burial. From Pfannkuche (1992) after Rowe et al. (1986). See Pfannkuche (1992) for details of calculations and source of estimates used.

including rates of organic carbon accumulation and chlorophyll-a in the sediment, indicate that highly variable carbon fluxes to the seabed occur over relatively small distances (e.g., DeMaster et al., 1994; Cahoon et al., 1994; Lohse et al., 1998).

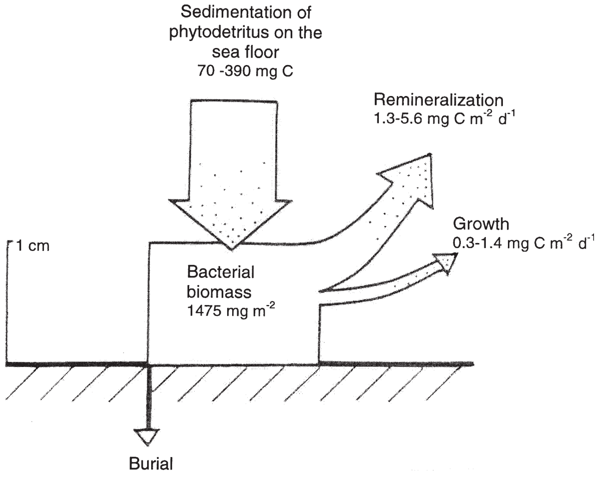

Fig. 11.18. Flux of particulate organic carbon through the biota of the phytodetrital layer lying on the seabed in July/August. From Pfannkuche (1992) after Rowe et al. (1986); data from Lochte and Turley (1988) and Pfannkuche and Lochte (1990).

Response by larger size classes of the sediment community to pulsed organic flux

In the Northeast Atlantic, changes in dietary volume and constituents have been documented from samples of the deposit-feeding sea urchin *Echinus affinis,* the gut contents showing a spring/summer peak in amount, but not in proportion of organic matter (Campos-Creasey et al., 1994). Seabed photographs also show that this species is attracted to phytodetrital patches (Billett et al., 1983). A survey of gut contents of a wide range of megafauna on the Porcupine Abyssal Plain was undertaken at three different times from September 1996 to July 1997 in the European BENGAL project, the results for both surface and subsurface deposit feeders showing seasonally varying proportions of fresh phytodetritus and sediment in the gut (K. Iken and T. Brey, personal communication). For most deposit-feeding species the proportion of phytodetritus was highest in September and lowest in March, whereas seasonal variability in gut content was low in predators/scavengers. A similar dietary association with detrital floc has been observed in the abundant, upper bathyal brittle star *Ophiocten gracilis* (Pearson and Gage, 1984). The brittle-star guts were found in summer to be full, mainly of mineral particles, flocculent material and foraminiferans, but empty, feeding apparently having ceased, later in the year. Observations have been made on the North Carolina slope of rapid subduction of viable diatoms and phytoplankton pigments to cause subsurface maxima of pigments or radiotracers deep in the sediment within days of bottom sedimentation of material (Cahoon et al., 1994). This has been associated with the feeding activities of dense populations of burrowing, surface-deposit feeding invertebrates, such as sipunculans and polychaetes, which may be very abundant in areas experiencing phytodetrital accumulations (Romero-Wetzel, 1987; Blair et al., 1996). These animals may transport material rapidly to depth at a rate >1 cm per day from the sediment surface (Graf, 1989). Jumars et al. (1990) suggested that this behaviour may be characteristic in the deep sea in order to sequester or hoard scarce food resources away from smaller, often specialized, meiofaunal organisms, such as Foraminifera. Hoarded material may be in the form of faecal pellets, or as labile food plastered to the burrow lining so that it is available for re-assimilation later when resources are scarce at the sediment surface. Although this is an appealing idea, it may be more important for animals to ingest seasonal bonanzas immediately, for conversion to reproductive production (see Tyler et al., 1992, 1994).

Pulsed variability in organic flux to the bottom, not surprisingly, has been linked to seasonal variability in responses at the population level, such as reproduction, recruitment and growth (Gage and Tyler, 1991; Tyler et al., 1994), and possibly macrofaunal–microbial interactions (C.R. Smith, 1994). The larger elements of the benthic community, with lifespans that may encompass several pulsed detrital inputs, may also respond in terms of accelerated somatic growth. In shallow-water fauna this is frequently expressed as banding patterns in the growth of skeletal elements such as mollusc shells. Such seasonal variability in growth provides a useful age marker, which has been used in numerous studies of population dynamics based on unbiased samples aged by this method, or on growth trajectories back-calculated from the pattern of skeletal zones. In the deep sea, similar growth-zone patterns occur across a broad range of fauna (e.g., Gage, 1987, 1990, and unpublished data; Gage and Tyler, 1985). These growth marks reflect the fact that growth is typically intermittent, responding to the increased availability of food after detrital maxima.

Data on behavioural differences have also started to emerge. Motile epibenthic megafauna, such as echinoids and holothurians, monitored with time-lapse photography were twice as active in the presence of detrital aggregates on the sea floor in the abyssal Pacific (K.L. Smith et al., 1994). De Wilde et al. (1998), on the European continental rise off Ireland, noted that large, motile ’vacuum cleaner’ holothurians, such as *Psychropotes*, were plentiful on the bottom when heavy deposition occurred, but were absent at the same time the following year when no deposition occurred. It is possible that the animals may migrate to areas of deposition, which may have a patchy distribition in the area, but whether long-distance olfaction may be involved as suggested by De Wilde et al. (1998) needs further evidence.

Response of larger, non-deposit-feeding size classes

Predators constitute a higher link in the food chain, less directly connected to variability in organic input than the consumers of passive organic inputs such as carrion or large plant remains; but there are few data on predators in the deep ocean. The benthopelagic fauna, which includes macrobenthic organisms such as peracarid crustaceans, makes up an important part of the diet of motile megabenthos such as larger decapod crustaceans and fish such as macrourids. Population increases in some of these prey groups have been linked to variability in advected organic flux on the continental slope in the western Mediterranean, and this results in increased abundance of benthopelagic predators (Cartes, 1998). That episodic flux may also affect even larger size classes higher up the food chain may explain seasonal changes in response times of scavenging grenadiers to bait detected by using acoustic tracking techniques (Priede et al., 1994b), although how such effects are mediated remains unknown.

Response to interannual variability in organic flux

As seasonal changes have become better understood over the past 15 years, so opportunities have been provided from the long-term time-series mentioned in previous Sections to make between-year comparisons in order to detect any interannual variability in the deep-sea benthic system. Such data are very difficult and costly to obtain, and resolution is usually poor. But just sufficient is available, particularly from the Northeast Atlantic and Northeast Pacific to provide strong indications of long-term variability in the benthic populations, which is most likely driven by interannual variability of organic flux to the deep-sea bed. For example, data from the long-term studies at Station ‘M’ off California by K.L. Smith and his associates provide evidence for significant changes over a seven-year study period in sediment community oxygen consumption, and in the abundance of benthic macro- and megafauna (K.L. Smith and Druffel, 1998; K.L. Smith and Kaufmann, 1999; Drazen et al., 1998; Lauerman and Kaufmann, 1998). Dramatic changes in relative abundance of invertebrate megafauna have also been recorded on the Porcupine Abyssal Plain at the BENGAL site (Billett et al., 2001). Abundance of a single species of small, elasipod holothurian, *Amperima rosea,* seems to have increased from 2–3 to 6000 individuals per hectare over a nine-year period. Other fauna, including the brittle star *Ophiocten hastatum,* and another holothurian *Ellipinion* sp., have also shown large population increases, although as yet it is not known whether the changes apply to a wider area, or whether the changes reflect patterns in migration of more motile species. Gut contents analysis by Iken et al. (2001) indicate these species ingest phytodetritus, and Billett et al. (2001) speculate that the changes have been driven by interannual variability, and a long-term, upward trend in organic-matter supply to the seabed.

PASSIVE ORGANIC INPUTS TO THE DEEP-SEA BENTHIC BOUNDARY – LARGE PACKAGES OF PLANT ORIGIN

The significance to the benthic and benthopelagic fauna of the food source provided by terrestrial and coastal plant debris was commented on by Moseley (1880) in the results of the *Challenger* expedition, and later by Agassiz (1888) in the cruises of the *Blake.* This material consists of various branches, leaves, nuts and fruits. Sampling by the Danish *Galathea* expedition in the 1950s provided the basis for a systematic review of the occurrence, and possible utilization by the deep-sea fauna, of such large, fast-sinking, plant remains in the deep sea (Wolff, 1976, 1979, 1980). Because large plants exist only on land and in shallow water, these inputs might be thought to be important only in the deep sea just beyond the continental-shelf edge. However, a great deal of this material may float for a long time before sinking, so that a significant proportion finds its way into the abyssal realm. Various downslope hydrodynamic processes (see below) also transport detrital particles, some of coastal and terrestrial plant detritus, onto the continental rise.

A number of macrobenthic species have become adapted to utilization of plant remains in the deep sea (see Wolff, 1979 for a systematic review). The overall significance, however, of such inputs to the nutritive budget of the deep-sea ecosystem, and to carbon mineralization on the deep-sea bed in global terms, remains obscure. However, deep trenches located near island arcs may act as sumps for coastal sediment and particulate terrestrial detritus advected from nearby land masses (Wolff, 1976; George and Higgins, 1979; see also Chapter 6) and then support much higher benthic biomass than occurs on the adjacent abyssal plain (Belyaev, 1972; Rowe, 1983). In this respect the deep trenches reflect the importance of such organic inputs, because mid-water consumption of small-particle flux from surface production through such great depths might otherwise result in an extremely low benthic standing crop.

Macroalgae and seagrass

Seagrasses and macroalgae of coastal origin are often encountered in samples from the seabed, and from sediment traps set in mid-water. Furthermore, observations from manned submersibles and ROVs (remote-operated vehicles) have provided many images of such material lying on the deep-sea bed. Although such material may play only a small role in the overall flux of organic material to the deep-sea bed (Schoener and Rowe, 1970), considerable quantities of material, such as the seagrass *Thalassia,* are washed into deeper water during tropical storms (Menzies et al., 1967; Menzies and Rowe, 1969). Debris from macroalgae may be important adjacent to the coasts over a wide geographic area (e.g., Alongi, 1990). At high latitudes its availability may help to modulate the short energy pulse from planktonic production, so that food may be available to foraging benthos throughout the year (Reichardt, 1987), and its availability at middle latitudes may actually be intensified during winter (Harrold et al., 1998).

Debris from macroalgae and seagrasses becomes concentrated at the head of submarine canyons off southern California (Harrold et al., 1998), supporting dense benthic populations (Vetter, 1994; Vetter and Dayton, 1998).

Evidence for the importance of macroalgae and seagrass debris to the benthic community comes from two sources. First, there may be a large associated standing crop of macrofauna (e.g., Vetter and Dayton, 1998). Second, there is evidence from gut contents that large epifaunal deposit feeders consume such remains, along with terrestrial plant detritus including wood (Wolff, 1979, 1980; Pawson, 1982; Young et al., 1993). Carbon isotope (^{13}C) analyses of gut contents indicate that seagrass which has been storm-washed off the coast, or rafted out to sink in deep water, may provide an important part of diet of megafaunal sea cucumbers and sea urchins in the Caribbean (Suchanek et al., 1985). Other observations in the western North Pacific suggest that parcels of kelp such as *Macrocystis pyrifera* are rapidly consumed by megafauna (C.R. Smith and Hamilton, 1983).

The pelagic macroalga *Sargassum* has a wider recorded distribution on the deep-sea bed than seagrass; but *Sargassum* usually occurs in clumps, whereas seagrass usually occurs as small blade fragments that may be easily overlooked (personal observations). *Sargassum* occurs in considerable quantities out to abyssal depths in the Northwest Atlantic in the Sargasso and Caribbean Seas, in the Gulf of Mexico and in the central Pacific, and less frequently in the Northwest Atlantic off New England (Grassle and Morse-Porteous, 1987). *Sargassum* may be driven down to depth by storms causing the gas bladders to collapse so that it sinks to the seabed (Johnson and Richardson, 1977). Rowe and Staresinic (1979) estimated that sinking *Sargassum* might provide up to 10% of the total organic input to the abyssal benthos in the Sargasso Sea. Observations of the author, P.A. Tyler and C.M. Young off the Bahamas suggest that macroalgae are recycled more rapidly than seagrass.

Land plant remains

Pieces of plants washed out to sea from the land may float for some time before becoming sufficiently waterlogged to sink onto the deep-sea bed far from land. Not surprisingly, the presence of branches and twigs, pieces of wood, bark and fruits in deep-sea trawlings has been regularly noted from the time of the great oceanographic expeditions right up to the Danish *Galathea* Expedition in 1950–52. Results from the *Galathea* cruise were discussed by Wolff (1979), together with earlier records. These inputs seem to be particularly noticeable in the deep sea near the mouths of large rivers in the tropics.

Response of deep-sea biota to macroalgae, and land plant drops

Observations and *in situ* experiments using a deep-diving submersible show that amphipods and the echinoid *Stylocidaris lineata* are able quickly to locate patches of *Thalassia* and *Sargassum* on the bottom. The results show that algal/seagrass food-falls are rapidly colonized by animals such as amphipods, while plastic-bag controls were not. This indicates that these food-falls provide a significant energetic imput to the deep-sea bed (Lawson et al., 1993; Young et al., 1993). Other data indicate that benefits to the smaller sediment-dwelling benthic fauna are less direct, and that 'normal' macrofauna may even be negatively affected by the proximity of fresh kelp falls (Levin and C.R. Smith, 1984).

Wolff (1979) recorded various animal species employing sunken wood and other land-plant material as substratum, shelter or food. Few metazoans are able to utilize the lignin and cellulose content of wood as food, but exceptions include the highly specialized, wood boring bivalve molluscs, and ostracods (Turner, 1973, 1977; Maddocks and Steineck, 1987). The response of such organisms may be extraordinarily rapid; colonization and population growth of *Xylophaga* on wood blocks resulting in extensive utilization within a few months (Dean, 1993; Romey et al., 1994; R. Harvey and P.A. Tyler, personal communications).

PASSIVE ORGANIC INPUTS TO THE DEEP-SEA BENTHIC BOUNDARY – LARGE PACKAGES OF ANIMAL ORIGIN

The overall significance of large packages of highly concentrated organic material sinking from the upper water column in the form of the dead carcasss of large animals, such as marine mammals, fish and large invertebrates such as squid, has long been largely conjectural (Stockton and DeLaca, 1982). In his early review of the characteristics of the deep-sea environment, Bruun (1957) suggested that the sinking remains of whales and sharks might constitute an important food source. However, there was little support for an important role being played by such large packages of organic material from dead animals in the nutrition of the deep-sea benthic system until the 1960s. Nevertheless, the overall importance of large food falls of animal origin, and the degree of dependence on scavenging by deep-sea biota, is still far from clear (Britton and Morton, 1994).

Response by the specialized scavenger community to large packages of animal origin

There has long been good evidence from analyses of gut contents demonstrating that the remains of such carcasses may be important in the diet of many deep-sea species (see e.g., Litvinova and Sokolova, 1971; Sedberry and Musick, 1978; Tyler et al., 1993).

However, it was the dramatic results from moored seabed cameras focusing on bait, or traps baited with fish or other carcasses, that provided the most convincing evidence of the role of large carcasses as a source of food to deep-sea organisms (Isaacs and Schwartzlose, 1975; Thurston, 1979; Stockton and DeLaca, 1982). These experiments showed that such concentrated food sources attract dense aggregations of a range of scavenging species, ranging from amphipod crustaceans to large fish, virtually anywhere on the deep-sea floor. The efficiency and rapidity of the response, which results in the carcass being reduced to bone within hours, or days in the case of a large cetacean, testifies to the high degree of specialization of scavengers for such food sources. Even if the dead bodies of fish provide less persistent packages of food than a large whale, they must be quantitatively more important on the deep-sea bed. Even the bones are eventually utilized, as it is unusual to encounter fish bones in deep-sea sediments, although the hard dentine of shark teeth is more persistent, and such teeth are well preserved in abyssal sediment.

The unpredictability in where they fall, and their low density, makes such concentrated food inputs difficult to estimate quantitatively. Certain areas underlying the seasonal migration routes of fish or marine mammals may experience these inputs more frequently (Tyler, 1988; C.R. Smith et al., 1989; Tyler et al., 1993). Another potential source of input is from the discarded by-catch of trawling in deep-sea fisheries on the continental slope. Such fisheries are as yet unregulated and highly selective, meaning that often a large proportion (up to around 50%) of trawled biomass re-enters the sea as highly localized, and relatively massive, dead food falls (Connolly and Kelly, 1996).

Dead whales

I shall deal with whales separately, as such megacarrion provides the largest amount of biomass from a sinking carcass, and therefore the most persistent food-fall. C.R. Smith et al. (1998) have estimated that adults of the nine largest species will provide in excess of 10 000 kg wet weight of organic matter. Even if the number of large cetacean food-falls to the deep-sea bed may have declined greatly since the development of modern whaling, such food-falls represent a colossal concentration of organic enrichment in a food-poor environment. That biological specialization to such windfalls is well developed is shown from seabed experiments using autonomous lander vehicles, which show tissue removal rates by fish and invertebrate scavengers of between 0.05 and 0.4 kg h^{-1} (Jones et al., 1998). This is a similar rate to that observed with large fish carcasses (C.R. Smith, 1985), and means that a small cetacean (50 to 100 kg) may be reduced to skeleton within 15 days. For larger carcasses, scavenging and decomposition may remove 1 kg h^{-1}, equivalent to 9 t yr^{-1}, sufficient to skeletonize small whales within a year (Jones et al., 1998). There is also a slow loss of particulate and dissolved organics into the surrounding water and sediment (C.R. Smith et al., 1998). Such falls may be locally important (Katona and Whitehead, 1988; Britton and Morton, 1994). Estimates of carbon input to the deep-sea benthic system based on whale population size and natural mortality are 2 to 3 orders of magnitude less than that provided directly from primary production at the surface by phytodetritus (Jelmert and Oppen-Berntsen, 1996). At the basin-wide scale in the Northeast Pacific, the input of dead whale falls is probably of the order of only 0.1% of published estimates of detrital sedimentation to the sea floor (C.R. Smith and R.S. Lampitt, personal communications). Butman et al. (1994) have given a speculative account of changes in such effects as inputs to the deep-sea bed ecosystem caused by changes in whale populations through whaling.

Whale skeletons located on the deep-sea bed seem to be persistent features whose large bones typically contain 10% lipid and 25% protein. In one experiment a dead dolphin measuring 2.04 m long was put on the abyssal seabed (4800 m water depth) in the Northeast Atlantic for 276 days. This was estimated to provide 500 kg of organic carbon from the skeleton, equivalent to 325 years of average daily background flux per square metre (Jones et al., 1998). Such a rich substrate encourages anaerobic decomposition with development of *Beggiatoa* bacterial mats over the surface. Sulphide generated by these microbial processes is utilized by chemoautotrophic bacterial endosymbionts in a variety of attached bivalve molluscs, such as the genera *Calyptogena, Vesicomya* and species of the families Lucinomidae and bivalves, hyalinoecid Thyasiridae, which normally are associated with reducing environments (see Chapter 4) (C.R. Smith et al., 1989; Bennett et al., 1994; Naganuma et al., 1996).

Adaptation to necrophagy: giant amphipod scavengers

The response to animal carcasses by highly specialized, motile scavengers is best known in the 'giant' amphipods belonging to the family Lysianassidae (Shulenberger and Hessler, 1974; Shulenberger and Barnard, 1976; Thurston, 1979; Hargrave, 1985). The largest of these amphipods, such as *Alicella gigantea* (measuring up to ~34 cm in body length in females) and *Eurythenes gryllus* (up to ~14 cm in body length), probably have a worldwide distribution (Barnard and Ingram, 1986; De Broyer and Thurston, 1987). The foraging of scavenging lysianassids has been reviewed by Sainte-Marie (1992). They represent a highly specialized response to isolated, discrete food-falls in the deep ocean.

Olfaction, possibly combined with rheotactic swimming behaviour, is almost certainly the principal means of detecting and finding carrion food-falls. The amphipods possess shearing mandibles and capacious guts, well equipped for rapid and voracious feeding on carrion (Dahl, 1979; Thurston, 1979). *In situ* experiments by Hargrave et al. (1994) on *Eurythenes gryllus* show that they are able to process meals as batch reactors (a term borrowed from industrial chemistry where food is processed as discrete batches in a large gut – see Penry and Jumars, 1987). This method is suited to the need for surviving for long periods without feeding. Furthermore, enhanced activity by barophilic bacteria in the intestinal tract represents hot-spots in microbial degradation of organic material in the deep sea (Wirsen and Jannasch, 1983); while high oil content from lipid energy storage in these animals may aid buoyancy as well as providing for concentrated energy storage. Hargrave et al. (1994) thought that *Eurythenes gryllus* might survive a year without food by utilizing its most recent meal and stored lipids. The added buoyancy from lipids may allow energy-efficient hovering, like a buzzard or mosquito, in the uppermost part of the benthic boundary layer (Jumars and Gallagher, 1982). Here, increasing flow velocity, and increasingly horizontally orientated turbulent mixing, widen the disemination of the odour plume from a target. As a consequence most *Eurythenes gryllus* are caught in baited traps set at about 15 metres above the bottom, although adults occur to about 300 metres above the bottom (Ingram and Hessler, 1983; K.L. Smith and Baldwin, 1984a; Charmasson and Calmet, 1987; Christiansen et al., 1990). Scent from carrion may diffuse upwards from below as well as laterally, but baited-camera observations show large scavenging amphipods approach from the down-current direction, with the response maximized during peaks in tidal flow (Thurston, 1979; Lampitt et al., 1983; Desbruyères et al., 1985; Jones et al., 1998), indicating efficient location of carrion. An alternative "sit-and-wait" strategy might involve amphipods lying burrowed in the sediment until they sense a target, but no hard evidence is available, and this now seems unlikely. However, aggregations of lysianassids are reported to persist, "roosting", possibly in a torpid state, in the sediment for days near bait after gorging themselves (C.R. Smith, 1985, 1986; Sainte-Marie, 1986).

A second group includes smaller, less specialized, amphipod species (including genera of the *Orchomene* complex) having a less specialized morphology and a lifestyle withstanding perhaps shorter periods of starvation. Experiments in aquaria have shown that the species *Orchomene obtusus* may not survive longer than about six weeks without food, but it reacts within seconds to odours emitted from carrion (Tamburri and Barry, 1999). Tamburri and Barry found that the smell also triggered a strong positive geo-, or possibly thigmo-tactic response, resulting in a search restricted to the bottom where food-falls will naturally occur. Even though members of the first group of amphipods are extremely well adapted, the prevailing view is that it is unlikely that any deep-sea species is an obligate necrophage; the extensive vertical range of lysianassid species enabling them to compensate for deficient bottom resources by foraging for living prey in the water column (Jumars and Gallagher, 1982; Sainte-Marie, 1992; Britton and Morton, 1994). Such feeding may contribute towards active transport of organic material from the bathypelagic zone to the sea floor. However, against the idea that these animals may feed on live prey is the experimental evidence that *Orchomene obtusus* when tested showed no response to the odour of live, rather than dead prey (Tamburri and Barry, 1999).

Other benthic necrophages

Britton and Morton (1994) have provided a general survey of marine scavengers, including those in the deep sea. Scavenging is not a sharply defined category of feeding and, like deposit feeding and carnivory where large 'vacuum cleaner' deposit feeders, such as elasipod holothurians, may take in small invertebrates as well as sediment particles, it also merges with detritivory (Walker and Bambach, 1974). I shall therefore only include macrophagous animals that do not necessarily kill their food. As mentioned earlier, there are a number of benthic and benthopelagic fauna groups, other than highly motile lysianassid amphipods and fish, that are known to consume carrion on the deep-sea bed. These include onuphid polychaetes, such as *Hyalinoecia* (Dayton and Hessler, 1972), large neogastropods such as *Neptunea* (e.g., C.R. Smith, 1985), octopods (Isaacs and Schwartzlose, 1975), ophiuroids (e.g., C.R. Smith, 1985), elasipod holothurians (Pawson, 1976; Massin, 1982) and perhaps asteroids and echinoids. Among peracarid crustaceans other than amphipods, isopods are known as scavengers (e.g., Sekiguchi et al., 1982; Briones-Fourzán and Lozano-Alvarez, 1991; Tso and Mok, 1991), as are many decapod crustaceans, including large, swimming caridean prawns such as *Acanthephyra* (e.g., Desbruyères et al., 1985). The large stone crab *Neolithodes grimaldi* has also been photographed attracted to bait set on the bottom in the deep Northeast Atlantic (Gage and Tyler, 1991, fig. 4.27). It is entirely possible that there are many deep-sea species belonging to the wide range of invertebrate groups known as occasional scavengers in shallow water and reviewed by Britton and Morton (1994) that may also function as facultative scavengers on the deep-sea bed.

Tamburri and Barry (1999) found that the large neogastropod *Neptunea amianta*, and the hagfish *Eptatretus stouti*, able to survive for at least nine months without food. Perhaps surprisingly, *N. amianta* showed no apparent response to the odour from carrion when tested, and Tamburri and Barry (1999) speculated that the sensitivity to such chemical cues is related to degree of motility of the scavenger.

Scavenging by fish, and the idea of an independent trophic pathway based on scavenging

The extent to which scavenging is important in deep-sea demersal fish is still debatable. Merrett and Haedrich (1997) doubted whether many demersal deep-sea fish are important scavengers at all. They pointed out that direct evidence supporting scavenging is rare, only the grenadier *Coryphaenoides (Nematonurus) armatus* (family Macrouridae) being known from baited-camera studies actually to feed on the bait. Study of stomach contents has provided evidence for scavenging only in the eel *Synaphobranchus kaupi*) and in *C. armatus*. However, the jawless hagfish are thought to contribute significantly to the rapid removal of carrion on the continental slope (Martini, 1998). Like lysianassid amphipods, hagfish are highly sensitive to the water-borne odour from carrion; the odour triggering characteristic searching activity (Tamburri and Barry, 1999). In addition, hagfish defend carrion from some other competitors by releasing slime during feeding (Isaacs and Schwartzlose, 1975).

The idea of an independent and specialized trophic pathway based on scavenging was first put forward by Isaacs (1969). He envisaged a trophic pathway quite independent from that of carnivores and organisms exploiting the rain of fine detrital particles (Haedrich and Rowe, 1977). This idea of divergence in trophic strategies has also been developed by Mahaut et al. (1990). However, for deep-sea fishes, the very substantial body of data that has accumulated from studies on diet, particularly in the large and widely spread family Macrouridae, and in sharks and chimaeroids, does not support the great importance of scavenging (Mauchline and Gordon, 1986; Merrett and Haedrich, 1997). As predators, opportunism seems to play an important part in foraging strategies of many species, as much as specialized trophic behaviour targeting preferred prey. Hence the evidence that deep-sea benthopelagic fish may play an important rôle as scavengers is still equivocal. Merrett and Haedrich (1997) have argued that predation by fish on pelagic organisms impinging on the bottom at slope depths, as discovered by Mauchline and Gordon (1991) and, in deeper water, on suprabenthic invertebrates in the benthic boundary layer, is more important.

For invertebrates, the evidence from dietary studies is much more fragmentary, and morphological and behavioural data have as yet failed to provide the definitive evidence that even species as highly adapated as large lysianassid amphipods rely entirely on scavenging for their nutrition. This view is supported in the important review of marine carrion and scavenging by Britton and Morton (1994), on the basis that as a food source it is too ephemeral, and in any case there would be too little of it available to encourage evolution of obligate scavengers. Although lysiannasid amphipods, and perhaps hagfish, approach this concept most closely, the unpredictability and very low density of natural carrion favour the evolution of facultative, rather than obligate, marine scavengers. Because most carrion comes from the surface, the observed increasing importance of scavenging with increasing depth (Stockton and DeLaca, 1982) is at least partly because of the declining flux of small particles arriving at the bottom, so that quantitatively detrivory becomes relatively less important.

Recent studies using stable-isotope analysis combined with gut-contents analysis in the European BENGAL study site on the Porcupine Abyssal Plain support this view of facultative scavenging combined with predation on living prey. Iken et al. (2001) found that highly motile organisms – large amphipods, decapod crustaceans and benthopelagic fish, such as *Coryphaenoides (Nematonurus) armatus* – show levels of ^{13}N enrichment below those of known predators. This was interpreted as reflecting dependency on both abyssopelagic prey and large food-falls.

Effect of food falls on the 'background' sediment community

It has been thought that relatively large carcasses might attract small benthic trophic opportunists, such as capitellid and dorvilleid polychaetes, cumaceans and leptostracans, as well as the more specialized scavenging fauna such as lysiannasid amphipods. Observations suggest that fish visiting carcasses prey on smaller animals such as the scavenging amphipods always attracted to such falls (e.g., Jones et al., 1998), so that such links form part of the wider deep-sea food chain. These, and more recent observations on the sediment macrofaunal response to a whale skeleton on the seabed off California (C.R. Smith et al., 1998), however, seem to confirm earlier suppositions (e.g., Dayton and Hessler, 1972; Rowe et al., 1974) that the 'background' sediment fauna is little affected. They certainly do not support the hypothetical enrichment by consumption of scavenger faeces suggested by Stockton and DeLaca (1982). Fish and epifaunal invertebrate scavengers consume and disperse the package so efficiently that little remains for direct utilization by the infaunal sediment community. Any local sediment enrichment perhaps resulting from scavenger faeces might be counterbalanced by direct effects through smothering by the carcass, or by secondary smothering caused by debris from megafauna colonizing whale skeletons (C.R. Smith et al., 1998).

Significance of large animal food-falls and the biomass of the scavenging community

It is immensely difficult to estimate the total amount of organic matter entering the deep-sea ecosystem as large food falls. Bait experiments on the deep-sea bed (see below) show that scavenging animals are an integral part of deep-sea food webs through the ingestion and redistribution of organic matter. Quantification of these scavenger populations is a good way to understand the importance of such large food falls, but this has proved difficult. Although a large biomass of sharks and chimaeras has been observed from baited cameras and manned submersibles, quantification of their importance as scavengers is problematic. Mahaut et al. (1990) concluded that carcasses falling to the bottom, at a depth of 2100 m on the Meriadzek Terrace (Northeast Atlantic), are exploited exclusively by selachians (sharks and rays). However, the baited-camera data showed that teleosts (bony fish such as species of the families Macrouridae, Moridae and Synaphobranchidae always attended the bait before the arrival of large-sized selachians, such as the enormous sleeper shark, *Somniosus microcephalus* (Fig. 11.19). This is confirmed in work using cetacean carcasses as bait in the abyssal Northeast Atlantic where macrourids arrived along with lysianassid amphipods after about an hour (Jones et al., 1998); but their numbers declined when much of the bait had been consumed. Overall, data are not inconsistent with the supposition by Haedrich and Rowe (1977) that the biomass of the motile scavengers is roughly the same as that of sedentary epifauna and infauna. It may seem unlikely that these populations could be sustained by feeding as carnivores on other deep-sea organisms such as epifauna, as suggested by Dayton and Hessler (1972).

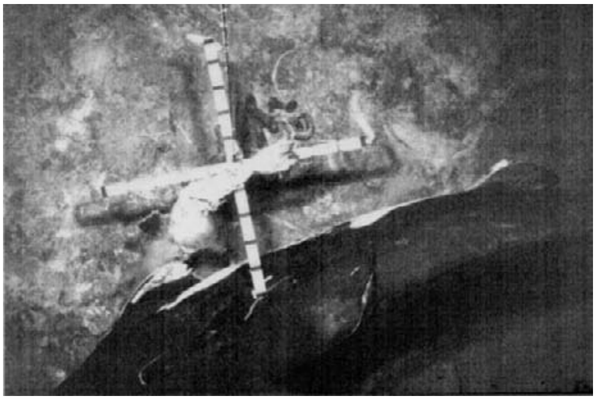

Fig. 11.19. Large shark, probably the sleeper shark, *Somniosus,* attacking bait at the deep-sea bed. Courtesy Dr Monty Priede, Aberdeen University.

The important role of deep-sea demersal fishes, such as rat-tails, *Coryphaenoides* spp. (family Macrouridae) has been shown in elegant experiments tracking individual fish which have ingested acoustic tags. These experiments have given rise to astonishingly large estimates of population densities (Armstrong et al., 1992; Bagley et al., 1994; Priede et al., 1990, 1991). Accurate range data using scanning sonar (Bagley et al., 1994; Priede et al., 1994a) confirm that the foraging pattern of scavenging fishes is important in dispersing organic material from a food-fall laterally over a wide area (Collins et al., 1998).

DISSOLVED ORGANIC CARBON AT THE DEEP-SEA BENTHIC BOUNDARY

Quantities and sources

Quantities of dissolved organic material are produced by phytoplankton in the euphotic zone. However, the amount produced still remains controversial. A new method for measuring dissolved organic carbon using high-temperature catalytic oxidation (HTCO) revealed far higher levels of dissolved organic carbon in the upper water column than previously thought (Sugimura and Suzuki, 1988). Here, bacterioplankton are important in the transformation of dissolved organic matter (DOM) into particulate organic matter (Azam and Hodson, 1977. Some of this may be transported downwards (Toggweiler, 1989); zooplankton are thought to contribute towards this dissolved organic matter flux by diel vertical migrations (Dam et al., 1995). Vertical profiles in the water column show marked increases in concentration at the benthic boundary layer of the deep ocean. Within the benthic boundary layer and sediment, dissolved organic matter is produced by free-living bacteria, by excretion of metabolites by metazoans, and by microbial degradation of dead organisms.

The deep-ocean pool of dissolved organic carbon, like that of suspended fine organic matter, is now thought to be very large – far larger than that of sinking particulate organic carbon (Bauer and Druffel, 1998). The source of this dissolved organic carbon, however, is also controversial. The annual global discharge of dissolved organic carbon from rivers is sufficient to cover turnover of the entire pool in sea water (Hedges et al., 1997). What happens to this ultimately land-derived carbon remains a mystery. However, although Bauer and Druffel (1998) suggested from mass-balance calculations, that input from the continental margins may be much greater than that from the ocean surface, most of this is of marine origin. Support for this comes from recent measurements of high efflux of dissolved organic carbon from the sediments on the continental margin off southern Ireland (Otto and Balzer, 1998). Because this dissolved organic carbon on the continental margin tends to be old, deep open-ocean carbon appears to be older than might be expected if its main source is from new production at the surface.

Dissolved organic matter thus typically consists of two main fractions. First, there are labile compounds readily metabolized by heterotrophic bacteria, and thus maintained at threshold levels. Second, and by far the largest part, consists of much more refractory compounds. These are mostly of very high molecular weight (in the region of 20 000 or more), such as lignins, humic acids and proteins, which are by no means as available for utilization by bacteria.

Dissolved organic carbon as a food source

Williams (1975) reviewed the issue of dissolved organic carbon as a possible food source. The majority of free-living bacteria subsist partly on the smallest organic particles, and also on dissolved organic compounds. The interstitial water of deep-sea sediments contains concentrations of dissolved organic matter about ten times those in the overlying water column (Tanone and Handa, 1980), but unlike that in the water above the dissolved organic matter is much more analytically identifiable. Free amino acids can reach concentrations of $5.6\,\mathrm{mg}\,\ell^{-1}$ and free sugars $0.4\,\mathrm{mg}\,\mathrm{g}^{-1}$ dry weight of sediment (Southward and Southward, 1982). The importance of dissolved organic carbon in the nutrition of deep-sea biota is still speculative. However, it seems likely its utilization may be widespread, and is certainly very likely to occur among deep-sea Foraminifera (Gooday et al., 1992). Free amino acids are taken up by certain free-living metazoans, particularly those living in reducing conditions in the sediment in shallow water. However, the importance of such sources to deep-sea taxa usually can only be guessed from the absence of obvious structures for ingestion of particulate food.

For example, a mouthless deep-sea nematode, described from the surface layer of sediment in the abyssal Northeast Atlantic at 47ºN (Riemann, 1993), may be able to utilize pore-water dissolved organic carbon. Xenophyophores (large agglutinating protozoans found only in the deep sea) are also thought to be able to utilize dissolved organic carbon, and also act as sites of microbial enhancement (Levin and Gooday, 1992). The Pogonophora are a group of worms lacking mouth and gut whose nutrition is thought at least partly to be dependent on dissolved organic matter (Southward and Southward, 1982). Examination of different species by these workers has shown that dissolved organic carbon supplies the total energy need of the adult in only one species, *Siboglinum eckmani*; however, most other pogonophores examined had an energy deficit of up to 70%. Southward and Southward (1982) also estimated that the uptake of dissolved organic carbon by the bathyal sea star *Plutonaster* and the polychaete *Tharyx* may provide up to 30% of their energy requirements. George (1981) was able to maintain the solitary coral *Thecopsammia* and the polychaete worm *Hyalinoecia,* collected from depths of 1000 to 1800 m, for long periods without food in water containing high levels of dissolved organic carbon. Organisms potentially able to benefit from dissolved organic carbon possess soft bodies with a high surface-to-body ratio, such as sponges and suspension-feeding cnidarians.

FOOD WEBS, ENERGETICS AND CARBON FLOW AT THE DEEP-SEA BENTHIC BOUNDARY

Food webs

It has been established above how the benthic sediment-dwelling community responds to the various sorts of organic flux to the bottom, derived either from sinking particles or laterally advected particulate material, from the finest particle to the largest dead body. I have also touched on some of the early trophic links, from these first consumers to secondary trophic links dependent on their faeces or on them as prey. Food webs provide a graphical conceptualization of these links as a map of food chains describing which kinds of organisms in the community eat, or use the ejecta, of other kinds. These linkages, as prey and predator, competitors, mutualists or symbionts, make a complex mesh of interactions (Lawton, 1989). They are not only interesting in their own right as windows on the natural complexity and organization of ecosystems, but important in understanding the functional basis for biodiversity and, as here, in terms of mapping and quantifying energy flow within the system.

The benthic ecosystem classically is considered as a complex web of energy and material flows fuelled by many different chemical reactions, and with substrates supplied by a variety of physical processes. In shallow water, diversity in chemical pathways allows benthic organisms to extract energy from reduced organic matter over a range of oxic and anoxic conditions. In the deep sea the options usually are more limited. This is because organic inputs are rarely sufficient for labile particles to escape utilization at the sdiment surface. Hence, in the absence of reducing conditions at depth, modelling the deep-sea benthic ecosystem need only concern itself with oxidant flux. However, because of the practical difficulties of work in deep water, and limitations in tools available, only a limited number of the food-web flows can be sampled. These either provide a sample of abundance and biomass, or measure rates of community or (more rarely) individual metabolism using *in situ* methods; while, as has been described, the most usually measured fluxes are those from, or to, the overlying water. These are the particle flux usually estimated by sediment traps, or as an oxidant flux measured from concentration changes in a benthic chamber, or modelled from a vertical concentration gradient in pore-water composition.

It is very difficult to measure the energy content of shallow-water marine organims, let alone those in the deep sea. Therefore to understand the energetics of material flows in food webs by this approach presents a daunting task. In practical terms carbon, being the essential building block for organic matter, is used as a proxy for energy. Nitrogen can also be used, this and carbon having a roughly constant ratio in marine organisms (the Redfield ratio). Carbon is taken up in inorganic form during photosynthesis and returned to sea water as carbon dioxide during respiration, and thus can be tracked through the system when labelled using radioactive carbon, ^{14}C. One important universal constraint on the length of food chains is the energy loss at each step. At most only about 50%, and often much less, of available energy is transferred over to the next upwards link in ectotherms. Two general features ought to apply to the deep-sea ecosystem. These are: a) the rapid rate of attenuation in energy transfer means that food chains tend to be short, even in the most productive systems; b) food chains also tend to be scale-invariant, independent of the number of links in the web such as the proportions of bottom, intermediate and top species. Additionally, the density of links in the food web might be expected to be high because of the high species richness among deep-sea sediment-dwelling invertebrates (see Chapter 10). The number of food-chain links has often reflected the intensity of study of a system (Hall and Rafaelli, 1991). The claim that longer chains are less stable than shorter ones, which would encourage severe population fluctations, has held sway for for nearly two decades in the ecological literature as a result of models, dating from May (1973), demonstrating the destabilizing effect of complexity in food webs. The recognition that in nature complexity is of common occurrence has encouraged new work and modelling, which has succeeded in demonstrating the stabilizing effect of complexity as deduced by intuition, in terms of an interwoven matrix of interaction holding the community together. This does not employ an approach with nonlinear terms in predator–prey relationships. Predators are constrained so they cannot maintain high feeding efficiency on many different prey organisms at the same time, thus relaxing pressure on low-density resources and so preventing their extinction. These many weak links, with few strong interactions, in the system connecting species in the community dampen oscillations between consumers and resources, and thus tend to stabilize, rather than destabilize, the dynamics of the component species (McCann et al., 1998; Polis, 1998).

Although it has been thought that food-web relationships among individual species in the deep sea are still too poorly understood to allow construction of the benthic food web for any single deep-sea station (Sibuet, 1992), there is steady movement towards the realization of this goal. Because of high local species richness, a high degree of taxonomic resolution in food-web description is difficult, but it seems unlikely that the number of food-web links approaches those found in the tropical rain forest, even if similar sorts of interaction occur. However, one interesting consequence of the patchy system caused by spatially uneven detrital deposition (which may also help explain high species richness – see Rice and Lambshead, 1994) is that food chains will be shorter in small habitat patches (Pimm et al., 1991).

Stable-isotope analysis has been applied in order to track sources in marine food webs involving deposit feeders (see overview of subject in Michener and Schell, 1994). Use of such natural tracers involves a number of assumptions. For example, measurements of δ^{13}C may be biased by lipid contents, with differing rates of ^{13}C enrichment occurring depending on relative amount of carbohydrate, proteins and lipids present in the tissue. It is claimed that ^{15}N ratios are more conservative among biochemical fractions, so that δ^{13}N is a more reliable tool in tracking trophic linkages (Hobson and Welch, 1992). However, stable-isotope studies conducted in tandem with analysis of stomach contents seem to provide most certain data. Iken et al. (2001), using δ^{13}N and analysis of gut contents, concluded that, although sedimented particulate matter seems to provide the major food source for the benthic community at the BENGAL site, food-web structure is not simple. Their analysis of 90 species shows that 35 macro- and megafauna are deposit feeders, with 17 suspension feeders, and 29 predators/scavengers. However, δ^{13}N values overlap between feeding types and cover a large range within them, indicating a considerable overlap in food sources, and probably high competition for food. Invertebrate predators, such as the polychaete *Nicon* sp. and the asteroid *Dytaster grandis* showed the highest ratios (i.e., greatest depletion). Interestingly, δ^{13}N values for the latter species are greater than those for highly motile predator/scavengers, such as amphipods, decapod crustaceans and benthopelagic fish (see pp. 354–359).

Modelling food webs, energy flow and carbon dynamics on the deep-sea floor

Perhaps one of the best-developed models of food web structure and energy flow has been put together by fisheries biologists for the Grand Banks off Newfoundland. This model aims at a better understanding of species interactions for the purposes of stock management of the top predators, such as cod (*Gadus morhua*). A study of a subset of seven consumer species used augmentation or depletion of single species in order to test effects on the resilience of the community, and found highly indeterminate outcomes (Gomes and Haedrich, 1992). No data of remotely comparable resolution yet exist for the deep sea, where incorporation of additional complexity in order to approximate biological realism will be even more necessary than for the Grand Banks. Therefore attempts to model trophic relationships in the deep sea will face much greater problems.

For this reason the approach up to now has been to categorize the entities of the deep-sea ecosystem in terms of size and functional groups, which have been sufficient as descriptive compartments in models of early diagenesis (e.g., Soetaert et al., 1996). Such models are typically constrained by particle-flux data from sediment traps, sediment porosity profiles and estimated sedimentation rates and bioturbation using radiotracers such as ^{210}Pb. These have made it possible to progress beyond describing links quantifying flows between broadly based compartments. But the difficulty is that the integrated values employed may have no relevance to rates in small size groups such as microorganisms and meiofauna, let alone individual species. Furthermore, biomass-specific respiration or feeding rates, when used to estimate carbon transfer between functional groups or model compartments, arguably have too broad a range to apply to individual links in a model (Eldridge and Jackson, 1992). Nevertheless it is only such bulk measurements that are presently available. Furthermore, despite the diversity of organisms comprising the various consumer groups, data plotted by K.L. Smith (1992) show a reasonably tight fit to a linear relationship between biomass and carbon demand. But the effort needed to construct a budgetary box model based on relatively large functional or size categories of organisms which includes contemporaneous flux data even for just one site is extraordinarily large.

One approach by French workers has been to link such diagenetic modelling with trophodynamic simulations. This employs numerical modelling to project behaviour of state variables (size of component categories of organisms) from measured parameter variables and initial conditions. A typical trophodynamic model consists of size- or function-determined compartments as state variables where interactions between compartments are modelled using known predation relationships and a forcing function provided by the measured organic carbon flux. The limitation of such models lies in uncertainty in feeding relationships among the large number of different species comprising the assemblage within a model compartment, and in uncertainty in assimilation efficiency and the true magnitude of organic flux. Because of this, there is a danger that output of such modelling may sometimes seem unrealistic. One solution to the frequent dilemma of incomplete data was developed for the planktonic food web (Vézina and Platt, 1988). Here, inverse analytic techniques use known information on state variables to estimate the parameter fluxes and initial conditions. The method then fits a “best” estimate of the complete set of flows in a way analogous to regression analysis. As yet, models have been limited to linear relationships, with flow parameters as constants, generating ‘snapshots’ in time. However, they have been robust and informative on the relative importance of different types of flows and compartments. For example, a flow network model applied to the diverse range of bathyal areas off the southern Californian coastal margin was able to include and assess the relative importance of anaerobic, as well as aerobic, pathways in the benthic system (Eldridge and Jackson, 1992, 1993).

Conclusions from organic carbon and energy flow models of abyssal ecosystems

Assuming that organic carbon arriving at the bottom represents approximately 0.5 to 4% of new carbon flux from the upper layer of the ocean (Deuser and Ross, 1980; Bender and Heggie, 1984; Martin et al., 1987), various studies suggest that about $50\,\mathrm{mg\,m^{-2}\,yr^{-1}}$ of meio- and macrofauna would be supported on a particle flux of $10\,\mathrm{mg\,m^{-2}\,yr^{-1}}$ – that is, about 0.5 to $2\,\mathrm{mg\,m^{-2}\,yr^{-1}}$ of fresh organic carbon (Sibuet et al., 1989). Various studies during the 1980s have indicated that most of the organic matter reaching the sediment would be consumed before burial within a few months (Honjo et al., 1984; Sibuet et al., 1984). Therefore burial flux, amounting to 0.5 to 2% of the total arriving at the deep-sea floor, may effectively be disregarded.

One obvious conclusion is that all studies, whether at bathyal depths or in the abyss, show the sediment community overall as the most important component of the benthic boundary layer community, followed by the epibenthic megafauna and the bacterioplankton, both of which are deserving of greater study (K.L. Smith, 1992).

Attempts at modelling energy flows using carbon have addressed sites in the abyssal benthic environment, because of its supposed simplicity and because the enormous area has an importance in carbon cycling at the global scale. One of the best known and most comprehensive of these has been developed over many years for the central North Pacific by K.L. Smith and his associates at Scripps Institution of Oceanography in California (K.L. Smith, 1992). Their budgetary model encompasses the entire sediment community and the organisms inhabiting the water up to 600 metres above the bottom (metres above bottom). It was assembled from an extensive existing data base, along with many new observations, for a site in the abyssal central North Pacific, where organic carbon pools and fluxes are better known than anywhere else in the deep ocean.

A similar box-model, flow-network approach has been undertaken by French workers in the Northeast Atlantic (Mahaut, 1990; Sibuet et al., 1993). In all approaches of this kind it is necessary to identify the different faunal compartments, in terms of size and feeding type, to determine the biomass of these compartments and the magnitude of the fluxes of organic material between them. This is accomplished in terms of known trophic relations and mass-specific metabolic rates (Mahaut et al., 1995), in order to estimate relationships of organic-carbon demand to biomass (K.L. Smith, 1992). Such work is extremely difficult and tedious, involving input from many different investigations. Categorization of trophic type is assembled using the sort of information summarized above on page 362. Careful study of body size and trophic behaviour, as well as stomach contents, is required in order to avoid mis-categorization. The question may arise, for example, whether large motile megafauna or fish are top predators in a benthic food web, or whether they rely on nekton falls from the surface, thereby short-circuiting the benthic food web (Mahaut et al., 1990). Furthermore, possible spatial and temporal variability in rates of processes mean that "snapshot" measurements incorporated, such as those from measurements of sediment community oxygen demand (see above), carry high uncertainty.

Quantification of trophic energy-flow models: caveats

The work so far discussed shows that it is now possible to put some figures for carbon and energy in and between the boxes corresponding to the compartments in trophodynamic models of energy flow. But even at the most comprehensively studied site – that studied by K.L. Smith in the central North Pacific – not all compartments and flows could be estimated from real data, and the budget fails to balance inputs and outputs. One suggestion, that the 'missing' carbon in these studies might be supplied by dissolved organics (K.L. Smith, 1989, 1992), was prompted by the inverse relation found by Sugimura and Suzuki (1988) between apparent oxygen utilization and dissolved organic carbon measured in the water column. This suggested that a more utilizable, labile fraction present is being turned over much more rapidly than that the old and highly refractory dissolved organic carbon previously thought to constitute this pool. This labile fraction, then, has a previously unrecognized importance, presumably by diffusion and turbulent mixing down to the benthic boundary layer, in carbon cycling in the deep ocean (Burdige et al., 1992). There are also tantalizing data indicating losses of dissolved organic carbon from the sediment larger than the requirements for sediment community oxygen consumption (Lampitt et al., 1995).

Other possible overlooked sources of organic carbon include net advection from other areas, although this seems much less likely in the central North Pacific than for sites nearer, and on, the continental margin. Also, the possible importance of large food-falls as another source of organic carbon in the central North Pacific, as is the case virtually everywhere else, cannot yet be quantified accurately. Finally, active transport into the benthic boundary layer by migrating fauna (which bypass sediment traps) could, both as active flux mediated by predation on diel migrators, and as passive flux from faecal ejecta at depth (see pp. 316–317), account for the total estimated consumption of the benthic boundary layer community in the central North Pacific. But this assumes that the migrators are feeding above the benthic boundary layer, and that their faeces represent a net gain (that animals leave the benthic boundary layer with empty guts). Neither assumption presently can be validated (K.L. Smith, 1992).

Finally, the problem of dealing with seasonal variation involves many uncertainties. Although intense seasonality may be seen in surface productivity, reflected in the measurements of exported particle flux, a corresponding variability in sediment community oxygen consumption, as an expression of seabed organic remineralization, has not always been seen (e.g., K.L. Smith, 1989; Lampitt et al., 1995). This is not to suggest that such coupling might not exist. Studies elsewhere have demonstrated rapid responses to pulsed sedimentation from the surface (see above). Improvements in the range, quality and duration of data, reflecting both the full size-range of inputs and the amounts utilized, will be necessary before a full understanding of the energetic links and dynamic responses can be said to exist for even one site in the deep sea. K.L. Smith et al. (1992) concluded that the inclusion of previously undetected episodic particle flux to the benthic boundary layer might substantially reconcile the imbalance between supply as particulate organic carbon flux and demand measured as sediment community oxygen consumption. Their studies at an abyssal station (Station 'M') off California utilizing a long time series of particle-flux measurements (2.3 years) succeeded in achieving agreement within 15%, compared to shortfalls of up to 97% in previous short-term measurements (K.L. Smith, 1987, 1989).

However, a more recently published study (K.L. Smith and Kaufmann, 1999) based on a much longer time series (7 years) has shown a widening, long-term deficit at this station. This may be related to increasing surface water temperature with reduced plankton biomass, resulting in a declining particulate export flux to the deep-ocean bottom. Whether this trend will prove to be persistent is as yet unknown.

Carbon dynamics at the deep-sea continental margin

The deep-sea continental margin beyond the shelf edge constitutes the continental slope and rise, the latter a wedge of sediment at the base of the slope where the gradient lessens into the flat area of the abyssal plain. Studies on the continental margin have provided some of the best, and most tantalizing, data. It is here that comparisons of supply and demand by the bottom community show the largest discrepancies (K.L. Smith, 1987; Jahnke et al., 1990).

This budgetary problem was uncovered during the 1980s on the upper continental slope along the Atlantic margin of the United States, where it was suggested that the large material flux to the continental slope is derived from material produced on the shelf and transported over the shelf edge (Walsh, 1991). The organic flux measured in sediment traps on the middle continental slope at about 1000 m depth was insufficient to account for the measured sediment community oxygen consumption (Rowe et al., 1994). When expressed as carbon equivalents (mg $C_{org}\,m^{-2}\,day^{-1}$), values of sediment community oxygen consumption on the continental slope are generally lower than near-bottom particle flux, except at mid slope depths where it was slightly higher; the general discrepancy may possibly be ascribed to along-slope and down-slope advection, anaerobic metabolism (not measured by oxygen demand), and burial. Net carbon flux to the bed might be thought best measured close to the bottom in order to collect near-bed advected material, as well as vertical flux. But there remains uncertainty arising from local resuspension and deposition – the so-called ‘rebound’ flux. However, if the measurements are made at greater depths more serious budgetary discrepancies have emerged. The differential in sediment community oxygen consumption on the continental margin is greater on the west coast of America than on the east, and increases with depth. This has been linked to resuspension by benthic storms along the continental rise in the western Atlantic, which results in relatively less bacterial decomposition of particles while they are on the bottom (Rowe et al., 1994). Furthermore, this turbulent regime on the continental rise may extend the effects of the continental margin far out onto the adjacent abyssal plain (Walsh et al., 1991).

Lampitt et al. (1995) found that particle flux collected by sediment traps set at mid-slope would be sufficient to fuel only 20% of measured sediment community oxygen consumption. Possible overestimation of oxygen demand might have resulted from the technique used, but it seems likely that very substantial quantities of detrital flux on the seabed are transported downslope in the bathyal Northeast Atlantic in order to provide the organic carbon consumed.

The issue of whether there is significant down-slope transport of particulate detrital material can be addressed by comparison of downward flux from surface production with estimates of benthic oxygen demand. Rowe et al. (1994) found seabed oxygen uptake, in terms of carbon equivalents ($mg\,C\,m^{-2}\,d^{-1}$) to be less than particle flux measured in sediment traps except at the mid-slope ‘depocentre’, where there is an accumulation of organic carbon laterally advected down the continental slope. Lampitt et al. (1995) also found that vertical flux measured from deep sediment traps at depths of 2000 m on the continental slope in the Northeast Atlantic was sufficient to fuel only 20% of demand. They concluded that substantial quantities of particulate material, not intercepted or properly collected by sediment traps (see Baker et al., 1988; Gust et al., 1994), must be transported down-slope in order to balance the discrepancy. The opposite imbalance found by Rowe et al. (1994) at other stations was partly attributed to lateral and near-bed down-slope transport.

Studies on the slope off Southwest Ireland studied in the OMEX program of the European Union has shown that both hydrodynamic and biologically mediated processes associated with lateral advection are of great importance (Heip et al., 2001). Even in low-flow conditions ($<5\,cm\,s^{-1}$), lateral particle flux is orders of magnitude greater than the vertical flux. Large-sized particles in the benthic boundary layer at the shelf edge are not deposited there, but transported to deeper, quieter areas. The processes involved of particle aggregation, biologically mediated modifications of near-bed fluxes, and a resuspension loop within the benthic boundary layer have been shown to be sufficient to fuel observed benthic demand on the slope and to account for the deficiency observed in sediment traps (Thomsen, 1999). However, these studies have also shown the importance of the resuspension loop in modifying the distribution and composition of organic carbon. Thomsen and Gust (2000) have suggested that an energy cascade occurs for benthic boundary layer aggregates. This begins with the most labile and nutritious particles freshly arrived from the euphotic zone, and ends with primary sediment particles containing very old refractory carbon of extremely low nutritive value to the sediment community, which accumulate in deep water.

Overall, the various studies measuring input (e.g., particle flux) and response (e.g., sediment community oxygen consumption) within the OMEX program indicate broad budgetary agreement in carbon flux, with no evidence of a significant carbon 'depocentre' beyond the shelf edge (Fig. 11.20).

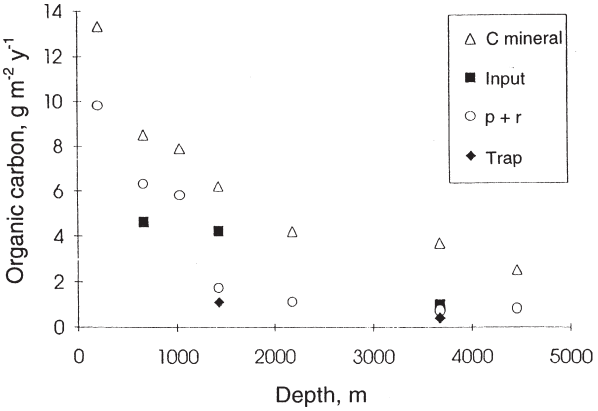

Fig. 11.20. Carbon fluxes (g C m^{-2} y^{-1}) at the West European margin along the OMEX transect; solid symbols represent input, open symbols utilization. Input points calculated from sediment trap data and from benthic boundary layer measurements and laboratory flume experiments on particle dynamics; benthic utilization points from sediment community oxygen consumption measurements and respiration-plus-production estimates for the metazoan benthos. From data in references cited by Heip et al. (2001).

The overall conclusion from several studies on the continental margin mentioned previously is that advective processes may be of equal or greater importance to some consumer groups compared with downward flux through the water column. These studies include slopes of varying physiography and related degree of locally focused intensity of downslope processes. Not surprisingly, advected flux has been shown to be important in the more complex, fissured margins, such as those in the Western Mediterranean (e.g., Buscail and Germain, 1997). This is subject to seasonal variability that can be mapped against changes in consumer populations (Cartes, 1998).

Exports from the continental shelf to the deep sea

The potential loss of organic production from the shelf to the deep sea raises important questions in the global carbon budget (e.g., Rowe et al., 1986). It has been suggested that biological production on the highly productive continental shelf is unbalanced, the large amount of phytoplankton produced during the spring bloom overwhelming the capacity of planktonic herbivores to consume and recycle it. Physical processes then largely result in its export over the shelf edge. Estimates of shelf export to the slope and abyss range from between 1 and 10% to about 90% of total phytoplankton production (J.J. Walsh, 1991; Biscaye et al., 1994). The excess organic carbon will eventually be sequestered by benthic populations living on the slope. This fuels enhanced biomass and remineralization through metabolism. Thus, from a global viewpoint, this utilization of organic carbon by the benthic boundary layer community (and its eventual burial) on the continental slope is of considerable importance in identifying sources and sinks in the planetary carbon cycle.

Whether the continental slope is, or is not, important in this way is a side issue in this Chapter, but the question has encouraged significant debate and research emphasis on organic-carbon dynamics at the continental margin. The typical pattern of exponential decline in benthic and benthopelagic biomass with increasing depth on the slope is associated with increasing separation from the source of primary production in the euphotic zone (Wishner, 1980; Rowe, 1983). But, at least for the much better known benthic community, it has also been recognized that this pattern is far from uniform. For example, markedly differing macrofaunal densities on the North Carolina slope are thought to reflect correspondingly different fluxes of labile material of marine origin caused by the pattern in surface boundary currents (Schaff et al., 1992; Blair et al., 1994). Another example is provided by the dissected topography of submarine canyons. This may act to channel down-slope transport of organic-rich particles from shallow seas into deep water. This enrichment may significantly enhance local benthic abundance and biomass (Rowe et al., 1982; Gage et al., 1995). Indeed, enhanced metabolism of the sediment community, measured as interfacial fluxes such as oxygen consumption, indicate enhanced rates of benthic carbon mineralization at the base of the slope. This led Jahnke et al. (1990) to suggest that about half of the total organic-carbon input to the deep-sea floor occurs within 500 km of the continental slope. The American SEEP programs in the Mid-Atlantic Bight in the Northwest Atlantic showed that, although rates characteriztically decline precipitously down slope, values at depths of about 1000 m may be almost as high as those on the continental shelf. This result supported the idea of an organic-carbon 'depocentre' and a corresponding peak in sediment community oxygen consumption (Rowe et al., 1994). The SEEP programs tested the idea that large amounts of fine particles including shelf phytoplankton production may be swept over the shelf edge and deposited on the adjacent slope; this phenomenon was periodically observed after storm-driven resuspension from shelf sediments (Biscaye et al., 1994).

Large-scale comparisons and projections

In the abyssal realm, comparisons between different latitudes and levels of primary production at the surface may show differences in the size, structure and composition of the community. These reflect differences in benthic response to amount and seasonal pattern of organic flux to the bottom (e.g., Sibuet et al., 1993; Rice et al., 1994). French work at contrasting sites at roughly the same latitude in the tropical Northeast Atlantic showed relatively high abundance of carnivorous necrophages (e.g., scavenging lysianassid amphipods) at the most oligotrophic station, despite the very low particle flux to the bottom. This was also consistent with the pattern in proportions of size classes, the largest organisms (megafauna) showing the least diminution in biomass from eutrophic to oligotrophic sites compared to macro- and meiofauna (Sibuet et al., 1993). K.L. Smith (1992) also found that the largest size groups formed a much larger component of the consumer community in the oligotrophic central North Pacific than at a more eutrophic, abyssal site near the California margin.

Such differences cannot easily be explained by differences in seasonality, as the stations were located at about the same latitude. Instead, possible body differences in foraging strategies related to body size may be implicated. Life-styles reliant on local particle rain become unrewarding at very low particle flux, with increasing importance of motile necrophages able to respond and scavenge large, albeit sparse, falls from the death of large surface swimmers (some perhaps migratory) which collect food over a wide area. Something similar may possibly explain the differing composition of abyssal necrophages at two sites further north in the Northeast Atlantic referred to earlier. One is dominated by crustaceans such as scavenging amphipods, and the other by macrourid fish; this difference possibly is a response to differences in relative proportions of mid-water zooplankton and nekton (Thurston et al., 1995). Sediment bacterial activity shows a better relationship to the particle rain intercepted by sediment traps, bacterial numbers being 3 to 4 times higher at the mesotrophic site than at the oligotrophic one (Sibuet et al., 1993). Otherwise, latitudinal comparisons in the Atlantic Ocean, from 30ºS up to about 80ºN, show a first-order relationship of meio- and macrofaunal abundance to particle rain, as integrated by the organic-carbon signal buried in the sediment during the Holocene (Sibuet et al., 1989).

Physical variables, such as hydrodynamics, are also important. The most extreme conditions are in areas experiencing frequent sediment-eroding benthic storms. Up to a point, strong flow may support a larger benthic standing crop than would be expected. But at higher energy it may have a negative impact on larger size classes such as motile megafauna, but lead to much enhanced abundances of certain smaller taxa, especially bacteria (Thistle et al., 1985, 1991). On the other hand, a large amount of microbial decomposition that would have occurred in the sediment has already been mediated by bacteria attached to suspended particles. Also, the finding that the macrofauna may consist largely of subadults indicates a constraint imposed on population size structure by such disturbances (Thistle et al., 1985).

Hydrodynamics also affects the efficiency of sediment traps as measures of passive particle rain. It has been shown above how vertical particle flux on the continental slope may be augmented by downslope processes, and by lateral advection of resuspended particles. Even in the abyssal basins, traps set within the benthic boundary layer may provide higher measurements than those a few hundred metres above, owing to resuspension. On the other hand workers have felt it necessary to measure particle flux as near the bed as possible in order to include near-bed advective flux in the total estimate of net accumulation on the bottom.

Epilogue

All these uncertainties, along with the need to model a highly non-linear system, may prompt despair in scaling models from particular sites up to the level of the regional, or even global-scale ecosystem. As an example of what might be possible, a comprehensive modelling approach using a mass-balanced ecosystem modelling package, Ecopath©, has been useful in developing a model of trophic energy flow in the Antarctic shelf ecosystem in the Weddell Sea (Schalk et al., 1993; Jarre-Teichmann et al., 1996).

Clearly projection of variables to the larger scale will involve large uncertanties. The studies reported above at single sites represent huge effort. Their budgetary deficiencies and the evidence for long-term changes (e.g., K.L. Smith and Kaufmann, 1999) reveal how little is really known about biological processes in the deep sea and about variability in coupling to processes in the upper ocean. But, despite their limitations, models assembled on such data as are currently available have proved at the very least useful and informative on what is, or is not, important, and also on what parts of the system are not being addressed.

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Chapter 12

REPRODUCTION, DEVELOPMENT AND LIFE-HISTORY TRAITS

Craig M. YOUNG

INTRODUCTION

From the earliest days of deep-sea exploration, it was assumed that animals living in the presumably "hostile" environments of the deep sea should show life-history attributes and reproductive modes differing from those of their shallow-water counterparts. Shortly after the *Challenger* expedition returned from its circumnavigation of the globe, H.N. Moseley (1880) one of the naturalists of the expedition, summarized the current state of knowledge about conditions in the deep sea. He suggested, as had Wyville Thomson (1878) before him, that brooding (parental care of offspring) is a predominant reproductive strategy in deep water. This idea was supported by the finding of large egg sizes in echinoderms and cnidarians during the same expedition (Agassiz, 1881; Moseley, 1881), and set the stage for a generalization, ultimately formalized as Thorson's Rule (Mileikovsky, 1971), which remained entrenched in the literature until very recent times, when numerous exceptions have been documented (reviewed by Young, 1994a; Pearse, 1994). A second idea first advanced by John Orton (1920) as a testable but untested hypothesis was that reproduction should be aperiodic in the constant thermal conditions of the deep sea. This hypothesis quickly became accepted as established fact and was questioned only when deep-sea seasonality and reproductive periodicity were documented after the 1960s (reviewed by Tyler, 1988).

Both Thorson's Rule and Orton's Rule were reasonable hypotheses when the deep sea was thought to be a completely monotonous habitat with no primary productivity, limited energy and virtually constant physical and chemical conditions. The predictive power of both proved inadequate once one began to understand something of the complexity, dynamics and variability of the deep-sea environment. Unexpected variability has been demonstrated dramatically in the past two decades by the discovery of vents and seeps (see Chapter 4; Lonsdale, 1977; MacDonald et al., 1989), benthic storms (Chapter 2; Gardner and Sullivan, 1981; Hollister and McCave, 1984; Hollister and Nowell, 1991), turbidites (Chapter 2; McCave and Jones, 1988), and other major sources of disturbance. Nevertheless, the vertical gradients of environmental stability and of nutrient availability that provided impetus for the earliest predictions remain a useful framework for considering how natural selection has shaped the life-history attributes of deep-sea animals.

In this chapter, I provide a phyletic overview of known reproductive parameters and developmental modes of deep-sea invertebrates, then apply various predictions of life-history theory to deep-sea animals, considering which predictions are supported or refuted by the available data. Both chemosynthetic and non-chemosynthetic systems are discussed, though the emphasis is on the latter, as a comprehensive summary of reproduction at hydrothermal vents and cold methane seeps has recently been published (Tyler and Young, 1999). Space limits the present treatment to benthic invertebrates; for portals into the literature on life-history attributes of deep-sea fishes, the reader is referred to Stein and Pearcy (1982), Gordon and Duncan (1985) and Merrett (1987).

PHYLETIC OVERVIEW OF REPRODUCTION AND DEVELOPMENT

In his seminal review of evolutionary ecology in the deep sea, Sanders (1977) noted that deep-sea benthic sediments are dominated by polychaetes, crustaceans, molluscs (especially protobranch bivalves and gastropods) and echinoderms, the peracarid crustaceans being the most speciose group. On hard substrata in the deep sea, cnidarians and sponges are especially abundant (Gage and Tyler, 1991) except at hydrothermal vents, where the hard-bottom fauna is dominated by polychaetes and molluscs (Grassle, 1986). As might be expected, the most speciose and abundant groups are also the best studied. I will discuss each of these major phyla in turn, then briefly consider a few others for which more limited information is available.

Annelida

Polychaete annelids are among the most abundant and diverse macrofaunal organisms in the deep sea (Hartman, 1965; Hartman and Fauchald, 1971). Most are deposit feeders depending directly on detrital material falling from above, and most live in the upper few centimeters of sediment. However, polychaetes are also well represented at hydrothermal vents and cold seeps, where they may take on bizarre life styles and spectacular forms. The giant tube worms of vents and seeps and the filamentous perviate pogonophorans are now recognized as polychaetes (family Siboglinidae) specialized for the use of chemosynthetic energy sources. Alvinellid polychaetes, which are common at hydrothermal vents, may be the most eurythermal metazoans (Cary et al., 1998). General aspects of polychaete life-history biology and development have been reviewed by Schroeder and Hermans (1975), Giangrande (1997) and Pernet et al. (2002).

Gonads, gametogenesis, and reproductive periodicity

Although many polychaetes are hermaphroditic, the majority of deep-sea forms that have been studied appear to have separate sexes. In polychaetes, the oocytes always originate within distinct ovaries, often found associated with the peritonea (Eckelbarger, 1986), but vitellogenesis, the stage of oogenesis in which oocytes are invested with yolk, may occur either within the ovary or while oocytes are floating freely within the coelom (Eckelbarger, 1986). In like manner, early spermatocytes released from the gonads often aggregate into plaques, then complete spermatogenesis while adrift in the coelom. Gametogenesis in the deep-sea polychaete *Pholoe anoculata* is coelomic in both sexes, with gametes concentrating near the acicula of the neuropodium (Blake, 1993). An unusual modification of the typical patterns occurs in the deep-sea cossurid *Cossura longocirrata.* In this species, oogenesis takes place in a single segment, which releases mature oocytes into more posterior segments for storage, making the abdominal region appear beaded (Fournier and Peterson, 1991; Blake, 1993). In the large bathyal terebellid *Biremis blandi,* scattered oocytes may be found throughout the coelom, but the highest concentrations are in the ventral region, where they pool between the peritonea (Young, unpublished observations).

With a single exception, all deep-sea polychaetes that have been examined appear capable of reproducing throughout the year, though several species may have “fluctuating” reproductive cycles (as defined by A. Scheltema, 1987), in which there are high and low periods of spawning. One non-vent species, *Cossura longocirrata,* reproduces more in the summer than at other times of the year (Blake, 1993). All of the other fluctuating species are associated with vents (McHugh, 1989; McHugh and Tunnicliffe, 1994; Zal et al., 1995), and in every case sampling is inadequate to determine the period of the fluctuation. The only truly seasonal species is the non-vent spionid *Aurospio dibranchiata,* which occupies an impressively broad bathymetric range (300–3600 m). Notably, evidence for a seasonal gametogenic cycle came not only from the shallowest animals, but also from collections at 2000 m depth. No mature animals were found in spring collections, but animals collected in the summer and fall were ripe (Blake, 1993). However, these data must be regarded as preliminary, since only 13 of 425 individuals examined were found to bear any gametes at all.

Gamete structure and fertilization

Sperm of some deep-sea polychaetes are of the primitive type associated with free spawning and external fertilization (e.g., *Amphisamytha galapagensis*: McHugh and Tunnicliffe, 1994), but the variety of modified sperm described in the literature is striking (Table 12.1). A number of species have elongate sperm, often with limited mobility, which are probably indicative of either internal fertilization, fertilization in tubes, or pseudocopulation in gelatinous egg masses (Franzen, 1956; Jamieson and Rouse, 1989). The sperm of *Paralvinella pandorae* have a convoluted structure of unknown function near the mitochondrion, and the flagellum emerges at an acute angle near this structure (McHugh, 1989), suggesting that motility is limited. On the basis of this sperm structure, McHugh (1989) has speculated that sperm are transferred from the male to the female in bundles rather than being freely spawned. The sperm of *Paralvinella grasslei* lack acrosome,

Table 12.1
Studies of reproductive periodicity and gametes in deep-sea polychaetes

Species	Site	Depth (m)	Egg size[1] (μm)	Sperm morphology	Periodicity[2]	References
NON-VENT OR SEEP SPECIES						
Aurospio dibranchiata	N. Carolina	300–3600	112	?	S	Blake (1993), Blake and Watling (1994)
Bathynoe cascadiensis	NE Pacific	2519–3021	?	?	C	Ruff (1991)
Benthoscolex cubanus	Bahamas	600	120	?	C	Emson et al. (1993)
Cossura longocirrata	N. Carolina	600–2000	180×80	?	F	Blake (1993)
Euchone bansei	NW Atlantic	1345–2495	100	?	C	Ruff and Brown (1989)
Fauveliopsis glabra	San Diego Trough	1240	?	?	C	Rokop (1977a)
Hyalinoecia arauncana	Chile	600	?	?	?	Carrasco (1983)
Microrbinia lineata	N. Carolina	800–3000	344 (mean)	elongate, aberrant	?	Blake (1993)
Nothria notialis	Antarctic	800–900	large	?	C	Hartman (1967)
Ophryotrocha labidon	NW Atlantic	225–2100	73	?	C	Hilbig and Blake (1991)
Ophryotrocha mandibulata	NW Atlantic	2020–3015	48	?	?	Hilbig and Blake (1991)
Ophryotrocha paralabidon	NW Atlantic	225–2195	56.5	?	C	Hilbig and Blake (1991)
Paronuphis antarctica	Antarctic	800–900	?	?	C	Hartman (1967)
Paedampharete acutiseries	NW Atlantic	4626–4830	23?	?	C?	Russell (1987)
Pholoe anoculata	N. Carolina	583–2000	141	?	C	Blake (1993)
Scalibregma inflatum	N. Carolina	600	190	?	C	Blake (1993)
VENT AND SEEP SPECIES						
Alvinella pompejana	East Pacific Rise	2000	200	modified	P	Jollivet et al. (1998), Pradillon et al. (2001)
Amphisamytha galapagensis	NW Pacific	2447–2725	240	normal	C,F?	Zottoli (1983), McHugh and Tunnicliffe (1994)
Branchipolynoe seepensis	Mid-Atlantic Ridge	1630–1685	390	elongate	A	Van Dover et al. (1999), Jollivet et al. (2000)
Hesiocaeca methanicola	Louisiana Slope	600	80	normal	C?	Eckelbarger et al. (2001)
Lamellibrachia c.f. *luymesi*	Louisiana Slope	600	105	elongate; bundles	A	Young et al. (1996b)
Opisthotrochopodus n. sp.	Mid-Atlantic Ridge	1700	390	elongate	A	Van Dover et al. (1999)
Paralvinella pandorae	Juan de Fuca Ridge	1570–2270	215	elongate, modified	C	McHugh (1989, 1995)
Paralvinella palmiformis	Juan de Fuca Ridge	1570–2270	260	modified	C,F	McHugh (1989)
Paralvinella grasslei	East Pacific Rise	2630	275	highly modified	F	Zal et al. (1995)
Ridgeia piscesae	Juan de Fuca Ridge	1853–2265	100	elongate; masses	C	Southward and Coates (1985)
Riftia pachyptila	East Pacific Rise	2500–2700	105	elongate; bundles	C	Cary et al. (1989), Gardiner and Jones (1985, 1993), Marsh et al. (2001)
Seepiophilia jonesi	Louisiana Slope	600	115	elongate; bundles	A	Young et al. (1996b)
Methanoaricia dendrobranchiata	Louisiana Slope	700	?	elongate	?	Eckelbarger and Young (2002)

[1] In most cases, egg sizes are the largest observed in histological sections and may not be representative of the actual sizes of eggs spawned.

[2] Periodicities are listed as either S, seasonal and synchronous; A, aseasonal, continuous, and asynchronous; and/or F, continuous breeding with fluctuating levels of gamete production.

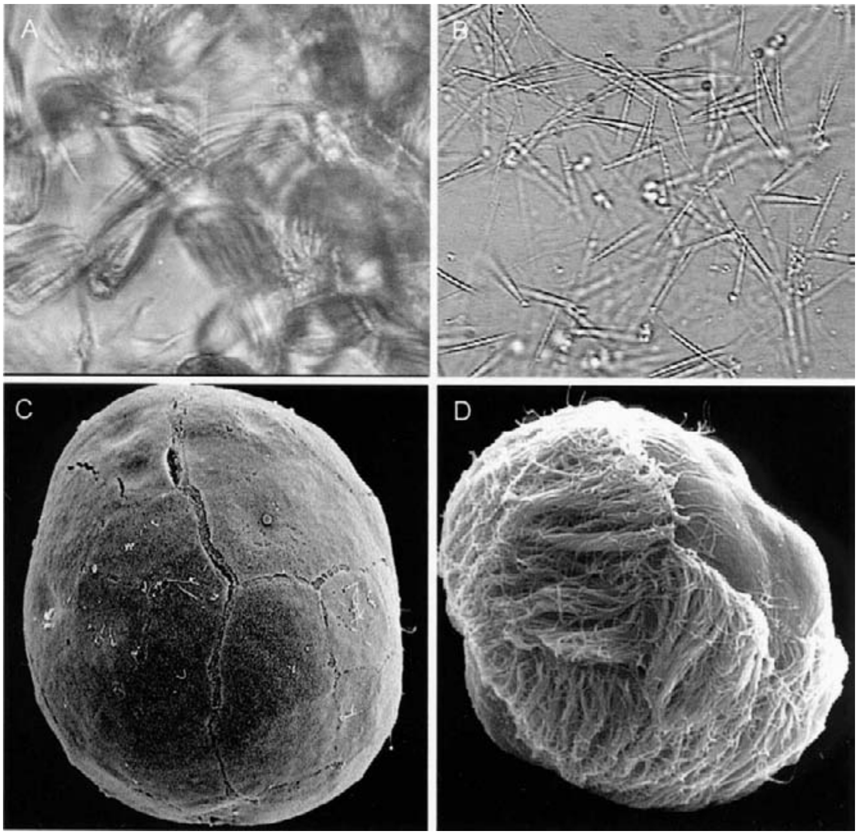

Fig. 12.1. Gametes and embryos of siboglinid tube worms. Sperm bundles (A) and free sperm (B) of *Riftia pachyptila* from 2500 m on the East Pacific Rise. Early larva (C) of *Riftia pachyptila,* showing newly formed cilia arising from trochoblast cells. Trochophore-like larva (D) of *Lamellibrachia* sp. from 600 m on the Louisiana slope.

flagellum and mitochondrion, but nevertheless have some mobility mediated by a flattened structure, apparently having an axoneme, which is believed to be homologous with the flagellum of a typical sperm (Zal et al., 1995). The egg of this species has a deep micropyle, which is interpreted as a mechanism that compensates for a sperm with no acrosome (Zal et al., 1995). *Alvinella pompejana* also has modified sperm (Jouin-Toulmond et al., 1997). Sperm of the orbinid polychaete *Methanoaricia dendrobranchiata,* a common inhabitant of *Bathymodiolus* beds at cold seeps on the Louisiana slope, achieve elongation with a huge acrosome (Eckelbarger and Young, 2002).

The reproductive system and fertilization mechanism of a scale worm, *Branchipolynoe seepensis*, from Atlantic hydrothermal vents has been described in detail by Jollivet et al. (2000). This species is sexually dimorphic and the complex genital tract of the female includes specialized chambers to store eggs and also sperm received by copulation from the male genital papillae. Upon leaving the ovaries, oocytes complete vitellogenesis in the coelom and are then collected by two pairs of ciliated coelomostomes, which lead to the proximal portions of the oviducts. The distal oviducts are enlarged to form spermathecae (seminal recepticles) that store sperm received by copulation from the males. Sperm are stored with their heads embedded in the thick epithelium of the spermatheca. The eggs pass through this chamber without being fertilized and are stored in an unpaired median ovisac until spawning. Jollivet et al. (2000), finding no fertilized eggs or embryos in the ovisac, infer that fertilization must occur at the time of spawning.

Perhaps the most modified of all polychaete sperm are found in the siboglinid (formerly vestimentiferan) tube worms associated with vents and seeps. All known siboglinid sperm are released in bundles or masses (Fig. 12.1). In at least one species, *Ridgeia piscesae,* sperm masses have been found attached to the vestimentum, near the gonopores of the female, suggesting that fertilization may take place either internally or just outside the gonopores (Southward and Coates, 1985). Upon breaking out of the masses, individual sperm of this species undergo a transformation in which the acrosome migrates from its extreme terminal position to surround and cap the tip of the nucleus. Although sperm have been reported from the terminal part of the oviduct in *Riftia pachyptila* (Gardiner and Jones, 1985), there is growing evidence that these and other siboglinids are free spawners. Apparent spawning events have been observed repeatedly in *Riftia pachyptila* (Van Dover, 1994; L. Mullineaux, T. Shanks, R. Lutz, J. Childress, personal communications; C. Young, personal observations) as well as the cold-seep siboglinid *Lamellibrachia* sp. (C. Young, unpublished observations). In these putative spawning events, gametes are expelled in a puff as the animal withdraws partially or completely into its tube. It is not known whether all of these observations are of sperm bundles or if eggs are also released in puffs. However, it seems unlikely that the sperm of other species are transferred to females in the same manner as occurs in *Ridgeia,* as the sperm bundles of these other species separate into individual sperm (Fig. 12.1) shortly after they are diluted in seawater (Cary et al., 1989; Young et al., 1996b). The heads of siboglinid sperm are extremely elongate and consist of a helical mitochondrion wrapped around a helical nucleus (Gardiner and Jones, 1985). The terminal acrosome, which is columnar rather than conical in shape, seems to hold the bundles together on the apical ends, while the posterior end is held together by the individual flagellae, which beat as a unit until the bundle breaks apart. Upon dilution in seawater, the acrosome changes shape and is lost before fertilization (Young, personal observations). The individual sperm, as well as the sperm bundles, are motile in seawater.

Spawning has recently been observed in the so-called “ice worm”, the hesionid *Hesiocaeca methanicola* that lives on exposed lumps of methane hydrate near cold seeps in the Gulf of Mexico (Fisher et al., 2000; Eckelbarger et al., 2001). Females apparently release eggs through nephridiopores, whereas males spawn their sperm through the cloaca, which is connected to the coelom by means of a ciliated duct (Eckelbarger et al., 2001). Fertilization in this species is indicated by a slight elevation of the fertilization membrane followed by production of unusually large polar bodies as the egg completes its maturation divisions.

Fecundity

Instantaneous fecundity has been estimated for only two species of non-vent deep-sea polychaetes, *Pholoe anoculata* and the orbinid *Microrbinia lineata*, both from the slope off North Carolina (Blake, 1993). The former has a fecundity of about 160 eggs and the latter bears only two large eggs in a single segment (Blake, 1993). These values are substantially lower than fecundities that have been reported for various polychaetes from hydrothermal vents, which range from less than 4000 in *Paralvinella grasslei* (Zal et al., 1995) through 230 000 in the much larger alvinellid polychaete *Alvinella pompejana* (Chevaldonné et al., 1997). The large hydrothermal-vent tube worm *Riftia pachyptila* holds as many as 700 000 ripe eggs in its ovisac, suggesting that as many eggs as this could be spawned at a time; but egg traps deployed *in situ* always yielded much smaller numbers (Young, unpublished data), suggesting that not all of these eggs are released at once. The smaller tube worm *Tevnia jerichonana,* also from the East Pacific Rise, is often the first colonist arriving at a newly formed vent habitat. Paradoxically, its fecundity is at least an order of magnitude lower than that of *Riftia pachyptila,* which generally arrives much later. Annual fecundities and lifetime fecundities cannot be estimated for any deep-sea polychaete because of inadequate information about longevity, spawning frequency, and the speed of the gametogenic cycle. It would not be surprising, however, if the annual fecundity of the continuously reproducting giant tube worm *Riftia pachyptila* greatly exceeds the fecundity of any lecithotrophic polychaete from shallow water.

Embryogenesis and larval development

Although the developmental modes of most deep-sea polychaetes remain completely unknown, a number of species are known to brood their young. Levin et al. (1994) listed eleven species of known brooders on the slopes of the Volcano 7 seamount in the eastern Pacific (Table 12.2). The mechanism of brooding varies among species, some brooding larvae in the tubes, others employing specialized brood pouches, and still others having the larvae attached directly to the segments of the mother, either laterally or dorsally (Levin et al., 1994). Because it is much easier to document brooding than other forms of reproduction, it is still not known whether brooding predominates among deep-sea polychaetes, or whether a majority of species have indirect development. Levin et al.

Table 12.2
Known and inferred modes and locations of development in deep-sea polychaetes[1]

Species	Location	Depth (m)	Mode of development	Type of larva or location of broods	References
Acrocirridae sp. A	E. Pacific	730–3350	direct[2]	brooded larvae attached dorsally	Levin et al. (1994)
Ampharete sp. A	E. Pacific	770–1800	direct[2]	brooded in tube	Levin et al. (1994)
Ampharetidae sp. B	E. Pacific	770–1800	direct[2]	brooded in tube	Levin et al. (1994)
Aricidea quadrilobata	E. Pacific	1300–1800	direct[2]	brooded larvae attached dorsally	Levin et al. (1994)
Aurospio dibranchiata	N. Carolina	300–3600	indirect (?)	planktotrophic larva (?)	Blake (1993)
Benthoscolex cubanus	Bahamas	600	indirect (?)	planktotrophic larva (?)	Emson et al. (1993)
Biremis blandi	Bahamas	500–700	indirect	planktotrophic larva (?)	Young et al., unpublished
Cirrophorus lyra	E. Pacific	730–860	direct[2]	brooded larvae attached laterally	Levin et al. (1994)
Euchone bansei	NW Atlantic	1345–2495	direct	unknown	Ruff and Brown (1989)
Euchone incolor	E. Pacific	770–3350	direct[2]	larvae brooded dorsally and in tubes	Levin et al. (1994)
Euphrosine sp.	E. Pacific	1300–1800	direct[2]	brooded larvae attached dorsally	Levin et al. (1994)
Hyalinoecia arauncana	Chile	600	direct	brooded in tube	Carrasco (1983)
Microrbinia lineata	N. Carolina	800–3000	direct (?)	brooded embryos and larva	Blake (1993)
Nothria notialis	Antarctic	800–900	direct	brooded in capsules on tube	Hartman (1967)
Nephthyidae sp. C	E. Pacific	2970–3350	direct[2]	brooded in dorsal brood pouches	Levin et al. (1994)
Ophryotrocha mandibulata	NW Atlantic	2020–3015	indirect (epitoky)	planktonic larva (?)	Hilbig and Blake (1991)
Paronuphis antarctica	Antarctic	800–900	direct	brooded in tube	Hartman (1967)
Paedampharete acutiseries	NW Atlantic	4626–4830	direct	unknown	Russell (1987)
Protodorvillea sp. A	E. Pacific	730–860	direct[2]	brooded in dorsal brood pouches	Levin et al. (1994)
Pholoe anoculata	N. Carolina	583–2000	direct (?)	unknown	Blake (1993), Christie (1982)
Terebellidae	E. Pacific	1300–3350	direct[2]	brooded in tube	Levin et al. (1994)
Tharyx sp. A.	E. Pacific	730–3350	direct[2]	brooded in dorsal brood pouches	Levin et al. (1994)
VENT AND SEEP SPECIES					
Alvinella pompejana	E. Pacific Rise (vent)	2500	indirect	lecithotrophic larva (?)	Jollivet et al. (1998), Pradillon et al. (2001)
Amphisamytha galapagensis	NW Pacific	2447–2725	indirect (?)	lecithotrophic, demersal larva	McHugh and Tunnicliffe (1994), Zottoli (1983)
Branchipolynoe seepensis	Mid-Atlantic Ridge (vent)	1700	indirect (?)	lecithotrophic larvae (?)	Van Dover et al. (1999), Jollivet et al. (2000)
Hesiocaeca methanicola	Gulf of Mexico (seep)	600	indirect	planktotrophic larvae	Eckelbarger et al. (2001)
Lamellibrachia cf. *luymesi*	Gulf of Mexico (seep)	600	indirect	lecithotrophic larvae	Young et al. (1996b)
Opisthotrochopodus n. sp.	Mid-Atlantic Ridge (vent)	1700	indirect (?)	lecithotrophic larvae (?)	Van Dover et al. (1999)

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Table 12.2, *continued*

Species	Location	Depth (m)	Mode of development	Type of larva or location of broods	References
Paralvinella grasslei	East Pacific Rise (vent)	2630	indirect (?)	demersal larvae (?)	Zal et al. (1995)
Paralvinella palmiformis	Juan de Fuca Ridge (vent)	1570–2270	indirect (?)	lecithotrophic, demersal larvae (?)	McHugh (1989)
Paralvinella pandorae	Juan de Fuca Ridge (vent)	1570–2270	direct (?)	embryos brooded in tubes (?)	McHugh (1989)
Ridgeia piscesae	Juan de Fuca Ridge (vent)	1540	indirect	lecithotrophic larvae (?)	Jones and Gardiner (1989)
Riftia pachyptila	East Pacific Rise (vent)	2500–2700	indirect	lecithotrophic larvae	Marsh et al. (2001)
Seepiophilia jonesi	Gulf of Mexico (seep)	600	indirect	lecithotrophic larvae	Young et al. (1996b)

[1] In cases denoted by queries (?) definitive data are lacking, and the inference represents the best guess of the original author.

[2] Classified provisionally as a direct developer because a brooding mechanism has been documented; may exhibit mixed development in which larvae are released following a brooded embryonic period.

(1994) found evidence for brooding in only a single species on the North Carolina slope, but emphasized that absence of data does not imply that other brooders are not present. It is possible to distinguish between species with planktotrophic development and species relying on yolk (either pelagic lecithotrophs or brooded direct developers) on the basis of egg size (Schroeder and Hermans, 1975). However, the situation is further confused in polychaetes by the prevalence of mixed development, in which embryos are brooded either in or on the adult, or held in an egg mass initially, but then hatch as either planktotrophic or lecithotrophic larvae and complete their development in the plankton (reviewed by Wilson, 1991). Thus, in most instances where brooding has been observed in deep-sea species (Table 12.2), it is impossible to state with certainty whether the developmental mode is direct or if it involves a later larval stage. Indirect development has been inferred more commonly for seep and vent species than for species in non-chemosynthetic habitats, though evidence in many cases is circumstantial (e.g., McHugh, 1989; McHugh and Tunnicliffe, 1994; Zal et al., 1995). Early trochophore larvae of the free-spawning hesionid *Hesiocaeca methanicola* from seeps have been reared in the laboratory and found to be planktotrophic (Eckelbarger et al., 2001). Three species of siboglinids have now been reared to lecithotrophic larvae in the laboratory. *Lamellibrachia* sp. and *Escarpia* sp. from 600 m on the Louisiana slope develop into lecithotrophic trochophores (Fig. 12.1) from buoyant eggs, and probably spend about three weeks in the plankton (Young et al., 1996b). *Riftia pachyptila* also has slightly buoyant eggs; these have been fertilized and the embryos reared in pressure vessels and on the sea floor to an early trochophore larval stage (Marsh et al., 2001). The yolk content and metabolic rate of the latter species suggests that it disperses for about five weeks (Marsh et al., 2001). Recent studies of the hot-vent polychaete *Alvinella pompejana* (Pradillon et al., 2001) show that embryos require temperatures around 10ºC for successful development. Embryos dispersing at 2ºC between vents apparently arrest development until sufficiently warm water is encountered. This is interpreted as a mechanism facilitating dispersal over very long distances. Despite the apparent prevalence of brooding in non-chemosynthetic polychaetes, there must be a number of species that produce larvae, as polychaetes are often among the most common organisms to appear in boxes of azoic mud deployed on or near the deep-sea floor and protected from invasion by burrowing adults or juveniles (Snelgrove et al., 1992, 1994).

Arthropoda

Crustaceans, particularly peracaridans such as amphipods, tanaids, cumaceans and isopods, are very speciose and abundant in the deep sea (see Chapter 9). The abyssal sites sampled by Sanders and Grassle (1971) contained approximately 85–90 species of

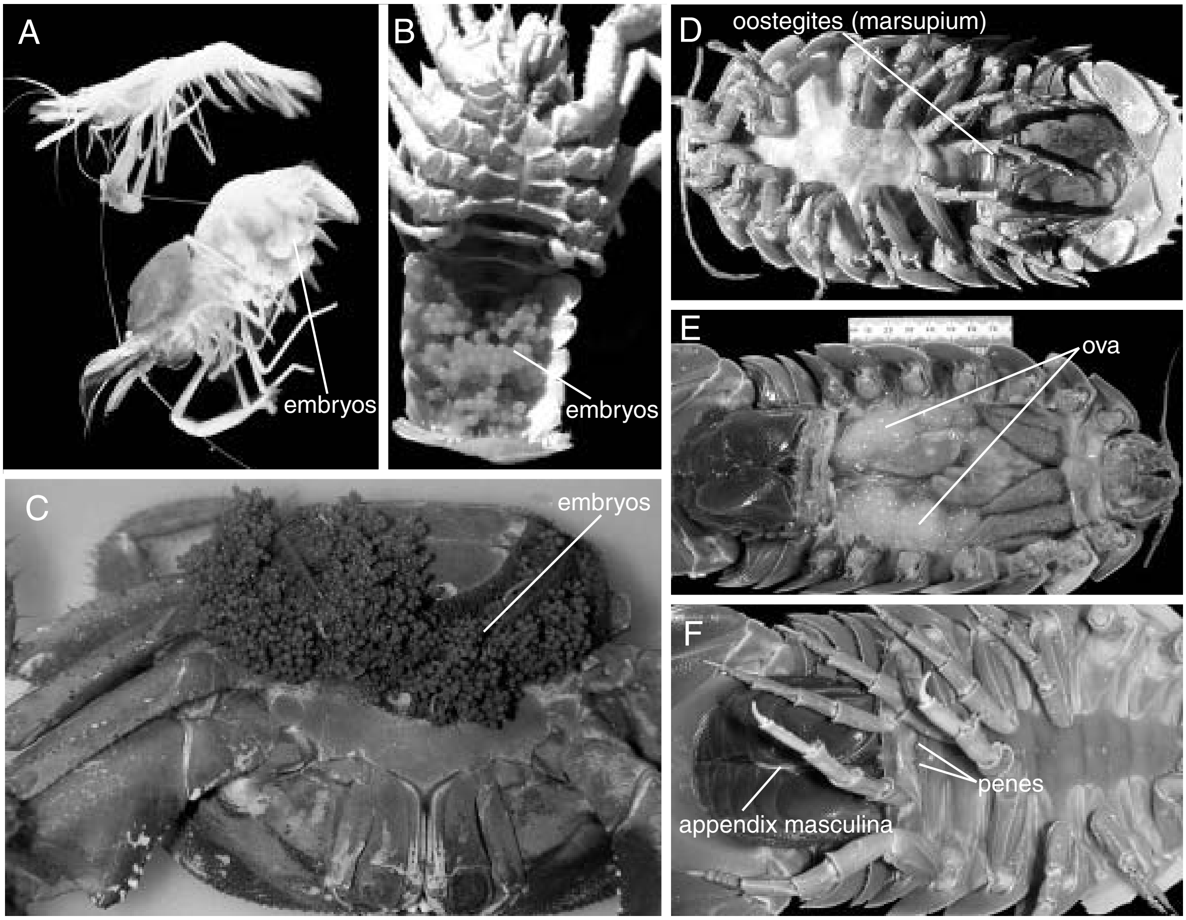

Fig. 12.2. A: Male (above) and female (below) wedding shrimp, from a bathyal hexactinellid sponge in the Bahamas. Note the extreme sexual dimorphism and the large embryos being brooded by the female. B: Galatheid crab of the genus *Munidopsis* from the Rockall Trough, showing very large eggs attached to the pleopods. C: Ventral view of a gravid female brachyuran crab, *Bythograea thermydron*, from hydrothermal vents on the East Pacific Rise. D: Female isopod, *Bathynomus giganteus*, from 800 m depth in the Gulf of Mexico. Oostegites (overlapping plates in the light colored region surrounded by walking legs) cover the brood of this large female, which measures nearly 20 cm in length. E: Female giant isopod, *Bathynomus giganteus*, dissected to show ovaries with very large (1 cm diameter) yolky eggs in the thoracic cavity. Note millimeter rule for scale. F: Ventral view of mature male *Bathynomus giganteus* showing external genitalia. Sperm are transferred to the female through paired penes on the last thoracic segment. The rod-like appendix masculina is also thought to have a role in sperm transfer.

peracarids in a sample of 1000 individuals, compared with 25 bivalve species and 3–5 species of ophiuroids, the next most speciose groups. Indeed, Hessler and Wilson (1983) estimated that peracarids comprise between one-third and one-half of all macrofaunal species in the deep sea. Caridean shrimps are among the most common organisms found at hydrothermal vents, especially in the Atlantic. Larger decapods such as geryonid, dromid and majid brachyurans and pagurid anomurans (hermit crabs) are especially common on the slope. Galatheid crabs (Fig. 12.2) are common at both bathyal and abyssal depths, whereas eryonids are mostly restricted to the abyss. The importance of decapods at slope depths is well illustrated by the spider crab *Encephaloides armstrongi* (Creasey et al., 1997), which occurs at very high densities in the oxygen minimum layer of the Arabian Sea. So-called marriage shrimps commonly reside within the spongocoels of hexactinellid sponges in the deep sea. Each sponge commonly supports two individuals, a male and a female (Fig. 12.2). Cirripedes, including lepadiform, scalpellid and verruciform barnacles, live on hard substratum (often hard parts of other organisms such as crabs, sea urchins and hexactinellid sponge stalks) at both bathyal and abyssal depths. Meiofaunal crustaceans, particularly harpacticoid copepods and ostracods, are very abundant in the deep-sea sediments.

Gonads, gametogenesis and reproductive periodicity

The gonads of decapod crustaceans are discrete, often paired or H-shaped organs that lie above the stomach within the cephalothorax and extrude gametes through gonopores on or near the bases of the pereiopods. The gonads of peracarids originate under the abdominal pereonites (Johnson et al., 2001), but eventually may extend forward to the cephalothorax region as vitellogenesis proceeds (Bishop, 1994). Gonads of barnacles lie at the proximal end of the visceral mass in acorn barnacles and within the peduncle of stalked barnacles (Green et al., 1994).

Most crustaceans brood their embryos either to the juvenile stage or to a larval stage, so that reproductive periodicity has often been documented by simply noting the presence of brooded eggs or embryos. In decapods, the egg mass or sponge is found attached to the pleopods on the underside of the abdomen of ripe “berried” females (Fig. 12.2). In barnacles, the eggs are brooded as plaques or lamellae within the mantle cavity, and in peracarids (including amphipods, isopods, tanaids, mysids, cumaceans and a few lesser known groups) they are brooded in a thoracic brood chamber called a marsupium. The vast literature on brooding in peracarids has been recently reviewed by Johnson et al. (2001). In its most typical form, the peracarid marsupium is formed by overlapping plates (oostegites) which originate from the coxae of the walking legs. Harpacticoid copepods carry their embryos in a single brood sac attached to and trailing behind the abdomen.

The gametogenic process of deep-sea crustaceans appears identical to that of their shallow water relatives, no special adaptations for deep-sea gamete formation having been reported. The deep-sea red crab *Geryon quinquedens* has an oogenic cycle illustrating the general pattern seen in bathyal brachyurans that have been studied (Haefner, 1977). The ovary begins as a small colorless organ with no central lumen, and consisting mostly of connective tissue. The germinal epithelium is columnar and contains only small, previtellogenic oocytes (Haefner, 1977). As it begins to grow, the ovary becomes more opaque, and growing oocytes replace the central connective tissue. The early previtellogenic oocytes are small (14–53 μm) and the nuclei are highly vacuolated. Vitellogenic oocytes containing cytoplasmic yolk granules are larger (74–278 μm) and have more compact nuclei. Each oocyte is surrounded by a single layer of follicle cells. The gonad grows and changes color as additional yolk is added to the expanding oocytes. Eventually, the mature ovum attains a diameter of 671 μm and the ovary fills the dorsal side of the ovary, completely obscuring the gut and hepatopancreas.

Wolff (1962) reported that the sex ratio of deep-sea asellote isopods is often biased significantly in favor of males. Indeed, of eleven families surveyed, all but one had a significantly skewed sex ratio. Wolff suggested that this pattern could be explained by gender-specific survivorship, as is known for some shallow-water isopods (Steel, 1961). Evidence for hermaphroditism has been found in four hadal tanaids collected from a depth of more than 6000 m (Wolff, 1956a), and Wilson (1981) reported a case of facultative hermaphroditism in a deep-sea isopod, *Eurycope iphthima.*

Table 12.3 gives a selection of studies of reproductive periodicity in deep-sea crustaceans. Although continuous breeding was predicted for deep-sea isopods early in the 20th century (Reibisch, 1927), the earliest data bearing directly on the subject of reproductive seasonality were anecdotal observations by Wolff (1962) and others who participated in the Danish *Galathea* Expedition between 1950 and 1952. In his monograph on the asellote isopods, Wolff (1962) noted that deep-sea asellote populations have fewer incubatory females (i.e., those with marsupium present) than did shallow-water isopods. Moreover, no brooding females at all were found among the samples of isopods ($n = 40$) and tanaids ($n = 30$) recovered from the hadal trenches during this expedition (Wolff, 1956a,b). Wolff (1962) considered several possible explanations for this pattern: 1) mortality may be greater for brooding females than for non-brooding ones; 2) brooding females may live deeper in the sediment, thereby avoiding the sampling equipment; 3) breeding occurs only once every few years; 4) the brooding period is much shorter than the preparatory period (the preparatory period is the moult stage when the marsupium is present, but the eggs have not been deposited in it). Although he had no access to seasonal samples from a given locality, he guessed that brooding should occupy a much longer period, perhaps 3–4 months, in deep water than the incubatory periods of 30 to 40 days known among shallow-water isopods, making the small proportion of incubating females even more surprising. After considering the various possibilities listed above,

Table 12.3
Reproductive periodicity and egg size in deep-sea crustaceans

Species	Site	Depth (m)	Egg size (μm)	Periodicity[1]	References
NON-VENT SPECIES					
MALACOSTRACA: PERACARIDA					
Mysidacea					
Boreomysis tridens	Rockall Trough	500–2500	1900–2100	S	Mauchline (1986)
Erythrops microps	Rockall Trough	500–1000	?	A	Mauchline (1986)
Michthyops parva	Rockall Trough	1500–2500	?	A	Mauchline (1986)
Cumacea					
Diastylis stygia	NW Atlantic	2065–2115	?	A	Blake and Watling (1994)
Leucon jonesi	Surinam	1500	?	A (?)	Bishop (1994)
Isopoda					
Eurycope californiensis	San Diego Trough	1171–1244	?	A	Rokop (1977b)
Ilyarachna sp.	NW Atlantic	1400–2178	?	A	Sanders and Hessler (1969)
Ilyarachna profunda	San Diego Trough	1171–1244	?	A	Rokop (1977b)
Natatolana borealis	Mediterranean	500	?	A,F	Kaïm-Malka (1997)
Storthyngura birsteini	Scotia Sea	1737–3804	?	S	George and Menzies (1967)
Storthyngura scotia	Scotia Sea	2450–2816	?	S (?)	George and Menzies (1967)
Storthyngura robustissima	Scotia Sea	884–1485	?	S (?)	George and Menzies (1967)
16 asellote species (pooled data)	N. Carolina Slope	515–5025	?	S (?)	George and Menzies (1968)
47 asellote species (pooled data)	Rockall Trough	1160–2925	?	A,F	Harrison (1988)
Amphipoda					
Eusirus perdentatus	Weddell Sea	176–799	2750	S	Klages (1993)
Harpiniopsis excavata	San Diego Trough	1171–1244	?	A	Rokop (1977a)
Pseudharpinia excavata	San Diego Trough	1171–1244	?		Rokop (1977b)
CIRRIPEDIA					
Poecilasma kaempferi	Rockall Trough	2000	120	A	Green et al. (1994)
DECAPODA					
Dendrobranchiata:					
Aristeus antennatus	Mediterranean	400–800	336 (max)	S	Demestre and Fortuño (1992)
Caridea:					
Plesionika acanthonotus	Mediterranean	165–1550	530	S	Company and Sardà (1997)
Plesionika edwardsi	Mediterranean	256–512	590	S	Company and Sardà (1997)
Plesionika gigliolii	Mediterranean	100–748	550	S	Company and Sardà (1997)
Plesionika heterocarpus	Mediterranean	82–699	530	A	Company and Sardà (1997)
Plesionika martia	Mediterranean	165–871	550	S	Company and Sardà (1997)
Macrura:					
Stereomastis nana	NE Atlantic	613–2642	700	A	Wenner (1978)
Stereomastis sculpta	NE Atlantic	486–2257	600	A	Wenner (1978)
Anomura:					
Chirostylus sp.	?	950	4280[2]	?	Van Dover and Williams (1991)
Eumunida picta	?	512	1556[2]	?	Van Dover and Williams (1991)
Munida propinqua	?	921	1001[2]	?	Van Dover and Williams (1991)

continued on next page

Table 12.3, *continued*

Species	Site	Depth (m)	Egg size (μm)	Periodicity[1]	References
Munida quadrispina	?	595	795[2]	?	Van Dover and Williams (1991)
Munidopsis spp. (35 species)	various	706–4390	2385–6560[2]	?	Van Dover and Williams (1991)
Parapagurus pilosimanus	Rockall Trough	350–5000	550	A	Tyler et al. (1985c)
Brachyura:					
Benthesicymus bartletti	NW Atlantic	2000m	?	S (?)	Wenner (1980)
Chaceon fenneri	Gulf of Mexico	311–677	610	S	Erdman et al. (1991)
Chaceon maritae	SE Atlantic	400–900	680	A	Melville-Smith (1987)
Chaceon quinquedens	NW Atlantic	200–1600	820 (max)	S	Haefner (1977, 1978)
Chaceon quinquedens	Gulf of Mexico	860–1043	850	S	Erdman et al. (1991)
Dorhynchus thompsoni	Porcupine Seabight	1205–1250	320	S	Hartnoll and Rice (1984)
Uroptychus nitidus	?	592	2889	?	Van Dover and Williams (1991)
VENT SPECIES					
DECAPODA:					
Caridea:					
Alvinocaris lusca	Galapagos Rift	2500	340×500	?	Van Dover et al. (1985)
Chorocaris chacei	Mid-Atlantic Ridge	840–3670	283	A,F (?)	Ramirez Llodra et al. (2000)
Mirocaris fortunata	Mid-Atlantic Ridge	840–3875	350	A,F (?)	Ramirez Llodra et al. (2000)
Rimicaris exoculata	Mid-Atlantic Ridge	2260–3875	320	A,F (?)	Ramirez Llodra et al. (2000)
Anomura:					
Munidopsis lentigo	East Pacific Rise	2500	2200 (max)	?	Van Dover et al. (1985)
Munidopsis subsquamosa	East Pacific Rise	2500	2300 (max)	?	Van Dover et al. (1985)
Brachyura					
Bythograea thermydron	East Pacific Rise	2500	480×540	?	Van Dover et al. (1985)

[1] Periodicities are listed as: S, seasonal and synchronous; A, aseasonal, continuous, and asynchronous; F, fluctuating levels of reproduction during continuous breeding.

[2] For comparative purposes, egg diameters were calculated from the egg volumes reported in the paper.

Wolff (1962, p. 221) concluded as follows with respect to abyssal isopods:

"However, in my opinion, the most likely explanation for the deficit of ovigerous females in the material presented here is to assume that the breeding in the bathyal and abyssal depths of the North Atlantic is to a certain extent seasonal, taking place in the winter months from which no material is available. The majority of the species originate from cold stenotherm shallow water ancestors which must be supposed to have had, as a rule, a seasonal breeding – as is the case with shallow-water species in the polar region today. As far as the asellotes are concerned, this mode of reproduction has also been maintained in the deep sea".

Wolff (1956b) proposed a different hypothesis to explain the absence of brooding females among hadal species, namely that these species live to advanced ages and reproduce infrequently, thereby reducing the likelihood that incubatory females will be collected in any given sample.

Some studies of deep-sea harpacticoids have shown a sex ratio biased strongly in favor of females (Hicks and Coull, 1983; Hicks and Marshall, 1985). This observation has been questioned by Thistle and Eckman (1990) who suggested that the skewed sex ratios may result either from gender-specific sampling bias or from males being more easily swept away by currents than females.

Empirical evidence to test Wolff's prediction of deep-sea seasonality came several years later when George and Menzies collected limited samples of isopods in the Scotia Sea (George and Menzies, 1967) and off North Carolina (George and Menzies, 1968). The evidence has been considered equivocal by most subsequent workers (e.g., Rokop, 1977b; Harrison, 1988; Bishop and Shalla, 1994), because many species were pooled and there was limited seasonal coverage of samples from any given region; nevertheless, the work stimulated interest in the possibility of seasonal reproduction in peracarids. Harrison (1988) pooled data for 47 asellote species in the Rockall Trough and concluded that there was no evidence for a distinct seasonal breeding pattern, though he did note a "fluctuating" breeding pattern in which more brooding females were found in some seasons than others. A fluctuating pattern of recruitment was also found in the cumacean *Diastylis stygia,* a species that recruits throughout the year in the northwest Atlantic (Blake and Watling, 1994). Strong evidence for seasonal breeding has been found at abyssal depth only for the mysid *Boreomysis tridens* (Mauchline, 1986), the Antarctic amphipod *Eusirus perdentatus* (Klages, 1993), and the cumacean *Leucon profundus* (Bishop and Shalla, 1994).

The careful study of reproduction in *Leucon profundus* by Bishop and Shalla (1994) sets a high standard that should be used in future studies of deep-sea peracarids. In this study, females were classified not only by the presence or absence of a brood, but also by the size and stage of the gonad and the developmental stages of brooded embryos. *Leucon profundus* was shown unequivocally to have a seasonal breeding cycle lasting approximately 14 months. This finding raises the possibility that other species in which brooding females have been found over much of the year may in fact be seasonal breeders with long reproductive cycles rather than aseasonal breeders with short brood times. This work raises an important challenge to virtually all previous studies; even though there are perhaps more observations of reproductive condition of peracarid crustaceans than most other groups of deep-sea animals, one still has only a very limited understanding of their breeding cycles and life histories.

Of the various caridean shrimp and other crustacea common at hydrothermal vents (Table 12.4), there is little evidence for periodic reproduction (reviewed by Tyler and Young, 1999). *Rimicaris exoculata,* probably the most abundant metazoan at vents on the mid-Atlantic ridge, appears to have multiple cohorts of eggs in its gonad, suggesting periodicity at the individual level (Ramirez Llodra et al., 2000), but insufficient seasonal coverage is available to infer any sort of population-level synchrony. Extensive collections of these abundant carideans have yielded a surprisingly small number of berried females (P.A. Tyler, personal communication). As with abyssal isopods, there is no completely satisfying explanation for this pattern. One hypothesis that remains untested is that females brood their young far away from the vents in order to protect the embryos from elevated temperatures (Tyler and Young, 1999).

A number of crustaceans living at depths less than 1000 meters breed seasonally, as might be expected (Table 12.4). These include bathyal dendrobranchiate and caridean shrimps in the Mediterranean (Demestre and Fortuño, 1992; Company and Sardà, 1997) and some species of brachyurans in the northwest Atlantic and the Gulf of Mexico (Haefner, 1977; Hartnoll and Rice, 1984; Erdman et al., 1991). It is interesting that various species of the slope crab genus *Chaceon* found in the northeast Atlantic are seasonal breeders (Haefner, 1977, 1978; Erdman et al., 1991), but the congeneric *C. maritae*, living at comparable depths in the Southeast Atlantic, is aseasonal (Melville-Smith, 1987). There are insufficient data to infer seasonal reproduction in any abyssal brachyuran, though Wenner (1980) suggested that *Benthesicymus bartletti* from 2000 m may have a synchronous breeding pattern.

Most species of pandalid shrimp in shallow water are protandrous hermaphrodites, changing from male to female as they grow. King and Moffitt (1984) presented evidence that several species of deep-water tropical pandalids are fully dioecious and that they never undergo sex reversal. The reason for this difference between deep-sea and shallow species is not known.

Gamete structure and fertilization

Spermatozoa of all crustaceans are aflagellate and are modified for internal fertilization. There have been no detailed studies at the ultrastructural level of oogenesis or spermatogenesis in deep-sea crustaceans, though the general structure of the reproductive system is well known from gross dissections and paraffin histology. Spermatozoa are often packaged into sperm packets which are deposited in the oviducts of the female as sperm plugs. These have been commonly seen in the hydrothermal-vent crab *Bythograea thermydron* (G. Perovich, personal communication). The various studies of gonad morphology that have been conducted at the light-microscope level (e.g., Ramirez Llodra

Table 12.4
Studies of reproductive periodicity in deep-sea molluscs

Species	Site	Depth (m)	Egg size[1] (μm)	Periodicity[2]	References
APLACOPHORA					
Prochaetoderma yongei	NW Atlantic	1470–2030	226	A	Scheltema (1987)
GASTROPODA					
Benthonella tenella	NW Atlantic	3806–5042	82.5	A	Rex et al. (1979)
Calliotropis ottoi	Rockall Trough	990–2450	150–260	A	Colman and Tyler (1988)
Colus jeffreysianus	Rockall Trough	2200	170	A	Colman et al. (1986a)
SCAPHOPODA					
Cadulus californicus	San Diego Trough	1162–1244	240	S	Rokop (1977a)
BIVALVIA					
Acharax alinae	Lau Basin (vent)	?	600	A	Beninger and Le Pennec (1997)
Bathyarca sp.	San Diego Trough	1200–1240	~132	A	Rokop (1979)
Bathymodiolus childressi	Gulf of Mexico (seep)	500–700	90	S	Eckelbarger and Young (1999)
Bathymodiolus elongatus	Fiji Back-Arc Basin	?	50–60	A	Le Pennec and Beninger (1997)
Bathymodiolus puteoserpentis	Mid-Atlantic Ridge	3480	50–60	S	Le Pennec and Beninger (1997)
Bathymodiolus thermophilus	E. Pacific Rise (vent)	2500	50	A	Berg (1985)
Bathymodiolus n. sp.	Mid-Atlantic Ridge	840–865	50	S	Comtet and Desbruyères (1998)
Calyptogena kilmeri	Monterey Bay (seep)	900	180–237	S	Lisin et al. (1996)
Calyptogena lauberi	Tenryu Canyon (seep)	?	200	A	Fiala-Médioni and Le Pennec (1989)
Calyptogena magnifica	E. Pacific Rise (vent)	2500	309	A	Berg (1985)
Calyptogena pacifica	Monterey Bay (seep)	600	180–220	A (?)	Lisin et al. (1996)
Ledella pustulosa	NE Atlantic	2880–2921	120	S	Tyler et al. (1992a)
Malletia cuneata	NE Atlantic	2880–2921	240	A	Tyler et al. (1992a)
Deminucula cancellata	San Diego Trough	1200–1240	?	A	Rokop (1977a), Scheltema (1972)
Nucula darella	San Diego Trough	1200–1240	~154	A	Rokop (1979)
Nuculana pontonia	San Diego Trough	1200–1240	~176	A	Rokop (1979)
Tindaria cervola	San Diego Trough	1200–1240	?	A	Rokop (1979)
Xylophaga spp	W. Atlantic	600–2000	45	A	Turner (1973), Tyler and Young, unpublished
Yoldiella jeffreysi	NE Atlantic	2880–2921	120	A	Tyler et al. (1992a)

[1] In most cases, egg sizes are the maximum observed in histological studies and may not be representative of the actual sizes of eggs spawned.

[2] Periodicities are listed as either S, synchronous or seasonal; or A, aseasonal or continuous.

et al., 2000) suggest nothing about gametes in deep-sea Crustacea that differs from related species in shallow water (reviewed by Adiyodi and Subramoniam, 1983).

Fecundity

Fecundity has been studied mostly in slope decapods that have fishery importance (e.g., Clarke et al., 1991), though instantaneous fecundities have also been reported for many deep-sea peracarids. For example, Wolff (1962) indicated that egg numbers in the asellote isopods range from 2 to 80, being correlated with the size of the brooding animal. Shallow-water isopods generally have much higher fecundities and smaller egg sizes (Zirwas, 1910).

The most comprehensive study of fecundity in deep-sea crustaceans is that by Van Dover and Williams (1991) of 52 species of squat lobsters in the superfamily Galatheoidea, which related fecundity and egg size to depth of occurrence. They found a positive correlation between fecundity and body size, but no indication of reduced fecundity in deep-sea species that could not be explained by phylogenetic constraints. Hines (1988) reported that fecundity of two species of deep-sea geryonid crabs is significantly lower than those of shallow-water crabs with similar body sizes, but that reproductive output is in fact higher; the low fecundity values result from partitioning the reproductive effort into larger eggs. The reproductive effort of brachyuran crabs seems always to be limited by the amount of space available in the cephalothorax for yolk accumulation (Hines, 1982), and this rule applies equally well to the deep-sea forms as to those in shallow water (Hines, 1988). Ramirez Llodra et al. (2000) noted the same relationship between brood size and body size in deep-sea caridean shrimps whether they lived in mid-water or at Atlantic hydrothermal vents. It should be noted that closely related crustaceans having very different fecundities may be successful in the same deep-sea habitats. Perhaps the most striking example of this occurs in two congeneric vent-associated galatheids, *Munidopsis lentigo* and *M. subsquamosa,* both of which live at Pacific vents; they have fecundities of 13 eggs and 294 eggs, respectively (Van Dover et al., 1985).

Ramirez Llodra et al. (2000) examined fecundity of three caridean species from hydrothermal vents. One of these, *Mirocaris fortunata,* had highly variable fecundity, the number of eggs carried by a female ranging from 25 to 503. Based on a single berried female from each species, *Chorocaris chacei* and *Rimicaris exoculata* had much higher fecundities than *M. fortunata*, carrying 2510 and 988 eggs, respectively.

Embryogenesis and larval development

Peracarids have direct development, brooding their young to a stage that resembles a miniature adult. Apart from the study by Tso and Mok (1991) on development of the giant isopod *Bathynomus doederleini,* there have been few specific studies of embryology in deep-sea peracarids, though Bishop and Shalla (1994) carefully monitored changes in embryo number and size in the cumacean *Leucon profundus.* They found that embryogenesis was synchronous for the first eight months of development (their stages I–III), but a pattern of asynchronous development began with the last two embryonic stages. Specifically, females with advanced embryos always contained a single stage V individual which was about to hatch, while the remaining embryos in the brood were still at stage IV. This observation suggests that large juveniles (manca stage) grow to full size one at a time and are released singly, the individuals in the brood hatching over a period of several months. A similar pattern of hatching has been found in the aseasonal congener *Leucon jonesi* (Bishop, 1994).

One of the first deep-sea larvae to be described in the literature was that of the deep-sea eryonid crab *Willemoesia suhmi,* a drawing of which appeared in the *Challenger* reports. Embryological development has since been described for several deep-sea decapods (e.g., Brattegard and Sankarankutty, 1967; Herring, 1974; Ingle, 1979; Sulkin and Van Heukelem, 1980; Williamson, 1982). In all cases, the patterns of development and the early larvae resembled closely those of shallow-water relatives. Caridean shrimps, including the very abundant vent shrimps *Chorocaris chacei, Mirocaris fortunata* and *Rimicaris exoculata,* have been studied extensively in recent years. Vereschaka (personal communication) has found embryos in the water column which he ascribes to *Rimicaris exoculata,* but there is some controversy about their identity. If this observation is correct, *R. exoculata* would be the only caridean that does not brood its embryos on the pleopods until hatching. However, this observation would help explain why very few berried vent shrimps have been collected. Larvae of Atlantic vent shrimps have been collected in midwater plankton samples near the mid-Atlantic Ridge, and postlarvae have been collected as far as 1000 km away, suggesting that dispersal potential is substantial (Herring and Dixon, 1998).

Fage (1956) reported that the eggs of pycnogonids (sea spiders) collected from a depth of more than 6000 m in the Banda Sea are brooded on the ovigerous legs of the males, in exactly the same manner as those of their shallow-water counterparts.

Mollusca

Deep-sea sediments contain a tremendous variety of gastropods (Clarke, 1962). Although some larger buccinids and pleurotomariids are encountered at slope depths (Harasewych, 2002), the deep-sea gastropods fauna is dominated by diminutive caenogastropod predators such as turrids. Ectoparasitic forms living as epizoites on other organisms such as sea urchins are also common.

Bivalves are represented mostly by protobranchs (Allen, 1979; Zardus, 2002), though xylophagid bivalves are commonly found in waterlogged wood (Turner, 1973), and a number of other orders also live as infauna in the soft sediment. Deep-sea mussels and clams are among the most abundant animals living at cold seeps and hydrothermal vents (Van Dover, 2000).

Gonads, gametogenesis and reproductive periodicity

Prosobranch gastropods are mostly dioecious, though hermaphroditic species, especially protandric hermaphrodites, are known. The gonad is a discrete organ located on the upper part of the body whorl and connected to the outside by a gonoduct, which passes through the pericardium. In the more advanced forms, the gonoduct may be divided into pallial and cardiac portions, which in turn may be elaborated into various kinds of glands for the secretion of fluids, mucus or capsular material to protect the embryos. Scaphopods are all dioecious (Reynolds, 2002), as are aplacophorans and, with very few exceptions, bivalves. The gonad in mussels and clams is found dorsally, often in close association with the digestive gland.

Gametogenesis has been described at the ultrastructural level in only a few species of deep-sea molluscs, all from chemosynthetic ecosystems (Le Pennec and Beninger, 1997; Eckelbarger and Young, 1999). Eckelbarger and Young (1999) described oogenesis and spermatogenesis in the methanotrophic mussel *Bathymodiolus childressi*; the gametogenic mechanisms were shown to be similar to those of seasonally breeding shallow-water mussels. Spermatogenesis has also been described for the gastropod *Bathynerita naticoidea* from the same habitat (Hodgson et al., 1998). Ongoing studies of gametogenesis in limpets from hydrothermal vents show that some species have rapid mechanisms of vitellogenesis virtually identical to those found in certain intertidal limpets (Eckelbarger, unpublished data).

Reproductive periodicity has been inferred from gonad histology in a number of deep-sea molluscs (Table 12.4), most of which have asynchronous gametogenesis indicative of continuous breeding. Seasonal breeders are found not only at relatively shallow slope depths (Rokop, 1977a; Eckelbarger and Young, 1999), but also at depths greater than 2000 m on the lower slope (Tyler et al., 1992a) and at 3480 m in a hydrothermal vent system on the Mid-Atlantic Ridge (Le Pennec and Beninger, 1997). It is somewhat surprising that several species of mussels breed synchronously at vents and seeps, since these animals are presumably exposed to a continuous source of chemical energy that can be allocated to gonadal development.

Gamete structure and fertilization

Sperm have been described at the ultrastructural level for deep-sea gastropods from several families (Healy, 1988, 1989b, 1990; Hodgson et al., 1998) as well as for a midwater cephalopod, *Vampyroteuthis infernalis* (Healy, 1989a), and some chemosynthetic mussels (Eckelbarger and Young, 1999). In every case, the sperm structure was similar to that of shallow-water members of the same groups.

Transfer of spermatophores has been described in a deep-sea octopus (Lutz and Voight, 1994). Although no other specific studies of fertilization have been undertaken in deep-sea molluscs, it is presumed that deep-sea gastropods follow the strongly conservative patterns known for shallow-water taxa. Thus, archaeogastropods (with the exception of the Neritidae) spawn their gametes and fertilize externally, while other groups all fertilize internally by copulation.

Fecundity

Scheltema (1994) has reviewed the literature on fecundity in deep-sea molluscs. Instantaneous fecundity in bivalves ranges from two eggs in two species of pristoglomid protobranchs on the continental slope (Sanders and Allen, 1973) to more than 30 000 eggs in opportunistic xylophagids that colonize wood (Turner, 1973). There are almost no reliable data on the fecundity of deep-sea gastropods despite reported counts of embryos in egg capsules (Gustafson et al., 1991), since the number of capsules produced by a single female is generally impossible to determine.

Embryogenesis and larval development

Egg masses from deep-sea snails have been found and described several times (Gustafson et al., 1991; Bouchet and Warén, 1994), but there are no descriptions of early embryology, nor has a complete sequence of larval development been reported for any deep-sea mollusc. The known patterns of larval development have been reviewed by Bouchet and Warén (1994) and Scheltema (1994). Most of what is known about larval development has been inferred from the apex of the adult shell, where the larval protoconch (in gastropods) or prodissoconch (in bivalves) is retained as a permanent record of larval size and growth (Thorson, 1950; Jablonski and Lutz, 1983; Scheltema, 1994). The shell-apex method permits discrimination between species with non-planktotrophic and planktotrophic larvae, but does not resolve differences between species with pelagic lecithotrophic larvae and species that brood their young or hatch as juveniles from benthic egg capsules (Jablonski and Lutz, 1983). Despite this limitation, the method has been applied to a very large number of deep-sea species. Many such studies have focused on species from distinct geographical regions of the Atlantic (Bouchet, 1976b; Rex and Warén, 1982; Colman et al., 1986b) and on species from cold seeps and hydrothermal vents (reviewed by Gustafson and Lutz, 1994). A selection of these studies is summarized in Table 12.5. Although both planktotrophic and non-planktotrophic development are common among bathyal and abyssal molluscs, some groups have peak numbers of lecithotrophic species at slope depths (Rex and Warén, 1982), and others, exemplified in Fig. 12.3 by the Turridae (the most speciose family of gastropods in the deep sea), show a regular increase in the incidence of planktotrophy with increasing depth (Potter and Rex, 1992). Supporting evidence for planktotrophic larval development comes from the work of Bouchet (1976a) and Bouchet and Warén (1979), who have obtained the larvae of several species of abyssal gastropods in shallow-water plankton tows. Moreover, Bouchet and Fontes (1981) and Killingley and Rex (1985) have shown, by oxygen-isotope ratios in abyssal snail shells, that larvae develop at a warmer temperature than is found in the adult environment. A number of planktotrophic larvae from deep-sea gastropods have eyes (Bouchet and Warén, 1994); but, in the only study of phototaxis in deep sea larvae, Bingham and Young (1993) showed that the eyed larvae of a bathyal snail, *Pelseneeria* sp., do not respond to unidirectional white light.

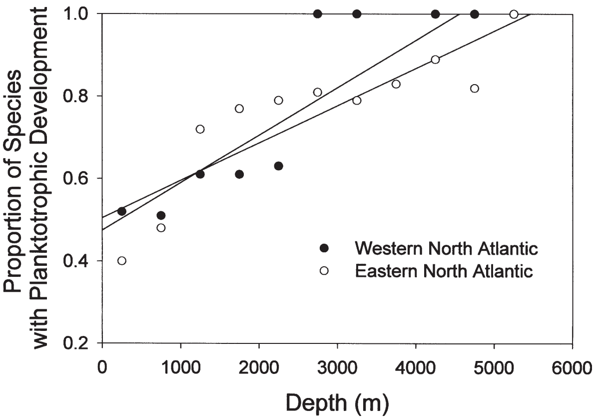

Fig. 12.3. The relationship between developmental mode and depth in deep-sea gastropods of the family Turridae. Redrawn from Potter and Rex (1992).

Bouchet and Warén (1994) have argued that planktotrophy in deep-sea gastropods is not only an ancestral condition (Strathmann, 1978), but also a plesiomorphic character constrained by phylogeny in most groups. They note that some species, particularly members of the exclusively deep-sea family Laubierinidae, produce very large veligers, males of which are neotonous and attain sexual maturity before settlement (Bouchet and Warén, 1994).

Knudsen (1961, 1970) provided detailed discussions of reproduction in non-chemosynthetic deep-sea bivalves, and the more recent literature in this field has since been reviewed (Knudsen, 1979; Schein, 1989; Scheltema (1994). Using criteria proposed by Ockelmann (1965) for inferring bivalve developmental mode from egg size, these studies suggest that pelagic lecithotrophy, not direct development or planktotrophy, prevails among sediment-dwelling deep-sea gastropods. The major exceptions appear to be in the Xylophaginidae, which are nearly always associated with waterlogged wood or other plant material. Turner (1973) showed that some xylophagids have small eggs and wide dispersal, while Knudsen (1961) documented several species with large eggs that appear to brood their young on the outside of the shell (Fig. 12.4). The reasons for these divergent reproductive modes within a single family remain unexplained (Scheltema, 1994).

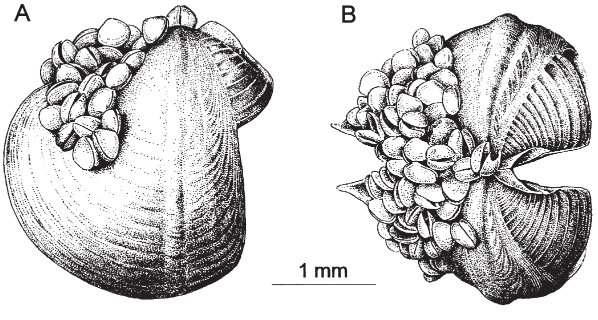

Fig. 12.4. Brooded juveniles on the valves of a bathyal xylophagid bivalve. Reproduced with permission from Knudsen (1961).

At hydrothermal vents, most molluscan species appear to have non-planktotrophic development, though planktotrophic species are also known (reviewed by Gustafson and Lutz, 1994). Craddock et al. (1997) predicted that non-planktotrophic species should have

Table 12.5
Modes of larval development for deep-sea molluscs, as inferred from protoconch and prodissoconch sizes and morphologies

Taxon	Region	Depths (m)	Planktotrophic		Non-planktotrophic		References
			Families	Species	Families	Species	
NON-VENT AND SEEP SPECIES							
Archaeogastropoda	NW Atlantic	478–4970	0	0	–	22	Rex and Warén (1982)
Mesogastropoda	NW Atlantic	478–4970	–	12	–	21	Rex and Warén (1982)
Neogastropoda	NW Atlantic	478–4970	–	33	–	19	Rex and Warén (1982)
Gastropoda	NE Atlantic	2500–5300	15	(30%)	–	–	Bouchet and Warén (1979)
Gastropoda	Norwegian Sea	2500–4000	–	3	–	11	Bouchet and Warén (1979)
Prosobranch gastropods	NE Atlantic	various	–	10	–	B	Bouchet (1976b)
Prosobranch gastropods	NE Atlantic	2200–2900	–	6	–	8	Colman et al. (1986b)
Gastropoda	world	1000–5400	27	–	5	B	Bouchet and Warén (1994)
Bivalvia	Norwegian Sea	2500–4000	–	1	–	5	Bouchet and Warén (1979)
VENT AND SEEP SPECIES							
Gastropoda	Atlantic, Pacific	various	–	3	–	39	Gustafson and Lutz (1994)
Archaeogastropoda	Pacific	2500	–	0	–	4	Craddock et al. (1997)
Bivalvia	Atlantic, Pacific	various	1	5	–	2	Gustafson and Lutz (1994)

limited dispersal, but genetics did not bear out this prediction. However, Etter and Rex (1990) showed that genetic differentiation decreases concomitantly with a shift away from lecithotrophy along a depth gradient. Some of this confusion probably results from an inability to distinguish pelagic lecithotrophs from direct developers and some is probably because lecithotrophs living at low temperatures (and therefore having low metabolic rates) can disperse substantial distances without the benefit of feeding. Just as mode of development is not a good predictor of geographic range in deep-sea ascidians and echinoderms (Young et al., 1997), it may not predict dispersal potential or genetic differentiation in deep-sea molluscs.

Echinodermata

From the standpoint of reproduction, echinoderms are the best-studied group of deep-sea animals. Table 12.6 gives a summary of some reproductive parameters for all species studied. Most deep-sea echinoderms have separate sexes, though hermaphroditism is known among the holothurians (Tyler et al., 1992b) and occasional hermaphroditic echinoids have been observed (e.g., *Allocentrotus fragilis, Lytechinus euerces*: Young, personal observations). With few exceptions, the reproductive mechanisms and patterns found in shallow-water echinoderms are also represented among their deep-water relatives. Echinoderm reproduction has been thoroughly reviewed elsewhere (see Giese et al., 1991 as a convenient portal to the literature).

Gonads, gametogenesis and reproductive periodicity

Echinoderms were among the first deep-sea animals shown conclusively to have seasonal reproduction (Lightfoot et al., 1979; Tyler et al., 1982a) and recruitment (Schoener, 1968), though it is now known that seasonal breeding is the exception in this group rather than the rule. In the Rockall Trough, where numerous species have been examined in multiple seasons, only a small proportion of species breed seasonally (Table 12.6). However, at shallower bathyal depths on the Bahamian Slope, the majority of species are seasonal breeders. All known deep-sea species with seasonal breeding produce planktotrophic larvae, and all known species of continuous breeders produce non-planktotrophic larvae (Tyler and Young, 1993). Gonadal development is essentially the same as that of other echinoderms, proceeding through sequential stages of gamete proliferation, vitellogenesis and gamete storage prior to spawning. However, in semicontinuous breeders such as *Echinus affinis,* the gonad contains multiple cohorts of gametes, and the cycle may take more than one year to complete (Tyler and Gage, 1984a).

Eckelbarger (1994b) has listed 34 species of bathyal and abyssal echinoderms whose ovaries have been examined by electron microscopy; but modified ovaries have been found only in four species of deep-sea holothuroids. In *Bathyplotes natans, Hansenothuria benti, Holothuria occidentalis* and *Mesothuria* sp., the inner epithelial cells of the oocytes resembled podocytes, cells which are generally associated with excretion in other invertebrates (Eckelbarger and Young, 1992; Tyler et al., 1994). In the case of sea-cucumber ovaries, it has been suggested that podocytes may function in exchange of nutrients between the genital haemal sinus and the ovary during vitellogenesis (Eckelbarger and Young, 1992).

Fecundity

Ramirez Llodra (2002) has reviewed the literature on fecundity in marine animals, including echinoderms in the deep sea. Fecundity has been estimated for many of the echinoid, asteroid and holothuroid species listed in Table 12.6. In general, deep-sea species follow the expected pattern (Vance, 1973) in which lecithotrophic species with large eggs have a smaller number of eggs than planktotrophic species. Thus, for example, the planktotrophic species *Plutonaster bifrons* produces about one million eggs (Tyler and Pain, 1982a), whereas co-occurring lecithotrophic starfish such as *Bathybiaster vexillifer* (Tyler et al., 1982b) and *Benthopecten simplex* (Pain et al., 1982a) produce only a small number of mature oocytes at any given time. Body size, gonad structure and depth all covary with fecundity in echinoderms. This is illustrated well in the forcipulate starfish of the Rockall Trough (Tyler et al., 1984). The brisingid starfish *Brisingella coronata* has an egg size (1250 μm) identical with that of the confamilial *Freyella spinosa,* yet the former has a fecundity of about 60 000 eggs and the latter produces only 2500 eggs. *Freyella* lives deeper (below 4000 m) than *Brisingella* (750–2450 m).

Gamete structure and fertilization

Eckelbarger et al. (1989c) and Eckelbarger (1994b) have reviewed the sperm morphology of deep-sea echinoderms. The majority have sperm of the primitive (Franzen, 1956) or ect-aquasperm (Rouse and

Table 12.6
Reproductive periodicity and egg sizes in deep-sea echinoderms

Species	Site	Depth (m)	Egg size (μm)	Periodicity[1]	References
ASTEROIDEA					
Bathybiaster vexillifer	Rockall Trough	2200	650	A	Tyler et al. (1982b)
Benthopecten simplex	Rockall Trough	2170–2300	950	A	Pain et al. (1982b)
Brisinga endecacnemos	Rockall Trough	1860–2200	1250	A	Tyler et al. (1984)
Brisingella coronata	NE Atlantic	750–2200	1250	A	Tyler et al. (1984)
Dytaster insignis	Rockall Trough	2170–2910	120 (?)	S	Tyler et al. (1982a)
Freyella spinosa	Porcupine Abyssal Plain	4000–4212	1250	A	Tyler et al. (1984)
Hymenaster gennaeus	Rockall Trough	2200	1100	A	Pain et al. (1982b)
Hymenaster membranaceus	Rockall Trough	1862–2300	1100	A	Pain et al. (1982b)
Hyphalaster inermis	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
Paragonaster subtilis	Rockall Trough	2200	900	A	Tyler and Pain (1982b)
Pectinaster filholi	Rockall Trough	1752–2515	850	A	Pain et al. (1982b)
Plutonaster bifrons	Rockall Trough	2200	120	S	Tyler et al. (1982a)
Pontaster tenuspinus	Rockall Trough	588–1050	800	A	Pain et al. (1982b)
Porcellanaster ceruleus	Rockall Trough	2900	600	A	Madsen (1961), Tyler, unpublished.
Pseudarchaster parelli	Rockall Trough	2200	900	A	Tyler and Pain (1982b)
Psilaster andromeda	Rockall Trough	1050–2965	950	A	Tyler et al. (1982a)
Styrachaster chuni	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
Styrachaster horridus	Madeira Abyssal Plain	5000	650	A	Ramirez Llodra et al. (2002)
Xyloplax medusiformis	New Zealand	1000	viviparous	?	Baker et al. (1986)
Xyloplax turnerae	Bahamas	2000	"large"	?	Rowe et al. (1988)
Zoroaster fulgens	Rockall Trough	2170–2450	950	A	Tyler et al. (1984)
OPHIUROIDEA					
Amphiophiura bullata	NW Atlantic	1330–4750	350	?	Schoener (1972)
Amphilepis ingolfiana	NW Atlantic	1330–4750	400	?	Schoener (1972)
Homalophiura tesselata	NW Atlantic	1330–4750	400	?	Schoener (1972)
Ophiacantha bidentata	Rockall Trough	2200	600	A	Tyler and Gage (1982)
Ophiacantha normani	San Diego Trough	1250	~430	A	Rokop (1974)
Ophiocten gracilis	Rockall Trough	1000	100	S	Sumida et al. (2000)
Ophiomusium lymani	NW Atlantic	1100–2000	600	S	Schoener (1968, 1972)
Ophiomusium lymani	Rockall Trough	2200	600	A, S	Gage and Tyler (1982b)
Ophiura ljungmani	NW Atlantic	1330–3834	90	S	Schoener (1968, 1972)
Ophiura ljungmani	Rockall Trough	2900	100	S	Tyler and Gage (1980), Gage and Tyler (1982a)
ECHINOIDEA					
Allocentrotus fragilis	NE Pacific	50–1150	110	S	Boolootian et al. (1959)
Araeosoma fenestratum	Rockall Trough	631	1250	A	Tyler and Gage (1984b)
Archaeopneustes hystrix	Bahamas	300–625	~100	S	Young et al. (1997)
Aspidodiadema jacobyi	Bahamas	350–600	90	S	Young and George (2000)
Brissopsis lyrifera	Mediterranean	60–1000	80	S	Ferrand et al. (1988)
Calveriosoma hystrix	Rockall Trough	640–1075	1250	A	Tyler and Gage (1984b)
Cidaris blakei	Bahamas	500–750	110	S	Young, unpublished

continued on next page

Table 12.6, *continued*

Species	Site	Depth (m)	Egg size (μm)	Periodicity[1]	References
Cidaris cidaris	Rockall Trough	508–1500	110	S	Tyler and Gage (1984b)
Echinus acutus	Rockall Trough	500–1271	90 (?)	S	Gage et al. (1986)
Echinus affinis	Rockall Trough	2200	120	S	Tyler and Gage (1984a)
Echinus elegans	Rockall Trough	500–1271	90 (?)	S	Gage et al. (1986)
Hygrosoma petersi	Rockall Trough	990–2965	1150	A	Tyler and Gage (1984b)
Linopneustes longispinus	Bahamas	608–683	109	S	Young and Cameron (1989)
Lytechinus euerces	Bahamas	300–500	96	S	Young, unpublished
Palaeobrissus hilgardi	Bahamas	575–650	128	S	Young, unpublished
Phormosoma placenta	NE Atlantic, Bahamas	616–2240	1100	A	Tyler and Gage (1984b), Young and Cameron (1987)
Poriocidaris purpurata	Rockall Trough	990–1075	1500	A	Tyler and Gage (1984b)
Salenia goesiana	Bahamas	90–540	57	S	Young, unpublished
Sperosoma grimaldi	Rockall Trough	1210	1100	A	Tyler and Gage (1984b)
Stylocidaris lineata	Bahamas	600	120	S	Young et al. (1992)
HOLOTHUROIDEA					
Bathyplotes natans	NE Atlantic, Bahamas	625–1694	280	A	Tyler et al. (1994)
Benthodytes sordida	Porcupine Abyssal Plain	3680–4515	>1000	A (?)	Tyler and Billett (1987)
Benthogone rosea	Porcupine Seabight	1387–2120	750	A	Tyler et al. (1985b)
Cherbonniera utriculus	Rockall Trough	2878–4050	200	(S)	Tyler et al. (1987)
Deima validum	Porcupine Abyssal Plain	4080–4795	700	A (?)	Tyler and Billett (1987)
Laetmogone violacea	NE Atlantic	960–1506	350	A	Tyler et al. (1985b)
Molpadia blakei	Porcupine Abyssal Plain	1991–4510	200	A	Tyler et al. (1987)
Oneirophanta mutabilis	Porcupine Seabight	2900–4795	950	A (?)	Tyler and Billett (1987)
Paroriza pallens	NE Atlantic, Bahamas	900–1785	350	A	Tyler et al. (1992b)
Paroriza prouhoi	NE Atlantic	4080–4780	450	A	Tyler et al. (1992b)
Peniagone azorica	Rockall Trough	2220–2965	300	A	Tyler et al. (1985a)
Peniagone diaphana	Porcupine Abyssal Plain	3976–4780	300	A	Tyler et al. (1985a)
Psychropotes depressa	Porcupine Seabight	2405–2440	>750	A (?)	Tyler and Billett (1987)
Psychropotes longicauda	Porcupine Abyssal Plain	4043–4795	>3000	A (?)	Tyler and Billett (1987)
Psychropotes semperiana	Porcupine Abyssal Plain	5432–5440	>3000	A (?)	Tyler and Billett (1987)
Ypsilothuria bitentactulata	Rockall Trough	2175–2907	350	A	Tyler and Gage (1983)

[1] Periodicities are listed as either S, seasonal or synchronous; or A, aseasonal or continuous.

Jamieson, 1987) type, characterized by small spherical or conical nuclei. Such sperm are indicative of free spawning and external fertilization; both processes have been observed for more than 20 species of bathyal echinoderms (Young, 1994b). There is, however, an unexplained tendency toward gigantism in the sperm of deep-sea echinoderms (Fig. 12.5). For example, the sperm of soft-bodied echinothuriid sea urchins, which fertilize yolky eggs exceeding 1 mm in diameter (Tyler and Gage, 1984b; Young and Cameron, 1987; Cameron et al., 1988) are very elongate. These sperm carry lipid bodies on the posterior end of the midpiece mitochondria (Eckelbarger et al., 1989a), a very rare feature in shallow-water sea urchins (an exception is the sand dollar *Echinarachnius parma.*) The lipid bodies are thought to serve as an energy store which permits the sperm to swim for an unusually long time after dilution (Young, 1994b), but could also provide some flotation, enabling the sperm to disperse upward with the rapidly floating eggs (Young and Cameron, 1987; Cameron et al., 1988). Sperm of even greater length are found in the deep-sea genus

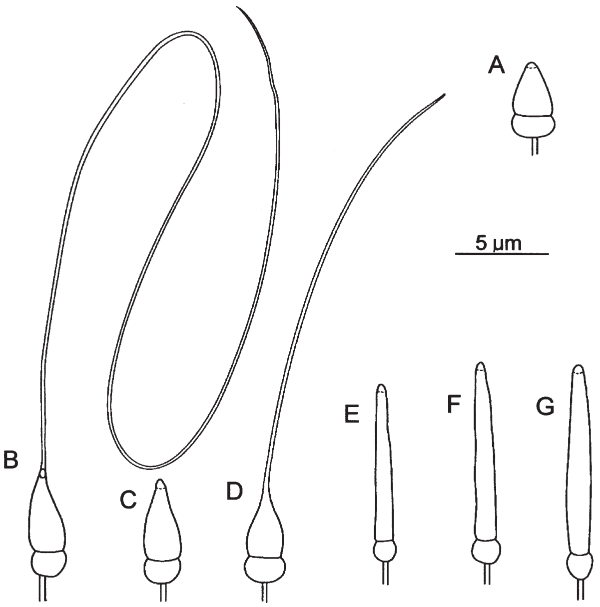

Fig. 12.5. Elongate and dimorphic sperm of deep-sea echinoids. The sperm of the arbaciid *Coelopleurus floridanus* (A) from the Bahamian slope is typical of a shallow-water echinoid. The elongate sperm from the genera *Araeosoma* (E, F) and *Phormosoma* (G) have lipid stores on the middle-piece, apparently to extend the swimming time. The elongate portion of the sperm head in *Aspidodiadema jacobyi* (D) consists of nuclear material, whereas the elongate anterior extension of the paraspermatozoan of *Phrissocystis multispina* (B) is a second flagellum. The euspermatozoan of *Phrissocystis* (C) is unmodified. Redrawn from Eckelbarger et al. (1989a–c).

Aspidodiadema (Fig. 12.5). The sperm nucleus of *Aspidodiadema jacobyi* from the Bahamian slope is 29 µm long, approximately an order of magnitude longer than a typical echinoid sperm (Eckelbarger et al., 1989b). Similarly elongate nuclei have been observed in *A. arcitum* from the Hawaiian slope (Young, unpublished data). The reason for these very long sperm heads is unknown; *Aspidodiadema* spp. freely spawn small (90 µm) eggs and fertilize them externally, apparently in the same manner as other echinoids with much smaller primitive-type sperm.

The Hawaiian deep-water echinoid *Phrissocystis multispina* is the only echinoderm known to have sperm dimorphism, and also the only known species with bipolar-tailed sperm (Eckelbarger et al., 1989b). Males produce not only normal-looking euspermatozoa, but also paraspermatozoa with two tails (Fig. 12.5), both of which originate from centrioles on the posterior end of the nucleus, but one pointing forward and one aft. As fertilization has not been observed in this species, the different roles of the two sperm types have not been discovered. The unusual concentricycloid asteroids of the genus *Xyloplax,* considered by some to constitute a separate phylum of echinoderms, apparently fertilize internally and consequently have sperm of a modified type. These unusual filiform sperm have been described in detail by Healy et al. (1988).

The mechanisms and problems of external fertilization in deep-sea echinoderms have been discussed by Young (1994b). Free spawning, often in response to chemical spawning inducers such as potassium chloride, has been observed in many species, though very few spawning events have been observed *in situ.* A number of Bahamian-slope species, including *Aspidodiadema jacobyi* (Young, unpublished), *Cidaris blakei* (Young, 1994b), *Salenia goesiana* (Young, unpublished) and *Stylocidaris lineata* (Young et al., 1992) form tight aggregations or pairs during the breeding season, apparently to cope with the problem of isolation at spawning (Fig. 12.6). Other species, including seasonally breeding spatangoids and cassiduloids, move about in herds during the entire year. Hermaphroditic holothurians in the genus *Paroriza* apparently pair for extended periods of time (Fig. 12.6; Tyler et al., 1992b; Mauviel and Sibuet, 1985).

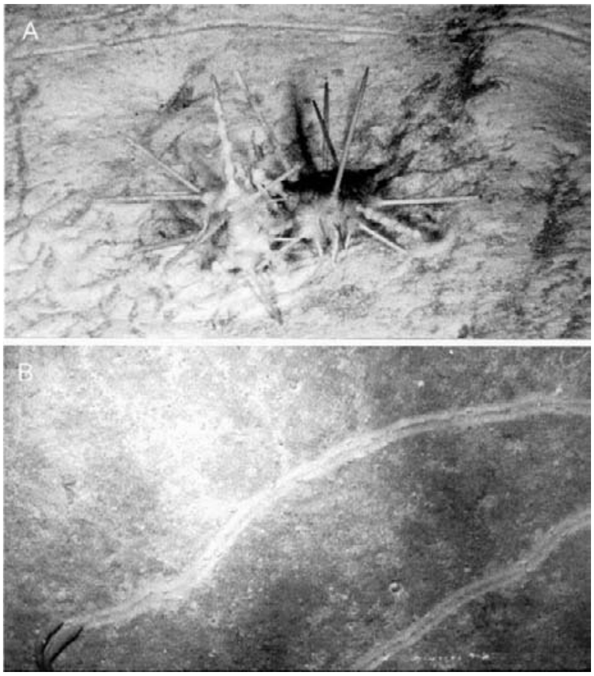

Fig. 12.6. Reproductive pairing in deep-sea echinoderms. A: a pair of ripe *Stylocidaris lineata* from the Bahamian Slope (Young et al., 1992). B: two individuals of *Paroriza* sp. leaving a long trail across the sea floor in the North Atlantic. Reproduced by permission from Mauviel and Sibuet (1985).

Embryogenesis and larval development

Early predictions notwithstanding, only two deep-sea echinoderm species, the holothurian *Oneirophanta mutabilis* (Hansen, 1968) and the concentricycloid *Xyloplax medusiformis* (Rowe et al., 1988), are known to brood their young internally, though it is likely that many ophiuroids and a few asteroids will also eventually be found to brood. Although a number of shallow-water or eurybathic species from Antarctica are known to be brooders (Thomson, 1878; Agassiz, 1881; Sladen, 1889), all other species of strictly bathyal or abyssal echinoderms, including many which were once assumed on the basis of egg size to be brooders (Agassiz, 1881; Thorson, 1946; Madsen, 1961) reproduce with either pelagic lecithotrophic larvae or planktotrophic larvae (Pearse, 1994; Young, 1994a). The lecithotrophs, exemplified by the echinothuriid echinoids (Tyler and Gage, 1984a), elasipod holothurians (Tyler and Billett, 1987) and porcellanasterid sea stars (Madsen, 1961; Ramirez Llodra et al., 2002), have yolky eggs approaching or exceeding 1 mm in diameter. Although it is clear from morphology and observation that these large eggs float (Young and Cameron, 1987; Cameron et al., 1988) and that these species do not retain their large eggs, lecithotrophic larvae have not been described for any deep-sea echinoderm. Indeed, Tyler and Billett (1987) have suggested that the large eggs of elasipod holothurians are direct developers which bypass a larval stage and develop directly into swimming juveniles of the sort commonly found in mid-water trawls (Gebruk et al., 1997).

Planktotrophic larvae have been reared for a number of echinoderm species living at bathyal depths, including the ophiuroid *Ophiocten gracilis* (Mortensen, 1898; Tyler and Gage, 1982) and the echinoid *Cidaris cidaris* from European waters (Prouho, 1888), the echinoid *Laganum diploporum* from Japan (Mortensen, 1921), and nine species of echinoids from the Bahamian slope: *Archaeopneustes hystrix* (Young et al., 1996c), *Aspidodiadema jacobyi* (Young et al., 1989; Young and George, 2000), *Cidaris blakei* (Young, unpublished), *Coelopleurus floridanus* (Young, unpublished), *Conolampas sigsbei* (C.M. Young and P.A. Tyler, unpublished), *Linopneustes longispinus* (Young and Cameron, 1989), *Lytechinus euerces* (Young et al., 1996c). *Palaeobrissus hilgardi* (C.M. Young and J.L. Cameron, unpublished) and *Stylocidaris lineata* (Young et al., 1996c, 1997). With the exception of *Aspidodiadema jacobyi* (Young and George, 2000), all of the larvae described are morphologically similar to shallow-water members of the taxa to which they belong.

The larvae of *Aspidodiadema jacobyi* are unusual in several ways. Like typical planktotrophs, they develop from a small egg (90 μm) but, unlike other species, development of a mouth is delayed for the first 21 days, as the blastocoel becomes filled with yolky cells from the vegetal plate (Young et al., 1989). The yolky cells permit dispersal and perhaps vertical migration (Young et al., 1996c) for up to two months before planktonic food is required (Young et al., 1989). Eventually, the larva becomes a very large and complicated echinopluteus having 12 arms, a long posterior process and convoluted ciliary lobes (Young and George, 2000).

Cnidaria

In the deep sea, benthic cnidarians including various octocorals, scleractinian corals and actinian and zoanthic sea anemones, are particularly common on hard substrata such as seamounts and boulders, and on the volcanic rocks at some hydrothermal vents. Many species that require a firm surface have adopted an epizoic lifestyle, often becoming specialized for life on a single species of echinoderm, sponge or gorgonian. The most common cnidarians on soft bottoms are pennatulids (sea pens), which anchor their rachises in the sediment like a root.

Gonads, gametogenesis and reproductive periodicity

Aspects of reproduction have recently been described for several deep-sea pennatulid octocorals. *Kophobelemnon stelliferum,* a sea pen from the Porcupine Seabight in the northeast Atlantic, produces large eggs (800 μm), has separate sexes and apparently breeds continuously (Rice et al., 1992). Members of the cosmopolitan pennatulid genus *Umbellula* have eggs of a similar size which originate on the mesenterial filament, then complete oogenesis while floating freely in the gastrovascular cavity (Tyler et al., 1995). Ultrastructural details of gametogenesis have been described for *Pennatula aculeata,* a species that lives in relatively shallow (110 m) water and to a depth of at least 1500 m (Eckelbarger et al., 1998). Females of this species contained oocytes of all sizes and at all stages of oogenesis, suggesting that breeding is aperiodic. Sperm were packaged in sperm cysts, each of which contained spermatocytes at a comparable stage of development. The sperm remain packaged in these cysts until after spawning, possibly as a mechanism for reducing sperm dilution (Eckelbarger et al., 1998).

Bronsdon et al. (1993, 1997) contrasted the reproductive patterns of two epizoic anemones, *Amphianthus inornata* which lives attached to gorgonians at depths between 2100 and 2300 m, and *Kadosactis commensalis,* which lives on sea cucumbers between 4500 and 4900 m. The shallower species breeds seasonally, releasing eggs in the spring, whereas the deeper-dwelling species has asynchronous breeding and probably spawns throughout the year. A species pair of zoanthid anemones which live epizoically on hermit crabs have also been studied at similar depths. In this case, however, the shallow species (*Epizoanthus paguriphilus* at 770–1065 m) and the deep one (*Epizoanthus abyssorum* at 3749 to 4400 m), are both continuous breeders (Muirhead et al., 1986).

Van-Praët and Duchateau (1984) and Van-Praët (1990) also provided evidence for seasonal reproduction in an abyssal sea anemone, *Paracalliactis stephensoni.* The timing and duration of reproduction has also been related to depth and seasonal flux of organic matter in congeneric actinians of the genus *Phelliactis* (Van-Praët et al., 1990). Both species are dioecious and produce large eggs. *Phelliactis hertwigi* lives between 719 and 1448 m in the Porcupine Seabight and produces an egg 180 μm in diameter. Gametogenesis takes 8–9 months and spawning occurs in October or November of each year. *Phelliactis robusta* lives at a greater depth (1600–2173 m) in the Bay of Biscay and produces a slightly larger egg (220 μm). Its gametogenesis takes 15–19 months and it spawns in April or May. These contrasting life cycles appear to be correlated with differences between the two habitats in the timing and intensity of phytodetritus flux (Van-Praët et al., 1990). Despite intense recent interest in deep-sea scleractinian corals such as *Lophelia pertusa,* there are no published data on the reproduction of these species, although fecundity appears to be very low (Waller and Tyler, pers. comm.).

Embryogenesis and larval development

Brooded planula larvae of two deep-water hydrocorals, *Cryptohelia pudica* and *Errina labiata,* were observed by Moseley (1881) during the *Challenger* expedition. Both male and female gametes of hydrozoans, actinians and octocorals were also described by the *Challenger* authors (von Kölliker, 1880; Hertwig, 1882; Allmann, 1883). Danielssen and Koren (1884) reported a developing embryo from inside the polyp of *Umbellula encrinus,* but no evidence of brooding has been reported since and it has been suggested (Tyler et al., 1995) that the earlier workers mistook a parasitic flatworm for an embryo.

The only study of larval biology in a deep-water cnidarian is of the alcyonacean *Anthomastus ritteri* from California (Cordes et al., 2001). A large individual of this species broods more than 4000 yolky embryos in its gastrovascular cavity. Larvae are released as fully formed demersal planulae capable of settlement within two days, but also capable of delaying metamorphosis for more than four months (Cordes et al., 2001).

Other phyla

Porifera

Hexactinellids dominate the sponge fauna of bathyal and abyssal depths, yet hexactinellid larvae have been described for only a single species from relatively shallow water, and embryos have only been observed in a few cases (M. Maldonado and C.M. Young, unpublished observations). Witte (1996) described reproduction in three deep-sea demosponges from 2300 m in the Norwegian Sea. One of these reproduced seasonally, the onset of yolk formation correlating closely with the maximum flux of particles collected in sediment traps.

Nemertea

Seven species of pelagic nemertean worms living at depths between 250 and 3250 m in the eastern Pacific had eggs substantially larger (0.5–1 mm diameter) than those typical of shallow-water nemerteans (Norenburg and Roe, 1998). Females tended to be larger than males, and the sex ratio was apparently biased toward females in all but one species. The polystyliferan nemerteans in this assemblage transfer yolk to the oocytes through cytoplasmic bridges attached to nurse cells, a vitellogenic mechanism unknown among shallow-water nemerteans. Reproduction was iteroparous in all species, though only two species of the genus *Phallonemertes* showed evidence of seasonal reproductive peaks (Norenburg and Roe, 1998).

Echiura

Selenka (1885) reported multiple dwarf males attached to a single female of the echiuran worm *Bonellia* *sumhi* dredged from a depth of 2451 m off Nova Scotia. This observation suggests that this species reproduces in the same way as its shallow-water congeners, which produce larvae that settle preferentially on the female worm.

Bryozoa

On the basis of skeletal morphology, it appears that some deep-sea bryozoans brood embryos and release coronate larvae similar to those of shallow-water ascophorans (Davidson, 1880). Although there has been considerable taxonomic work on deep-water bryozoans in recent years, beginning with the bryozoan volume of the *Galathea* reports (Hayward, 1981), there have been no studies specifically directed at reproduction.

Brachiopoda

Larvae of the deep-sea inarticulate brachiopod *Pelagodiscus atlanticus*, which lives at depths ranging from 365 m to 4435 m, were collected from shallow water by Ashworth (1915). Other inarticulate larvae have been taken in plankton samples between 1000 and 3000 m (Simroth, 1897; Eichler, 1911). There have been no recent studies of reproduction in deep-sea brachiopods.

Hemichordata

Enteropneust worms are relatively common in the deep sea, though reproduction has only been examined in a single species. The very elongate "spaghetti worm," *Saxipendium coronatum*, lives draped over rocks in areas of diffuse hydrothermal flow at about 2500 m depth on the East Pacific Rise. Most individuals that have been collected are male, suggesting a strongly biased sex ratio. The testes, which are easily visible through the transparent body wall, occur in series along most of the trunk of the worm, giving the worm the appearance of a double pearl necklace. The sperm ultrastructure, as described by Franzen et al. (1985), reveals mushroom-shaped primitive sperm suggestive of external fertilization. Franzen et al. (1985) also reported small eggs, from which they inferred planktotrophic development. However, a recent re-examination of this species (Young, unpublished data) reveals very large floating eggs suggestive of either lecithotrophic larval development (a developmental mode unknown in the enteropneusts) or pelagic direct development. Giant larvae (up to 22 mm diameter)of an enteropneust known as *Planktosphaera pelagica* have been collected from oceanic waters in both the Atlantic and Pacific (Spengel, 1932; Hadfield and Young, 1983). Although the adults remain unknown, it is generally thought that these are the larvae of an unknown enteropneust from the deep sea.

Chordata

Colonial ascidians collected from deep water have often been found to contain brooded larvae, like their shallow-water relatives (e.g., Herdman, 1886). A few deep-water solitary ascidians, including *Hypobythius calycodes* (Moseley, 1876) and some species of carnivorous octacnemid ascidians (Young and E. Vázquez, unpublished data) produce eggs much larger than those of any known shallow-water solitary ascidian. It is not known whether these gigantic eggs (nearly 1 mm in diameter) develop directly, bypassing the larval stage, or if they develop by means of lecithotrophic tadpoles like the majority of shallow-water solitary ascidians. Larval development has been described for only a single bathyal species, *Bathypera feminalba* (Young and Vázquez, 1995). Tadpoles of this species were very similar to those of shallow-water species in the same family.

LIFE-HISTORY TRAITS IN THE DEEP SEA: PREDICTIONS AND EVIDENCE

Life-history theory predicts traits that maximize fitness of an organism in the particular environment where it lives. These include brood size, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and variation in all of these traits among the progeny of an individual (Stearns, 1976). In the context of marine organisms, "brood size" is generally called "fecundity" and "size of young" may be equated with egg size, which often determines the mode of development. Most marine animals reproduce until they die, so the "age distribution of reproductive effort" is often equivalent to age at first reproduction. To these one may add a number of traits that are especially germane for marine animals, including developmental mode, degree of parental protection, and various traits that assure successful fertilization (the "breeding strategy": Young, 1999), including mating systems, spawning behaviors, sperm chemotaxis and pheromonal communication.

An extensive literature on life-history traits considers differences that are expected between species or populations occupying stable vs. unstable environments. Although there is considerable habitat variation at bathyal and abyssal depths, extensive regions (e.g., abyssal plains) are much more stable than most shallow-water habitats, and indeed are perhaps among the most stable and predictable environments on the planet (see Chapter 2). Because depth is roughly correlated with gradients in nutrient availability and habitat stability, it is useful to consider what life-history traits would be favored by natural selection at various depths in the sea. It is also interesting to consider how life histories might differ between normal (heterotrophic) deep-sea systems and autotrophic systems such as hydrothermal vents and cold seeps.

Environmental stability is not the only selective pressure in the deep sea that is expected to influence life-history traits. On the abyssal plain, low population densities, spatially uniform habitats, low temperature and limited food are all expected to influence life-histories, as are the extreme physical and chemical conditions found at hydrothermal vents.

Partitioning of energy between somatic and reproductive needs

Background

A fundamental idea in many life-history theories is the principle of allocation, a zero-sum game in which an organism has a fixed amount of energy and material to allocate among various reproductive tissues, somatic tissues and activities (Fisher, 1930; Williams, 1966). Theories about allocation are roughly divisible into deterministic models such as the familiar r–K selection idea of MacArthur and Wilson (1967) and stochastic models, such as the bet-hedging theories of Cohen (1966), Holgate (1967), Mountford (1968), Murphy (1968), Schaffer (1974) and others. These various models have been reviewed and summarized by Pianka (1970), Stearns (1976) and Todd (1986).

In the r-selection/K-selection dichotomy (MacArthur and Wilson, 1967), so-called "r-strategists" are organisms living in environments (e.g., hydrothermal vents), where mortality is caused largely by unpredictable events. Such organisms are expected to invest more energy in reproduction so as to spread the risk of mortality among habitats and times. "K-strategists" are organisms living in stable environments (e.g, the abyssal plain) where density-dependent mortality (e.g., from competitive interactions) occurs as the environment reaches carrying capacity. Such organisms are expected to allocate more of their energy to growth, efficiency, persistence, and competitive ability than to producing offspring which could ultimately be competitors. Proponents of the theory emphasize that most species occupy places along a continuum of r and K selection, but that a distinct dichotomy still exists between two very different kinds of animals (Pianka, 1970). However, Pianka (1970) also noted that aquatic organisms in general do not conform to the r/K dichotomy.

The stochastic "bet-hedging" life-history models have become more popular in recent years than deterministic models such as r–K selection, particularly for marine organisms with pelagic larvae and type III (Deevey, 1947) survivorship curves (Todd, 1986). These models predict the same combinations of life-history traits as r/K selection theory, but argue that these combinations should be found under circumstances opposite to those predicted by r/K selection. Specifically, the stochastic models predict short life, high reproductive potential and semelparity for species living in environments where the probability of juvenile (or larval) survivorship is quite constant and the opposite traits (long life, low reproductive output, iteroparity) where juvenile survival is variable.

Predictions

The r/K selection theory would predict that species in stable, food-limited habitats in the deep sea should tend toward the K end of the continuum, while vent species living in geologically unpredictable habitats should be r-strategists. The "bet-hedging" models are difficult to test for deep-sea animals because there are no data on the temporal variability of juvenile or larval survival. If juveniles or larvae develop in the relatively constant conditions of the abyssal plain or in the predator-poor abyssopelagic zone, then the "bet-hedging" models would predict a combination of traits similar to "r-selection". If, on the other hand, abyssal animals send their larvae into the upper water column where mortality processes are more severe and variable, then a combination of traits similar to K-selection would be expected. The latter traits would also be predicted for stochastically unpredictable hydrothermal vent habitats.

Evidence

Grassle and Sanders (1973) and Sanders (1979) considered the available evidence for a K-selected life-history strategy in the deep sea. Experimental tests of this hypothesis subsequently came from colonization experiments in which defaunated sediments were deployed in trays on the sea floor (Grassle, 1977; Desbruyères et al., 1980; Levin and Smith, 1984;

Grassle and Morse-Porteous, 1987; reviewed by Smith and Hessler, 1987) or deposited directly on the sea floor in mounds resembling the fecal deposits of burrowing infauna (Kukert and Smith, 1992). Results from these experiments have been variable. Most of the sediment-tray experiments indicated that colonization rates are significantly slower in the deep sea than in shallow water (Grassle, 1977; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994). In all of these studies, it took a very long time for the community to return to background levels. Both Desbruyères et al. (1980) and Kukert and Smith (1992) documented much higher rates of recolonization. However, in the study by Desbruyères et al., most of the colonists were polychaetes not represented in background samples; and some of the colonization in the study by Kukert and Smith is likely to have been invasion by adult burrowing, not larval settlement.

Can any of these colonization data be interpreted as evidence that species found in the deep sea allocate more energy to growth and maintenance than to colonization of new habitats by larval dispersal? Strictly speaking, recruitment rate is not a life-history trait that can be influenced by natural selection, but some factors contributing to recruitment rate (e.g., fecundity, larval defense mechanisms, larval habitat selection behaviors) are. One must therefore exercise extreme caution in making the leap from gamete production to colonization rate, as variable pelagic processes may result in large losses of animals with high fecundity or, conversely, occasional high recruitment of animals which invest relatively little in reproduction. Moreover, experiments deployed at different times may yield very different results for species with seasonal recruitment processes. The situation is further confused by the inclusion of some ophiuroids (Gage and Tyler, 1982b) and bivalves (Gage et al., 1980) with apparently continuous reproduction which still recruit seasonally or sporadically (Gage, 1991). In a community that contains several species with different periods of annual recruitment, slow colonization rates are not surprising; indeed, they would be expected in some proportion of experiments deployed at varying times of the year and lasting for only about two years. Thus, low colonization rates may be indicative of low investment of gametes, but should not be taken as direct evidence of K-selection. Finally, the use of colonization data to evaluate life-history strategy assumes that species with K-selected traits normally live at population equilibrium, and hence require little ability to colonize disturbed or newly available habitats. This point has been questioned by Caswell (1982), who stated categorically and with the support of population models that life-history traits cannot be used to distinguish equilibrium and non-equilibrium populations.

In making their case for K-selection in the deep sea, Grassle and Sanders (1973) noted that many deep-sea animals, particularly the highly diverse peracarid crustaceans (isopods, amphipods, tanaids, cumaceans, mysids), typically have low fecundity and some parental protection, and lack a pelagic larval stage. However, the K-selected traits of parental protection and direct development are also universal among shallow-water peracarids, suggesting that these traits are phylogenetically constrained (Eckelbarger and Watling, 1995). Sanders (1977) noted that brittle stars and some other deep-sea animals have high fecundity and produce pelagic larvae, but he supposed that these species must occupy peripheral deep-sea habitats such as slopes and boreal seas, where conditions are less stable and biological accommodation (and K-selection) is less likely to occur. It is now known that many deep-sea animals do in fact produce abundant pelagic larvae (reviewed by Young, 1994a) and that settlement rates of such animals may sometimes be very high in the deep sea (see Gage and Tyler, 1981, for an example of high ophiuroid settlement).

Turner (1973, 1977) provided dramatic demonstrations of apparently r-selected deep-sea species associated with ephemeral and patchy habitats such as waterlogged wood. Regardless of what time of year wood is deployed in the deep sea, xylophagid molluscs and associated polychaetes invade it and grow quickly to reproductive maturity (Tyler and Young, unpublished data). The speed and reliability of the colonization process indicates that there must be a “soup” of larvae always ready to invade wood as it becomes available. This is classic r-selection; indeed, it is one of the most extreme examples of a “weedy” or r-selected species anywhere in nature.

Rex (1979) provided evidence for a depth-related shift along the r–K continuum in *Alvania pelagica,* a gastropod common at shelf and slope depths in the western Atlantic. He inferred longevity and the relative amounts of energy devoted to growth and reproduction from careful measurements of the protoconchs and body whorls of the shell. The results indicated a clear shift to greater K-selection occurring below the shelf/slope break where the environment becomes more stable. Slope snails seem to allocate more energy to growth and less to reproduction than conspecifics on the shelf. A similar analysis within the protobranch bivalve genus *Nucula* was conducted by Scheltema (1972) over a depth gradient from the shelf to the abyss. He showed that species from the abyss allocated much less energy to reproduction than did their shallow congeners, and also that abyssal species tended to have lower fecundities and larger eggs. All of these observations are consistent with the predicted shift from r- to K-selection with increasing depth and environmental stability. However, the opposite may hold true for brachyuran crabs. Hines (1988) noted that deep-sea brachyurans in the genus *Chaceon* (formerly *Geryon*) have higher reproductive outputs than shallow-water crabs of comparable sizes, but that their fecundities were lower because of larger egg sizes.

The r–K selection theory predicts that animals should grow slowly, mature late, and live to a greater age in more stable environments. The most dramatic and oft-cited example of this is in the deep-sea protobranch bivalve *Tindaria callistiformis* from 3.8 km depth, which, on the basis of radioisotopic dating and shell sculpturing are estimated to attain reproductive maturity in about 50 years and to live for more than a century (Turekian et al., 1975). Gage and Tyler (1991) have discussed potential sources of error in this life span estimate, which has a confidence interval of 76 years. Similar longevities have been inferred for shallow-water bivalves using a variety of techniques (Breen and Shields, 1983; Jones et al., 1978), so long-lived clams are not unique to the very stable habitats of the abyss. Moreover, analysis of isotopes in deep-sea clams on the Galapagos Rise reveals very fast growth rates and shorter life spans (Turekian et al., 1979) Analysis of size-frequency data of protobranch bivalves in the Rockall Trough indicate that growth rates are fairly rapid, and that clams there live for only about eight years (Gage, 1985), which is similar to the expected longevity of a small clam from inshore waters (Gage and Tyler, 1991). Grassle (1977) found reproductively mature protobranchs (*Deminucula cancellata*) in colonization trays that had only been on the sea floor for about two years. Similar data from sediment trays indicate that the aplacophoran mollusc *Prochaetoderma yongei* attains full adult size in only two months and reproductive maturity in less than a year (Scheltema, 1987). Taken together, these data do not support the contention that deep-sea bivalves live longer, mature later, or grow slower than shallow-water species.

Gage and Tyler (1985) have analysed growth and longevity in the sea urchin *Echinus affinis* from a depth of 2200 meters on the Hebridean Slope. This species lives for up to 28 years and attains reproductive maturity after about five years. A shallow-water congener, *Echinus esculentus,* lives for only up to 12 years and attains maturity after about 1.5–2.5 years (Nichols et al., 1985). Other echinoids from various shallow temperate and tropical seas are likewise shorter-lived and attain reproductive maturity much faster (Ebert, 1982) than *E. affinis.* The limited data on echinoids are consistent with a shift toward K-strategy in the deep sea. However, other predicted attributes of a K-adapted species do not apply to *Echinus affinis.* This species has high fecundity, small egg size (Tyler and Gage, 1984a), produces a pelagic larva (Young and Tyler, 1993) and sometimes recruits in very large numbers (Gage and Tyler, 1985).

There have been no explicit analyses comparing “r-selected” and “K-selected” traits of deep-sea animals from vents and seeps with animals that rely on allochthonous food in the “normal” deep sea. The predictions would be ambiguous in any case, since the food supply of vent/seep animals is more predictable and constant, yet the environment itself may remain stable for much less time.

“Bet hedging” models are currently difficult to evaluate for deep-sea habitats because there are no data whatsoever on juvenile vs. adult survival probabilities in the deep sea. It would seem reasonable to assume that juvenile survival is less variable in the stable deep sea than in temporally more variable shallow systems. However, Jumars and Gallagher (1983) have argued that, in the virtual absence of physical disturbance, predation becomes the most important source of mortality and that predation pressure should be more intense on younger animals because more mouth sizes would be able to ingest them. An extreme case of heavy juvenile mortality has been documented in the ophiuroid *Ophiocten gracilis* (Gage and Tyler, 1981). Also, Gage et al. (1980) and Gage and Tyler (1981) have invoked temporally variable juvenile mortality as a possible explanation for apparent seasonal recruitment in species that reproduce continuously.

In summary, there is evidence for a depth-related increase in certain K–selected traits within species and families of a few taxa, but there is also abundant evidence to suggest that the opportunistic r-strategy is well represented in the deep sea. As in shallow water, the deep sea contains enough spatial and temporal variability to allow exploitation by species with various strategies of energy allocation.

Age distribution of reproductive effort

Background

In his classic paper linking life-history traits with population growth, Cole (1954) focused on the demographic advantages and disadvantages of one-time reproduction (semelparity) and repeated reproduction (iteroparity). His major finding, often known as "Cole's result" was that semelparous animals that reproduce early in life produce as many offspring over many generations (i.e., are "as fit") as iteroparous animals that produce more offspring over the course of an individual's life, but begin reproduction later in life. This result has been challenged as an oversimplification (Charnov and Schaffer, 1973) but the fact remains that both kinds of organisms are successful in the real world. Todd (1986) noted that virtually all intertidal invertebrates are iteroparous and used this observation in support of the bet-hedging models that predict iteroparity for habitats where organisms have variable survival in the early life-history stages.

Predictions

"Bet-hedging" models predict that semelparity should increase as a function of environmental stability; thus, "normal" deep-sea habitats should select for semelparity, particularly among species that do not produce pelagic larvae. The r/K-selection theory, by contrast, predicts a predominance of long-lived, iteroparous species in stable deep-sea habitats.

Evidence

The most extensive work on reproductive patterns in the deep sea is that of Tyler, Gage and their colleagues in the Rockall Trough. Of the many species of echinoderms, molluscs, cnidarians and other invertebrates they have studied, virtually all reproduce over a wide range of body sizes, a feature indicative of iteroparity. Moreover, the majority of deep-sea species for which seasonal samples have been obtained appear to reproduce more or less continuously, probably over a number of annual cycles. The large number of observations on echinoderm reproduction on the Bahamian Slope also indicate iteroparity in all species. However, Turner's observations on xylophagid bivalves living in wood are in stark contrast, as these species attain reproductive maturity quickly and must reproduce before they consume their own habitat. Not all xylophagids seem to follow this pattern. Knudsen (1961) found juveniles attached in some way to the adults of nine species. Although this was interpreted as evidence of brooding, the young might also have settled on the adults after a period of dispersal. Thus, although at first sight it seems that some xylophagids might not be opportunistic and iteroparous, definitive information is not available. Other kinds of opportunistic species which probably have semelparous reproduction include some cocculinid limpets which colonize palm fronds and wood (Young and Tyler, unpublished data), and sipunculans which recruit opportunistically into fibrous substrata (M.A. Rice, P.A. Tyler and C.M. Young, unpublished data). The latter appear to live longer than a year and can reproduce several times in laboratory culture. However, sipunculans differ from xylophagids ecologically in that they do not destroy their own habitat. Before concluding that iteroparity is more common than semelparity in the deep sea, it should be noted that semelparity is much more difficult to document than iteroparity in infrequent deep-sea sampling programs; indeed, it is probably common for semelparous species to have life spans shorter than typical sampling intervals.

Not all small-bodied animals are semelparous in the deep sea. Wolff (1956a) found that the females of at least two species of hadal tanaids "… pass through several egg-bearing periods lasting probably at least three months" and that "these periods may occur only once every second or third year, provided that the female reaches an age of, say 15–20 years." Wolff (1962) also found evidence of iteroparity in asellote isopods, and Bishop reported multiple cohorts of gametes in the gonads of abyssal cumaceans, a clear indication of iteroparity.

If Jumars and Gallagher (1983) are correct about the importance of juvenile predation, then the "bet-hedging" models correctly predict iteroparity; if not, then the predominance of iteroparity in the deep sea is best explained as a K-selected life-history trait. Empirical evaluation of these models requires demographic data, which, with the exception of a few echinoderms and bivalves in the Rockall Trough, remain scarce for deep-sea animals (Gage and Tyler, 1991).

At vents and seeps, many of the larger animals, including alvinellid polychaetes, siboglinid tube worms and bivalves, appear to reproduce over a wide range of body sizes, suggesting that reproduction is either continuous or iteroparous (reviewed by Tyler and Young, 1999). To date, no semelparous species have been documented at vents or seeps, but it seems likely that some of the abundant small gastropods might be opportunistic and semelparous.

Seasonal vs. continuous breeding

Background

At the individual level, gametogenesis may proceed rapidly or slowly depending on the mechanisms of yolk deposition, and with either single or multiple cohorts of eggs developing at any given time (reviewed by Eckelbarger, 1994a). The mechanism of vitellogenesis may be absolutely conserved in some groups, but in others, selection can modify the timing and speed of gametogenesis to produce life cycles that reflect the environmental cycles in which the animal lives. Some tropical animals, which live in environments with virtually constant temperature and daylength breed semi-continuously (reviewed by Giese and Pearse, 1974; Young, 1999), but the vast majority of shallow-water animals in both temperate and tropical latitudes are periodic, synchronous breeders with annual reproductive cycles being the most common (Giese and Pearse, 1974).

Predictions

Moseley (1880) thought that there might be some seasonality in the deep sea, but his tentative suggestion was soon overshadowed by an influential paper by Orton (1920) predicting that deep-sea animals living at constant temperature should reproduce continuously. Although Orton advanced this idea as a testable hypothesis, it was not tested for many decades. During the intervening period, it became practically canonized in the deep-sea literature, in part because seasonal samples were hard to obtain, but also because the dynamic nature of the deep sea was not fully appreciated by biologists.

Evidence

Tables 12.1 to 12.4 list by major group all bathyal and abyssal species for which gametogenesis has been studied sufficiently well to infer periodicity of reproduction. Only a small amount of evidence comes from populations sampled regularly for reproductive parameters throughout the years. Constraints in ship-time, so that different seasons are sampled in different years, often make it necessary to piece data together to make a composite year. It is not uncommon to find data sets with many months missing. As a poor alternative to seasonal sampling, patterns of reproductive periodicity have often been inferred from single gonad samples. This may be done by examining the cohort structure of gametes; the presence of multiple egg sizes and few mature gametes is suggestive of semi-continuous reproduction, particularly when numerous individuals of the population show a similar pattern. On the other hand, population-wide synchrony in which all individuals have a single gamete cohort is indicative of periodic, synchronized reproduction.

It is clear from the data that the majority of deep-sea species have aseasonal reproduction, but that seasonal reproduction also occurs at all latitudes and to depths of several thousand meters. Seasonal reproduction is known among sponges, cnidarians, peracarid and decapod crustaceans, molluscs, and echinoderms. Vent species are mostly continuous breeders. However, preliminary evidence suggests that some bivalves living at relatively shallow hydrothermal vents may breed seasonally (Comtet and Desbruyères, 1998; Comtet et al., 1999) as do many animals at cold seeps. The factors that drive seasonality remain unknown, as these animals may obtain all of the carbon and energy needed for maintenance from chemosynthetic sources. It is possible that they use phytodetritus as an energy source for gonad development, while relying on methane for maintenance and construction of somatic tissue.

Because the very existence of seasonal breeding came as a great surprise when it was first documented in the deep sea, it has perhaps received undue attention. It must be kept in mind that the vast majority of deep-sea animals, particularly at abyssal depths, reproduce aperiodically or continuously and therefore require no periodic cues for the entrainment of their gametogenic cycles.

Environmental control of gametogenesis

Background

Among marine animals, the timing of reproduction is almost invariably controlled on two different temporal scales: a long scale associated with initiation and progression of gametogenesis, and a shorter scale associated with spawning. Factors that entrain seasonal cycles of gametogenesis in shallow water include predictable changes in the natural light regime (e.g., sunrise, sunset, increasing daylength), and predictable variability in salinity, diet and energy availability (Giese and Pearse, 1974). Most of the periodic cues known to control reproduction in shallow water (e.g., daylength, sunrise, temperature, lunar period, salinity, wave action) are not available in the deep sea. Nevertheless, there are seasonal changes even at abyssal depths that could possibly entrain reproductive cycles (reviewed by Tyler, 1988). Some of these factors, all of which remain untested as controllers of gametogenesis or spawning, include eddy kinetic energy, spring or summer falls of phytodetritus, and turbulence during benthic storms.

Predictions

Phytodetritus on the sea floor might qualify as a reliable cue for the entrainment of gametogenesis, particularly in temperate habitats where food may not only entrain reproduction, but also provide the energy needed for gamete production. A number of workers have suggested that phytoplankton detritus is probably the main controller of gametogenesis (Tyler, 1988; Tyler et al., 1994; Campos-Creasey et al., 1994).

The phytodetrital entrainment hypothesis gives rise to three predictions about the distribution of seasonal or periodic reproduction among deep-sea invertebrates: 1) If phytoplankton entrains gametogenesis, then one would expect more seasonality at the sea floor underlying highly productive temperate seas than in oligotrophic tropical regions, where the seasonal signal should be less intense; 2) one would expect more seasonality at bathyal depths than at abyssal depths; and 3) seasonal reproduction should be more common among animals living in non-chemosynthetic systems than in vent or seep animals, since the latter should have food available to them throughout the year.

Evidence

Latitudinal and depth comparisons of reproductive periodicity are easiest with the Echinodermata, since this phylum has been most extensively studied. At least one common deep-sea group, the echinoid family Echinothuriidae, reproduce continuously at all depths and latitudes where they occur. This suggests that reproductive periodicity, as well as mode of larval development, may be phylogenetically constrained for this group. The data show that seasonal breeders are present among echinoderms at both temperate and tropical latitudes and to a depth of about 3000 m. However, the few data available for greater depths suggest that seasonal reproduction may indeed become less common. When tropical and temperate latitudes are compared, it appears that seasonal breeders are more common in tropical seas than in the temperate ones, a pattern not predicted by the phytodetrital entrainment hypothesis. However, the comparison is not entirely valid, since the only data set for tropical seas is for Bahamian Slope echinoids at depths less than 1000 m, whereas most data for temperate species are from greater depths. Greater geographic and bathymetric coverage is needed before these correlative tests are fully satisfactory.

In the past few years, my laboratory has undertaken experimental studies (as yet unpublished) to determine if detrital food entrains reproductive cycles in bathyal echinoids. Although the data remain preliminary, laboratory experiments and also experiments in field enclosures suggest that the timing of reproduction can be shifted at least slightly by providing excess food at certain times of year. Food quantity and quality control fecundity and egg quality in bathyal echinoids (S. George and Young, unpublished data), but can also shift the speed of the gametogenic process. Thus, evidence is beginning to accrue to support the hypothesis that the timing of food falls can control the onset or completion of gametogenesis.

Tyler et al. (1994) showed that *Plutonaster bifrons,* a seasonally breeding sea star from the Rockall Trough, shifts its diet to phytodetritus when this food source is available, whereas a continuously breeding starfish, *Bathybiaster vexillifer*, is predatory and therefore one trophic link away from the direct influence of the seasonal phytodetrital pulse. *Echinus affinis,* an echinoid from lower bathyal depths, shows a seasonal change in gut contents which reflects the composition of the sea-floor phytodetritus (Campos-Creasey et al., 1994). This species breeds annually in mid-winter, releasing eggs several months before phytodetritus becomes available to plankton at bathypelagic depths (Tyler and Gage, 1984a). If larval development is very slow, it is conceivable that planktotrophic larvae may be using this detritus as a food source. However, one does not know how long larvae take to reach the feeding stage in this species.

Fertilization success and the control of spawning

Background

Successful reproduction requires that eggs and sperm be mature and present at exactly the same time. Sperm generally have a short swimming time, and must occur at relatively high concentrations in order for fertilization to occur (reviewed by Levitan, 1995). In shallow water, fertilization success is assured by breeding behaviors that bring animals into close proximity (e.g., Run et al., 1988), by environmental cues that assure simultaneous release of gametes (reviewed by Giese and Kanatani, 1987), and, at least in some species, by chemical communication (e.g., Miller, 1989). Internal fertilization is the most secure method of assuring that eggs and sperm come together. In some species this follows copulation, and in others sperm are collected and maintained by the female until the eggs are ready to be fertilized. Internal fertilization occurs in many gastropod molluscs, in peracarid, cirripede and decapod crustaceans, in bryozoans, in colonial ascidians, and in many polychaetes. Among free spawners, the timing of gamete release is often controlled by photoperiodic cues such as sunrise and lunar period. Epidemic spawning, wherein the gametes of one individual provide a signal that stimulates spawning in another, is commonly thought to facilitate spawning throughout the animal kingdom (Thorson, 1946). However, evidence for epidemic spawning remains equivocal for most species (Young, 1999), and only a few experimental studies (e.g., Starr et al., 1990) have shown its importance in shallow-water animals.

Fertilization success may also be facilitated by gamete modifications that reduce dilution by water currents, or that increase gamete longevity (Eckelbarger, 1994b).

Predictions

Because photoperiodic spawning cues are absent in the deep sea and many animals occur at low population densities, an increase in the incidence of internal fertilization is expected. Among species that fertilize externally, behavioral mechanisms such as spawning aggregation and an increase in the importance of pheromonal communication have been predicted (Young, 1999). Gamete modifications are also expected (Eckelbarger et al., 1989c; Eckelbarger, 1994b).

Evidence

Internal fertilization is the rule among deep-sea peracarids, which are the most diverse animals in the deep sea, and also predominates among the deep-sea gastropods, which include many diminutive species that lay egg masses with developing embryos. Many of the polychaetes living at hydrothermal vents have sperm that are clearly modified for internal fertilization. For example, the alvinellid and polynoid polychaetes have spermathecae for receiving exogenous sperm from other individuals and storing the sperm until eggs are ready to be fertilized (Zal et al., 1994; Jollivet et al., 2000). Internal fertilization also appears likely in a vent siboglinid tube worm, *Ridgeia piscesae.* In this species, sticky masses of sperm are apparently captured on the vestimentum of the female worm, then transferred into the gonoducts (Southward and Coates, 1985). Although other siboglinids release unusual helical sperm in bundles (Cary et al., 1989), evidence suggests that they all fertilize externally (Van Dover, 1994; Young et al., 1996b).

Elongate and modified sperm are much more common among deep-sea free-spawning echinoderms than among their shallow-water relatives (reviewed by Eckelbarger et al., 1989c), and elongate sperm have also been described for a hydrothermal-vent bivalve (Beninger and Le Pennec, 1997). Some modifications, such as lipid reserves associated with the mitochondria of echinothuriid sea-urchin sperm (Eckelbarger et al., 1989b) appear to increase sperm longevity, whereas others, such as the bipolar tailed, dimorphic sperm of *Phrissocystis multispina* (Eckelbarger et al., 1989a), may reduce dilution. The release of sperm in swimming bundles by hydrothermal-vent and cold-seep siboglinids may also help to maintain high sperm concentrations in environment where buoyant, turbulent water could easily carry individual sperm away from the spawning females.

Many deep-sea echinoderms apparently facilitate fertilization by living in perennial herds (Young, 1994b), but others occur as scattered individuals, often at very low population densities. Many of the latter, including species of echinoids, holothuroids and ophiuroids, form pairs (Fig. 12.6) and other small-scale aggregations prior to spawning (Tyler et al., 1992b; Young et al., 1992; Young, 1994b, 1999). Indeed, breeding aggregations have been documented in many more deep-sea species than shallow-water ones, a pattern that is particularly striking when sampling bias is taken into account. Wilson (1975) posed the following hypothesis on the basis of his own work with insects:

> “It is plausible (but unproved) that swarming is most advantageous to members of rare species and to those living in environments where the optimal time for mating is unpredictable.”

Pairing behavior in rare deep-sea echinoderms that live in an environment with few spawning cues lends credible support to Wilson’s hypothesis.

Starr et al. (1994) demonstrated that phytodetritus can stimulate larval release in animals living in relatively shallow water but below the euphotic zone; but, to date, natural spawning cues have only been documented for a single deep-sea animal: a vesicomyid clam living at cold seeps in Sagami Bay, Japan (Fujiwara et al., 1998). In this species, spawning was correlated with small natural temperature rises in the environment, and was induced experimentally in an elegant experiment wherein seawater was artificially heated *in situ*.

Fecundity and egg size

Background

The relationships among parental investment, egg size, and fecundity in marine invertebrates have received much attention. It is assumed that an animal of any particular body size should have a fixed amount of energy available for reproduction and that this energy allotment may be divided into many small eggs with little energy invested per egg, or into fewer large eggs with more energy per egg. A portion of the available energy may also be used for parental protection of broods, for auxiliary structures such as egg capsules, or for assuring successful fertilization. Among shallow-water free-spawning invertebrates, the former strategy is most common, especially among species with relatively large body sizes (e.g., Menge, 1975). Broadcasting many small eggs with no parental protection and little yolk requires high fecundity to compensate for high mortality during a long planktonic life (Thorson, 1950; Chia, 1974). These tradeoffs were first formalized for marine invertebrates by Vance (1973), whose classic model was immediately challenged (Underwood, 1974; Strathmann, 1974) and has been updated many times since (Christensen and Fenchel, 1979; Havenhand, 1993). Recently, there has been discussion about the potential role of fertilization processes in driving the evolution of egg size (Levitan, 1995), though this idea has not yet been accepted as fully as Vance's initial premise that egg size evolves because of limitations in fecundity and mortality during the larval stage.

Vance's model and most subsequent formulations predict that the very large and small egg sizes are evolutionarily stable, and that few eggs of intermediate size will be found. Thus, species tend to have either very large yolky eggs and lecithotrophic development, or very small eggs with planktotrophic larval development. In all of these models, it is assumed that a species has a fixed amount of energy to allocate to reproduction, that an animal with small body size will have less energy for reproduction than one with large body size, and that mortality in the plankton will be greater for small eggs than large eggs.

Predictions

What egg sizes are to be expected in the deep sea? With the dramatic exceptions of a number of very large amphipods, isopods and pycnogonids, deep-sea animals tend to be smaller on average than related animals in coastal and littoral environments, a pattern that may be related to energy limitation in deep water (Rex and Etter, 1998). Small animals are expected to produce small numbers of large eggs not only because they have inadequate energy to invest in large fecundity, but also because space for brooding embryos may be limited (Strathmann and Strathmann, 1982). Thus, in the deep sea, models of reproductive partitioning predict large egg size, short or non-existent larval periods, and significant investment in parental care. Even in megafauna with large body sizes, limited energy in the environment might reduce the amount of energy that can be devoted to reproduction, thus driving the species toward decreased fecundity and large egg size. On the other hand, if mortality in the plankton is less important in the deep sea than in shallow water, then animals with small body size could perhaps reproduce successfully with low fecundities and smaller egg sizes than their shallow-water counterparts.

Reproductive output, which is sometimes but not always reflected in fecundity, is predicted to decrease with depth because of food limitation in deep water.

Evidence

The relationships among egg size, fecundity and depth have been examined for galatheid crabs (Van Dover and Williams, 1991), caridean shrimps (Ramirez Llodra et al., 2000), protobranch bivalves (Scheltema, 1994), and echinoderms (Pearse, 1994). Van Dover and Williams plotted the mean egg volume against depth for 52 species of galatheids ranging from intertidal to abyssal depths (Fig. 12.7). There was a general positive correlation between egg volume and depth. Statistical analysis within genera showed that this trend was significant in *Galathea* spp. and *Munidopsis* spp., but not in *Munida* spp. Apparent depth-related trends in fecundity in other groups of crustaceans are often caused by body-size differences or by a shift to larger

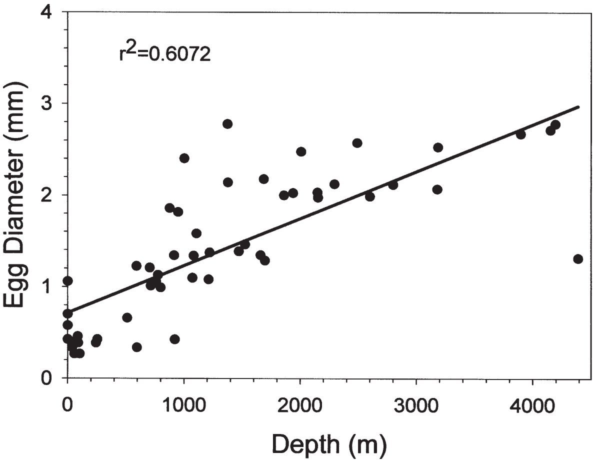

Fig. 12.7. The relationship between egg size and depth in deep-sea galatheids. Redrawn from Van Dover and Williams (1991).

egg sizes at greater depths (e.g., King and Butler, 1985; Mauchline, 1988; Company and Sardà, 1997). In Scheltema's (1994) review of fecundity data for bivalves, there is no obvious bathymetric trend in fecundity; indeed, two of the protobranch species with the lowest fecundities occur on the upper slope.

Sewell and Young (1997) have recently assembled all available data on echinoderm egg sizes for an additional test of the prediction by Vance's model that egg sizes should fall into a bimodal distribution. Combining data from all depths, they found clear bimodality in several echinoderm classes, though the pattern was obscured in taxa that brood their young or have other kinds of parental care. The bimodality remains when species occurring at depths less than 500 m are removed from the data set, suggesting that planktonic mortality is important in the deep sea, just as it is in shallow water.

Developmental mode

The reasons why larvae are present in some life cycles but not others have received considerable theoretical consideration in recent years (e.g., Strathmann, 1978, 1985, 1993; Wray and Raff, 1991; Wray, 1995; Hall and Wake, 1999; Hickman, 1999; Pechenik, 1999). Pechenik (1999) has reviewed in detail the advantages and disadvantages of having a larval form in the life cycle, and made some predictions about the environments where larvae are likely to have evolved or been lost. Many of the arguments relate to the advantages and disadvantages of dispersal. Potential advantages of dispersal include: 1) reducing competition between adults and their offspring; 2) minimizing competition among siblings; 3) colonization of new habitats; 4) decreasing predation by benthic predators; 5) reducing the negative effects of inbreeding; and 6) spreading the risk of mortality in spatially and temporally variable environments. The fossil record provides several examples where molluscan clades with larval development survived longer in geological time than species with more limited dispersal (Jablonski and Lutz, 1983). However, there is still no solid evidence that there is selection for larvae as dispersal agents *per se* (Pechenik, 1999). Studies that have attempted to assess the advantages of dispersal on different scales have generally concluded that only moderate dispersal is advantageous, even in shallow water where there is considerable temporal variability in habitats (Palmer and Strathmann, 1981; Strathmann, 1985; Hedgecock, 1986).

Predictions

Thorson (1946, 1950) predicted that deep-sea animals should brood their young or have direct development. He reasoned that planktotrophic larval development should be impossible in deep water because larvae would have to migrate too far before encountering food items required to complete development. This idea, which Mileikovsky (1971) named "Thorson's Rule", is so logically appealing that it became a virtual paradigm for deep-sea reproduction.

If larvae evolved primarily for dispersal, then one might predict that larval development should be less common in the deep sea, where conditions tend to be more stable and habitats more continuous than in shallow water.

Evidence

Although brooding was once predicted to be the predominant mode of development among deep-sea animals (Thorson, 1950), recent analysis of the egg-size data in North Atlantic echinoderms shows that pelagic lecithotrophy, rather than brooding, is the main reproductive mode in both deep and polar seas (Pearse, 1994). Many authors have assumed that large egg sizes indicate brooding (Madsen, 1961; Tyler and Gage, 1984b); but, to date, very few brooding echinoderms have been found at abyssal or bathyal depths. The notable exception is the holothurian *Oneirophanta mutabilis* (Hansen, 1968), the only deep-sea elasipod holothurian known to brood its young. All other deep-sea holothurians that have been studied apparently produce pelagic lecithotrophic larvae (Tyler and Billett, 1985, 1987; Tyler et al., 1985a, 1992b;

Sewell et al., 1998). Planktotrophic development is found in a number of north Atlantic echinoderms, including the sea stars *Plutonaster bifrons* and *Psilaster andromeda* (Tyler and Pain, 1982a), the echinoids *Cidaris cidaris* (Prouho, 1888) and *Echinus affinis* (Tyler and Gage, 1984a), and the ophiuroids *Ophiocten gracilis* (Sumida et al., 2000) and *Ophiura ljungmani* (Tyler and Gage, 1980). However, these represent only a small fraction of the species studied; the remainder have pelagic lecithotrophic development. In tropical seas, planktotrophic development is very common among echinoids (e.g., Young and Cameron, 1989; Young and George, 2000), though pelagic lecithotrophic development remains the most common mode of development in asteroids and holothuroids. Lecithotrophic echinoderm eggs that have been studied are buoyant and probably move great distances up into the water column. For example, the eggs of soft-bodied echinothuriid echinoids, which are more than 1 mm in diameter, float at a rate that should carry them to the surface from 1000 m depth in about 4 days (Young and Cameron, 1987; Cameron et al., 1988).

Many gastropods in the deep sea lay egg masses (Table 12.5), but some hatch in the capsule and emerge as crawl-away juveniles (Bouchet and Warén, 1994); the proportion of species that hatch from the egg mass to disperse in the water column as either lecithotrophic or planktotrophic pelagic larvae is unknown. Most of what is known concerning the development of deep-sea molluscs has been inferred from the dimensions of the protoconch (gastropods) or prodissoconch (bivalves) at the apex of the adult shell (Rex and Warén, 1982; Scheltema, 1994; Gustafson and Lutz, 1994), although also some deep-sea larvae have been captured in near-surface plankton hauls (Bouchet, 1976b). Xylophagid bivalves in the deep sea have very small eggs, planktotrophic larvae, and high fecundity, as might be expected for weedy species that rapidly colonize isolated and ephemeral substrata (Turner, 1973). Most vent and seep molluscs, including a myriad of tiny limpets, are apparently lecithotrophic, though some of the large-bodied mussels probably produce planktotrophic larvae (Gustafson and Lutz, 1994).

One could argue that brooding is the most typical reproductive mode in the deep sea, since peracarid crustaceans brood and are also the most speciose group in the deep sea. However, from an evolutionary standpoint, one cannot argue that there has been selection for brooding in the deep sea, since without exception shallow water peracarids also brood their young. Thus, it appears that these animals are constrained phylogenetically to brooding as a developmental strategy. Decapod crustaceans, including brachyuran crabs and caridean shrimps, generally produce planktonic larvae, many of which are probably planktotrophic. The larva of an abyssal eryonid crab was described at the time of the *Challenger* expedition (von Willemoes-Suhm, 1876). The abundant vent shrimp on the Mid-Atlantic Ridge, *Rimicaris exoculata,* is known to produce larvae, some of which have been captured in plankton trawls many hundreds of meters above the bottom (Herring and Dixon, 1998).

Developmental modes of deep-sea infaunal polychaetes have been inferred from egg size in a number of studies (Table 12.1). Planktotrophy, lecithotrophy and brooding strategies are all present in these species, though lecithotrophic development again predominates and phylogenetic patterns of developmental mode are generally conserved. At hydrothermal vents and cold seeps, a number of polychaetes have been studied, most of which probably have larval development. Deep-sea perviate pogonophorans, now considered polychaetes, brood their embryos in their tubes, eventually releasing larval forms that are probably short-lived and demersal (Baake, 1976), but the related siboglinid polychaetes from vents and seeps produce small yolky eggs (100–115 μm) which develop into lecithotrophic trochophore larvae (Young et al., 1996b; Marsh et al., 2001). Wax esters confer buoyancy on these eggs despite their small size (Marsh et al., 2001).

Larval dispersal and migration

Background

Both the role of dispersal in evolution and the functions of dispersal in the life cycles of individual animals remain somewhat controversial, but most arguments revolve around the genetic advantages of outcrossing and the spread of risk among spatially and temporally heterogeneous environments (Strathmann, 1974; Palmer and Strathmann, 1981). Dispersal could also be important for reducing competition when resources are limiting locally. In the marine environment, most species disperse by means of microscopic larvae. Larvae may disperse for very long distances or they may have short lives and limited dispersal. With few known exceptions, those shallow-water species that disperse for long distances have feeding (planktotrophic) larvae, whereas most philopatric dispersers have lecithotrophic larvae or direct development (reviewed by Jablonski and Lutz, 1983). Planktotrophic development requires that larvae find food before they exhaust the energy and nutrients sequestered by the mother in the egg, so most planktotrophic animals depend either directly or indirectly upon phytoplankton. Those species that do not produce larvae, including peracarid crustaceans, must disperse as adults or juveniles.

It is generally supposed that dispersal should be less crucial for the maintenance of genetic diversity in stable habitats than in habitats where there is a high likelihood of environmental change and a commensurate requirement for adaptive change in the genome. However, Hamilton and May (1977) have disputed this point with a model showing the population-wide importance of successfully competing for distant sites. Long-distance dispersal should not be advantageous where densities remain too low to foster competition among siblings or between siblings and offspring. Disadvantages of larval dispersal include high planktonic mortality and the improbability of locating a site as good as that of one's parents.

Predictions

One might predict that long-distance dispersal of larvae would not be favored by natural selection on the abyssal plain because great expanses of uniform substratum would make colonization of new habitats unnecessary. Moreover, in habitats like seamounts where a small area of suitable substratum is surrounded by extensive areas of marginal or unsuitable habitat, selection should favor only limited dispersal. Large eggs, parental protection and lecithotrophic development should be found in those deep-sea habitats where dispersal is not critical to the survival of the species. However, in ephemeral deep-sea habitats such as hydrothermal vents, the temporal variability of the system might compensate for the danger of gamete loss to unsuitable habitat, favoring the evolution of larval dispersal mechanisms.

Because the density of living phytoplankton declines rapidly below the deep chlorophyll maximum at about 200 m, and they are virtually absent below the permanent thermocline, it has been predicted that planktotrophy should not be a viable strategy for deep-sea animals (Thorson, 1946, 1950). Thorson argued that it would be impossible for a microscopic larva to migrate all the way to the euphotic zone without feeding, and Scheltema (1994) provided calculations in support of this contention.

Etter and Caswell (1994) used a cellular automaton model to explore the advantages of dispersal in habitats with various levels of disturbance in a competitive system. The model predicts that long-distance dispersal would only be advantageous at certain disturbance frequencies, and that the range of these frequencies would be influenced by reproductive output, competition and the intensity of disturbance. If it is assumed that the frequency of disturbance decreases as a function of depth down the slope, then the greatest advantages to dispersal may be expected at some intermediate depth, which would correspond to an intermediate level of disturbance.

Evidence

As indicated in Tables 12.1 to 12.6, planktotrophic larvae are produced by animals in many phyla living at slope depths and planktotrophy is common in some groups (notably prosobranch gastropods) even at abyssal depths. The mechanisms of nutrition for these larvae remain generally unknown. They may use nutritional resources available at depth (bacteria, dissolved organic matter, detrital seston) or they may migrate to a depth where sufficient food is available. Both possibilities have been discussed in the literature and explored experimentally. Young et al. (1997) presented a mathematical model incorporating swimming speeds, respiration rates and plankton concentrations to predict the likelihood that larvae could reach the euphotic zone by migrating from bathyal depths. When run with reasonable parameter estimates taken from deep-water echinoderm larvae where data were available and shallow-water larvae when the former were not available, the model showed that migration could be possible for many species if they were respiring at low rates and swimming at high (but realistic) speeds. However, larvae of some of these species cannot tolerate the temperatures or pressures found at or near the level where phytoplankton are abundant (Young and Cameron, 1989; Young and Tyler, 1993; Young et al., 1996a, 1997; Tyler and Dixon, 2000). Preliminary data (W. Jaeckle, A. Pile, I. Bosch and C. Young, unpublished) show that larvae of bathyal echinoderms can absorb dissolved organic matter and remove heterotrophic bacteria from the water column at relatively high rates. These various pieces of indirect evidence indicate that planktotrophic development may be a viable developmental strategy in the deep sea, even for species that cannot migrate to the euphotic zone.

Compelling evidence that some larvae migrate ontogenetically to the euphotic zone comes from the work of Ashworth (1915) and Bouchet (1976a,b), both of whom collected deep-sea larvae among the shallow-water plankton. Bouchet and Fontes (1981) and Killingley and Rex (1985) analysed oxygen isotopes in protoconchs; these data indicated that the carbonate in protoconchs was deposited at a warmer temperature than in the teloconchs.

Genetic studies of hydrothermal vent animals generally have demonstrated a high level of genetic exchange among remote sites, suggesting the strong possibility of larval dispersal (reviewed by Jollivet, 1993; Mullineaux and France, 1995; Vrijenhoek, 1997; Tyler and Young, 1999). Indeed, larvae from many phyla have been collected in vent plumes (Mullineaux et al., 1995, 1996), larval development has been inferred from shell apices of many vent molluscs (Gustafson and Lutz, 1994); and a handful of vent and seep species have been reared in the laboratory from larvae (Young et al., 1996b; Epifanio et al., 1999; Marsh et al., 2001; Pradillon et al., 2001). The swimming behavior of larvae of the vent crab *Bythograea thermydron* suggests that it disperses quite passively for long distances, then begins walking when it encounters the warm water of a vent. Similarly, the embryos of an alvinellid polychaete, *Alvinella pompejana*, undergo arrested development at 2ºC, then resume cleavages when encountering warmer temperatures (Pradillon et al., 2001). Using data on lipid reserves, metabolism and currents, dispersal distance has been estimated for the siboglinid polychaete *Riftia pachyptila* (Marsh et al., 2001). The lecithotrophic larvae of this species are capable of drifting for about 38 days. At 9ºN on the East Pacific Rise, this dispersal time is sometimes enough to permit dispersal over the transform faults that separate ridge segments.

Young et al. (1999) analysed the geographic ranges of deep-sea echinoderms and ascidians with known modes of larval dispersal. They found that the standard relationship between geographic range and mode of development (planktotrophs disperse farther and have broader ranges than lecithotrophs: see Jablonski and Lutz, 1983) breaks down in deep water. This is probably because lecithotrophs can drift much longer distances in the cold temperatures of the deep sea than in warmer surface waters. Some of the species with the broadest ranges were elasipod holothurians, which produce lecithotrophic larvae, but also are capable of pelagic dispersal in the juvenile and adult stages.

Etter and Caswell (1994) tested the prediction of their dispersal/disturbance model by examining the relative proportions at various depths of gastropod species with planktotrophic and nonplanktotrophic development (Rex and Warén, 1982). In the western Atlantic, the proportion of prosobranch gastropods with planktotrophic development increases with depth to 2000 m, where the number of planktotrophic and nonplanktotrophic species is approximately the same (Rex and Warén, 1982). This pattern fits the predictions of the model well, suggesting that disturbance frequency might interact with other factors influencing the evolution of larval dispersal in the deep sea.

CONCLUSIONS

It is now recognized that the deep sea is not a single, continuous habitat, but rather a mosaic of habitats in which many species have particular specialized requirements (Tyler, 1995). The insular, dynamic, often ephemeral, vent and seep habitats with abundant sources of autochthonous nutrition contrast markedly with stable, nutrient-poor and extensive abyssal plains where all energy is allochthonous in origin. Likewise, the continental slopes and rises contain many different habitats, each characterized by specific topographic features, food levels, and physical characteristics, and each occupied by distinct assemblages of species adapted to those conditions. It is not surprising therefore that reproductive modes and life-history traits of animals, as revealed by more than a century of study, show a rich assortment of tactics and strategies for responding to the diversity of habitats in the deep sea. With few exceptions, the reproductive strategies and tactics found in shallow-water systems are also represented in the deep sea, though there remain clear shifts in the relative importance of different strategies with depth. As in most other ecological systems, generalizations become harder to make as one learns more about the details.

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Chapter 13

ANTHROPOGENIC IMPACTS ON THE DEEP SEA

Hjalmar THIEL

DEEP-SEA IMPACTS

The deep sea has received broad attention in the preceding chapters of this volume, a recognition that it is the largest, continuous ecological unit on earth. However, it is also of all environments the most remote and least well known, both to scientists and to the public. But this remoteness has not protected the deep sea from anthropogenic impacts. Wastes released anywhere on the high seas or into the atmosphere may rapidly sink into the abyss, to be out of sight and out of mind. Invisible and visible wastes penetrate this vast volume of water from a variety of sources and via different pathways. There are few areas of the world's oceans that have not received any anthropogenic impact, invisibly and by slow-paced transport. Life is ubiquitous in the oceans. Since most species require oxygen, this essential gas must be transported to all locales with the currents; and these same currents transport invisible contaminants.

These invisible substances have travelled for long distances and periods of time, and may affect organisms many degrees of latitude and longitude away from their origin and their entrance to the oceans. In contrast, human intrusions into the deep sea are already direct sources of environmental disturbances, and these intrusions, visible and made with consciousness of their impact, may become more numerous and more serious in coming years.

Anthropogenic impacts in the deep sea deserve serious consideration and international legal regulation. Invisible deep-sea contaminants may eventually return to the ocean surface, add to the local pollution, and disturb species or communities and eventually man through direct or synergistic effects. Turn-over times in the oceans, depending on regional peculiarities, are estimated at a few hundreds to one thousand years or so. One has no idea what the pollution status of the ocean surface will be when contaminants resurface after such long time periods.

Visible contaminants, intentionally dumped into the deep sea, cannot be retrieved. Any realization that specific substances may not have found their final storage at great ocean depth will inevitably come too late; there would be no possibility to redress the situation. Similarly, impacts occurring in the deep sea as a consequence of mining mineral resources will have long-term effects.

A thorough knowledge of the ecology of the deep sea is essential to arrive at the right decisions. However, effective protective measures for the deep sea will be possible only if the impacts are known or their extent can be estimated. These are certainly difficult tasks, but impact prediction must be undertaken a long time in advance. Oceanographers of all disciplines must think ahead. Appropriate deep-sea research must be conducted, targeted so as to understand potential impacts, and experimental large-scale approaches are essential.

From a conservation point of view the deep sea is firmly within the ambit of the human community despite its remoteness. Besides ocean scientists, politicians, economists, and engineers must take the potential disturbance of the far-distant deep sea into account. They all share responsibility for the deep sea as part of the oceans and the human environment.

NON-VISIBLE CONTAMINATION

Radiation

On 4th July, 1986 Erlenkeuser and Balzer (1988) collected two box corer samples off mid Norway (at about 67ºN and 67º40′N) on the continental slope of the Norwegian Sea at a depth of 976 m and on the adjacent Vøring Plateau at a depth of 1426 m. The samples were analyzed several months later for radiocesium, and high levels of the radionuclides Cs^{134} and Cs^{137} were discovered in both samples. Bioturbation had carried this material about 10 mm into the sediment. Further analysis of the material proved that the radionuclides had originated from the Chernobyl accident on 26th April 1986. Strong fallout occurred on 10th and 11th May on Greenland and Svalbard, and it may be assumed that radioactive material had already contaminated the surface of the Norwegian Sea. Organic matter may have scavenged the cesium, and fast-sinking aggregates may have transported the material to the seafloor. This is an example of deep-sea contamination which can be traced back to its origin, and it can be confidently assumed that larger areas of the bathyal and the abyssal floors of the Norwegian and the Greenland Seas received radionuclides during the spring of 1986. By 1987 cesium-134 derived from the Chernobyl accident had certainly penetrated into the water column to a depth of 1000 m near the northern slope of the Barents Sea and to about 300 m in the adjacent Nansen Basin (Scholten et al., 1995).

Other fallout events originated from nuclear bomb tests. Nies (1988, 1989) presented vertical profiles through the water column in the Northeast Atlantic for cesium-137, strontium-90, tritium and plutonium-239/240. Although the highest concentrations were found in surface and subsurface waters, down to depths of more than 1000 m, these radionuclides could be traced to abyssal depths. Their vertical distribution depends partly on their reactivity with particulate matter. The concentrations of Cs-137 and Pu-239/240 in some instances show an increase in the nepheloid layer above the seafloor. However, for his most westerly samples (25ºW) Nies (1988) assumed that the higher values near the bottom originated from northern subpolar water-masses – that is, from sources other than fallout in the general area. In possible support of this conclusion, Scholten et al. (1995) discovered Cs-137, derived from atmospheric testing of atomic weapons and from the nuclear reprocessing facility at Sellafield, mixed throughout the water column in the Arctic Ocean. These water masses are those which will be transported into the Atlantic, and later the Indian and Pacific Oceans, together with their contamination load.

Although not specifically related to the deep sea, Kautsky (1988) summarized data collected in 1979, and between 1982 and 1985, on the distribution of Cs-134 and Cs-137 in surface waters of the Northeast Atlantic, the North Sea and the Norwegian and Greenland Seas. He traced the transport routes from their sources, the nuclear fuel reprocessing plants of Sellafield on the Irish Sea and La Hague on the English Channel, all the way through the North Sea, the Norwegian Sea, into the Barents Sea and to the Greenland Sea (see also Kershaw and Baxter, 1995). There, the water may be entrained into the downwelling processes (Rudels and Quadfasel, 1991; Schlosser et al., 1995a). It is this down-welled water with a high density which leaves the Norwegian and Greenland Seas, passing the Shetland–Greenland ridge, and contributing to the North Atlantic Bottom Water. Aarkrog et al. (1983, 1987) had calculated the transport time for the surface waters from Sellafield to the Greenland Sea to be seven years, Kautsky (1987) reported 7–9 years, and Nyffeler et al. (1996) 7–10 years. Adding to this the transport time from the Greenland Sea to the North Atlantic deep sea, probably in the same time range, the total time from Sellafield or La Hague to the deep ocean would still be well below the 30.2 years half-life of Cs-137.

This very rough calculation demonstrates that contaminants from terrestrial sources, if they are persistent and not deposited somewhere in shallow sediments, will reach the deep sea. Nies (1988) had discovered Cs-137 values in the bottom water layer to be higher than in the water column above. This is the North Atlantic Bottom Water which carries the signature of the water from Sellafield and La Hague. Other contaminants may originate from dumping sites in shallow water in Northern Siberia, and from rivers discharging into the Arctic Ocean (Khodakovsky, 1994; Nies et al., 1997). These contaminants may be transported into the deep Arctic basins by downslope convection. Indications from radionuclides for deep convection are presented by Cochran et al. (1995) and Wedekind et al. (1997) for the Norwegian and Greenland Seas, by Papucci et al. (1996, 2000), Yiou et al. (1997) and Merino et al. (1997) for the Mediterranean, and by Gulin et al. (1997) for the Black Sea. The tracers originated partly from the Chernobyl accident.

Chlorofluorocarbons

A number of substances exist today which are useful tracers for tracking water masses (Roether and Rhein, 1989). As tracers, they should be non-reactive in seawater, not metabolized by organisms, and not adsorbed to particulate matter. This characterizes them as perfect tracers, because they do not change their concentrations with time and clearly mark their specific water body. One such group of tracers are the so-called freons, the chlorofluorocarbons (CFCs)[1], and specifically F-11 (trichlorofluoromethane) and F-12 (dichlorofluoromethane). These substances are of anthropogenic origin and have been widely used as refrigerants, aerosol propellants, blowing agents for plastic foam, and solvents. They are volatile, and considerable proportions enter the atmosphere after their application. Transported into the stratosphere, they are known to destroy ozone. In the oceans they are carried with the water masses, so that their continuing distribution can be demonstrated. Bullister (1989) showed the distribution of F-12 in the North Atlantic and its penetration into the deep sea. For the South Atlantic he was able to trace the cold Weddell Sea water into the deep sea to become the Weddell Sea Bottom Water below 4000 m. The southward flow of deep Arctic Ocean water along the western Fram Strait, through the Greenland Sea and the Denmark Strait into the North Atlantic was studied by Smethie et al. (1988) using F-11 and F-12.

Doney and Bullister (1992) and Smethie (1993) have shown that chlorofluorocarbons penetrated more deeply into the western than into the eastern North Atlantic, which is in accordance with the known fact that the deep-sea water masses are formed in the western part of this ocean. For the deep sea of the Eastern Mediterranean, Schlitzer et al. (1991) were able to demonstrate with the help of chlorofluorocarbons that the source of bottom and deep waters is the Adriatic Sea, and Rhein (1996) described the processes of deep-water formation in the Greenland Sea by studying the distribution of chlorofluorocarbons. This water mass carries the contaminants into the deep North Atlantic and finally throughout the world ocean, as has been graphically described by Broecker (1991) in his postulated inter-oceanic conveyor-belt system.

Sültenfuß (1998) has presented results on the distribution of F-11, together with tritium, in the Weddell Sea, and demonstrated higher levels in surface, slope and bottom waters down to 5000 m depth compared to the open water column. The ratios of different chlorofluorocarbons in a water body provide true markers for water masses, and it was shown that surprisingly little mixing occurs in the interior of the ocean. Other useful tracers are, for example, helium isotopes, tritium and neon (e.g., Roether et al., 1996).

Organochlorine and organotin compounds

Another class of man-made substances found in the oceans are the synthetic organochlorine compounds, including the polychlorinated biphenyls (PCBs), the hexachlorocyclohexanes (HCHs), trichlorethane (DDT) and its metabolites, and the polychlorinated camphenes (PCCs). Their physicochemical properties show a broad range in respect of water solubility, vapour pressure, biodegradability, lipophilicity and particle affinity. In recent years it has been demonstrated that low-volatility organochlorine compounds are distributed by atmospheric transport from tropical and temperate to polar regions (Duce et al., 1991; Wania and Mackay, 1993; Iwata et al., 1993; Loganathan and Kannan, 1994; and literature cited therein). These substances have been discovered in relatively high concentrations in the Arctic and Antarctic Oceans, in various terrestrial and marine biota, and also in human populations of the high-arctic region. They have been traced from warmer localities at lower latitudes to cold environments at higher latitudes, where they precipitate with rain or snow after condensation (Hargrave et al., 1988; Patton et al., 1989; Oehme, 1991; Arctic Monitoring and Assessment Programme, 1998).

Since the renewal process of the deep-ocean water masses starts at the surface in polar regions, contaminants are likely to be transported into and widely dispersed in the deep sea, as shown above for radionuclides and chlorofluorocarbons. The existence of organochlorines in the deep sea has been described by Tanabe and Tatsukawa (1983), Knap et al. (1986), Schulz et al. (1988), Fischer et al. (1991) and Ballschmiter et al. (1997), but no impacts were observed.

In shallow waters, metabolites of some persistent organochlorines and detergent components were found to act as oestrogenic chemicals even at low concentrations, adversely affecting male and female gonads and the development of reproductive tracts (e.g., Jobling and Sumpter, 1993; Kelce et al., 1995; Ruiz et al., 1996; Colborn et al., 1996; Ide et al., 1997). Nothing of

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[1] For a list of acronyms see the appendix on p. 471.

this type of influence is known for deep-sea biota, but there is no reason to believe that fish and invertebrates there would not be affected at sufficiently high concentrations. Whereas infertility and other sexual deviations were discovered earlier in coastal regions, female gastropods in the open North Sea were found to be affected by tributyltin used in anti-fouling paints on ship hulls (Ten Hallers-Tjabbes et al., 1994). Takahashi et al. (1997) discovered this same contaminant to a depth of 980 m in Suruga Bay (Japan) in fish, crustaceans, cephalopods, gastropods and echinoderms. Although these observations were made close to shore, the data demonstrate the penetration of organotin compounds into offshore and deep-water food chains.

Flux to great depth and reactive contaminants

As noted above, predominantly inert substances such as the chlorofluorocarbons will enter the deep ocean, and be transported around in it, with the thermohaline circulation system. Consequently, although chlorofluorocarbons, like the radionuclides resulting from nuclear tests, occur throughout the earth's atmosphere, their main entry into the deeper parts of the ocean takes place through the formation of bottom water by downwelling of dense water masses, which occurs in rather limited regions around Antarctica and in the Greenland and Labrador Seas (e.g., Rudels and Quadfasel, 1991; Schlosser et al., 1995b). The bottom waters of enclosed deep basins like the Mediterranean and the Red Seas are also formed in fairly restricted areas and also carry contaminants into the deeper layers. Lipiatou et al. (1997) calculated mass budgets and dynamics for polycyclic aromatic hydrocarbons which enter the Mediterranean from atmospheric fallout and riverine input. Some of this material and other contaminants settle to the seafloor within the Mediterranean, but some find their way into the Atlantic with the Mediterranean outflow over the sill 300 m deep in the Strait of Gibraltar, to form a well-marked water mass slowly spreading throughout the North-east Atlantic at a depth between 600 and 1000 m.

A more direct and widespread route into the deep sea, particularly for those substances which enter the metabolism of living organisms or are scavenged by particulate matter, is through the sinking of particles, which may occur at all latitudes. This route into the deep ocean by the sinking of particulate matter has been recognized for more than hundred years, but it is only within the last twenty years or so that it has been realized that mass particulate transport to great depth can occur in a matter of weeks (Billett et al., 1983; Rice et al., 1986; Thiel et al., 1988/89; Smith et al., 1996; De Wilde et al., 1998). Although this transport mechanism probably exists throughout the world oceans, its extent varies markedly in space and time, being largely dependent upon the level of primary production and season. For example, aggregate formation and rapid sinking of organic matter, with any associated contaminants, occurs in the North Atlantic predominantly after the spring phytoplankton bloom, and this phytodetritus arrives at the seafloor after about six weeks. In tropical regions, where both the seasonal influence and the standing stocks are lower, aggregation and sinking are much less important, and it may be expected that contaminant transport to great depth by this means is smaller and less episodic.

Speculation on this rather direct route for deep-sea contamination finds support in the demonstration of various substances accumulating on particles and concentrating in deep-sea organisms. Flegal and Patterson (1983), Duce et al. (1991) and Mason et al. (1994) described vertical profiles in the water column for the concentrations of various metals; heavy metals were found in deep-sea shrimps and fish, for instance, by Kobayashi et al. (1979), Thiel et al. (1986), Karbe (1987), Steimle et al. (1990), Mason and Fitzgerald (1993) and Monteiro et al. (1996). However, not all high concentration values are due to anthropogenic inputs to the ocean; they may be due to age and food-chain relationships (Windom et al., 1987; Vas et al., 1993; Cronin et al., 1998). Data from the Red Sea (Thiel et al., 1986; Karbe, 1987) clearly indicate increasing concentrations in organisms above the Atlantis-II-Deep, a region subject to hydrothermal influence. Various organic contaminants in deep-sea fish were reported by Krämer et al. (1984) and Steimle et al. (1990).

Further transport mechanisms exist in the sedimentary environment. Reactive substances of riverine or atmospheric origin may be adsorbed to particulate matter and transported far into the open ocean, for instance by the large visible plumes shed into the Atlantic Ocean by the rivers Amazon and Congo. Sediment may accumulate in shallow waters on the outer shelf, the shelf edge or the upper continental slope. Sediment masses, predominantly below the shelf edge, may become unstable and mass flows may be triggered, transporting sediment and contaminants in slumps, slides or turbidity currents to great depths.

Although these events are rare in ecological terms, the amounts transferred into the deep ocean may be very large (Seibold and Berger, 1993). Quadfasel et al. (1990) reported the existence of turbidity currents in the Sulu Sea at intervals of several decades following long-term sediment accumulation.

Various other means of contaminant transport occur, although these may be rather weak and geographically limited. Contaminants scavenged during the freezing process together with sedimentary materials, or those precipitated on ice floes in polar seas, may be released from the ice cover into the ocean by the melting process, together with particulate matter, after drifting long distances over several years. Other contaminants are drained out of the ice much faster, together with salt brines concentrated during freezing (Arctic Monitoring and Assessment Programme, 1998). Absorbed to particulate matter, they settle to the seafloor. Those in solution are transported with the currents, and downwards-directed convection with cold water transfers them into deep water.

Quadfasel et al. (1988) and Fohrmann (1996) described and modelled the occurrence of sediment-laden or turbidity plumes, originating from melting ice and the release of the particulate load from ice floes, in the Arctic. Both types of plume probably drifted to the Svalbard and Bear Island regions from the far northern regions of Siberia, with added components from fallout of contaminants with snow. Because of its higher density, this particle-laden water mass sinks to great depth. The particulate matter is lost during this passage through the basin, predominantly along the continental slope of the northern Norwegian Sea and the Barents Sea, where further cold water masses from the shelf penetrate into the deep sea (Rutgers van der Loeff et al., 1995). Adsorbed reactive contaminants are distributed at the sediment surface below the paths of the currents.

Another example of downslope transport is known from upwelling areas, for instance off northwestern Africa. Primary organic matter (determined as chlorophyll a and its degradation products) and benthic organisms have their maximum downslope concentration at depths between 800 m and 1000 m – an unexpected increase with increasing depth (Thiel, 1982). Support for the deduction that food energy is transported may be derived from the existence of turbid bottom water layers (Kullenberg, 1978) and from indications of downslope transport of sediment (Bein and Fütterer, 1977). These phenomena may be partially explained by a downslope component of the undercurrent flowing to the north along the upper continental slope (Mittelstaedt, 1982), and internal waves may regularly interact with the upper slope, resulting in the resuspension of particulate matter (Fahrbach and Meincke, 1982). Downslope transport of water and particles was also observed by Thomsen and van Weering (1998) along a transect south of the Porcupine Seabight in the northeast Atlantic.

This short account of existing and potential contaminants in and pathways into the deep sea is far from comprehensive (see also OSPARCOM, 2000a,b,c). There are more results available from other ocean regions and more detailed descriptions of the processes involved. However, it shows that a variety of transfer mechanisms exist by which contaminants not visible to the human eye reach the deep sea. Their concentrations have so far not reached unacceptable levels (Ballschmiter et al., 1997) so that they cannot be classified as pollutants; but from the data available it seems that no region of the deep sea has escaped anthropogenic impact. No results are available from deep-sea trenches, but since vertical sinking is independent of depth and most trenches are situated close to the continents and to island arcs, and because some water renewal occurs down to maximum depths, contaminants are ubiquitous throughout the oceans.

VISIBLE AND CONSCIOUS CONTAMINATION

In contrast to the non-visible substances in the sea, visible contamination ranges from items of small litter thrown overboard by seamen and tourists to regular ocean disposal using the deep sea as a repository. This category includes deep-sea mining and fishing. Primarily, ore is extracted from the deep seafloor, but much of the material mined is discharged back into the ocean. Both disposal of wastes and mining of mineral resources must be economically feasible and therefore can be organized only on the basis of large-scale intrusions including the mobilization of large amounts of material. Fishing, if it is to be profitable, may not be sustainable at great depth. All these uses of the deep sea may have long-lasting and far-reaching effects.

The regular thoughtless and secret dumping of wastes at sea

Ever since man first crossed the oceans, the sea has been the recipient of all wastes produced on canoes, rafts, sailing ships, steamers and ocean liners. Trawling the bathyal or the abyssal seafloor recovers beer and medicine bottles, cans, dishes, furniture parts, plastic sheets, paint brushes, bricks and many other remains of civilization (Galil et al., 1995). The most abundant waste material, however, is clinker together with some unburnt hard coal (Thiel, 1972). During the steamship era thousands of tonnes of coal were burnt daily and all the ashes and clinker were shovelled over the rail. On the deep-sea floor the shipping routes are clearly marked by this material, as today there are oil residues and drifting tar lumps on the ocean surface (e.g., Day and Shaw, 1987; Golik et al., 1988) which may eventually sink to the seafloor. In 1972 regulations were adopted, the so-called London Convention ("LC", see p. 457), to prevent the pollution of the sea by dumping of wastes produced on land but loaded on board ships for disposal at sea. Whereas in 1979 an estimated 17 million tonnes of industrial wastes were dumped, the amount decreased to 6 million tonnes in 1987. Dumping of certain waste types in shallow waters is still considered a practicable and environmentally acceptable option, but the dumping of sewage sludge decreased from 17 million tonnes in 1980 to 14 million tonnes in 1985, with further reductions in the subsequent years (International Maritime Organization, 1991). Much of the material disposed of on the high seas will eventually sink down to great depths.

The MARPOL (MARitime POLlution) 73/78 Convention of the International Maritime Organization (IMO) regulates the discharge of residues from ships at sea, tank washing etc. and transportation of goods, including bulk chemicals and oil, to cover considerations of safety and pollution. Ports are required to provide facilities to collect all wastes; but it remains cheaper to dump at sea, and only signatory states are bound by the IMO regulations. Consequently, much of the waste accumulating during ship passages is still discharged into the ocean surface, but glass bottles and other rapidly sinking materials are now often released after crushing into small particles, which again mark the shipping routes along the seafloor. The amounts secretly discharged at sea are not known and may be high. Rumours in seamen's circles suggest that containers with unknown contents are often loosely lashed in the top layer of freighters and might get lost "occasionally" in stormy weather.

Wastes with hard surfaces arriving at the bottom of the deep ocean may disappear in the soft ooze, but may also extend into the near-bottom water and constitute a hard substrate for colonization by sedentary species. Regions which have been contaminated with high amounts of hard-surface wastes, for instance below the main shipping routes, may be expected to exhibit secondary ecological impacts through alterations in community structure. Since the average amount of food for all the benthos remains the same over geological time spans, an increase in hard substrate and subsequently in sedentary fauna will inevitably result in a decrease in the density of soft-bottom fauna due to competition and changed energy partitioning.

Losses of ships at sea

With increasing traffic and tonnage, increased loss of ships can be expected. Most wrecks are situated in coastal regions, but many have sunk on the high sea to great depth. Specifically, during World Wars I and II, many warships and merchant ships were sent to the deep-sea floor. In peace-times during the period from 1971 to 1990, according to Lloyd's Register (1990, 1996), a total of 3701 ships comprising 12 861 975 gross tonnes were lost due to foundering, fire or explosion, or went missing, not including shallow-water losses. If 10% of these ships are assumed to be lost on the high seas, this would amount to an average of 18 ships and 65 000 tonnes per year arriving on the deep-sea floor. For 1996, corresponding figures are 11 ships and 47 000 tonnes.

Those ships were totally lost with all their equipment, installations, fuel and cargo, certainly including poisonous and persistent substances. These potential pollutants may be sealed off in the ships' hulls, but eventually, after decades, they may be released, contaminating the nearby area or drifting away with the currents, probably for long distances, and then returning to the surface. The impact of wrecks on the abyssal seafloor has never been investigated, although modern techniques are suitable for studying their effects. This is demonstrated by the discovery of the *Titanic*, corroding away at a depth of 3800 m in the Northwest Atlantic since 1912, and by the detection of the *Lucona* at a depth of 4511 m in the Indian Ocean, as part of the investigation of an insurance fraud since 1977 (Mullen, 1991).

Waste disposal in the deep ocean

The production of wastes in human societies is tremendous – up to 40 kg per person per year in industrialized countries (Oslo Commission, 1989). Although efforts are made to reduce the production of wastes that need permanent storage in repositories, the amounts will increase through industrialization of developing countries. In principle, avoidance of waste production must have priority over the overcoming of storage problems. However, waste disposal remains necessary, and negotiations regularly include consideration of ocean and deep-sea options. Few ethical arguments exist to support protection of 60% of the earth surface, the deeper ocean regions, when mankind already uses the terrestrial and shallow marine 40% of the planet. Careful comparative evaluations are prerequisites for finding the best practical solution to waste treatment. In the future it may be that, for certain wastes, deep-ocean disposal becomes the optimal option after balanced consideration of all environmental, technical, commercial and social arguments.

Marine scientists, specifically deep-sea ecologists, must be aware of the fact, that one day, probably not far into the future, they may be asked to contribute to environmental impact assessments. They should ask themselves, whether hard data on deep-sea ecology are sufficient for the evaluations that will be needed. The time scales over which environmental assessments will be required may be short in relation to the time required to mobilize research activities and obtain adequate results.

The discrepancy between the current level of scientific effort and the likely future demand for advice should lead to precautionary research activities. Deep-sea ecologists should think ahead, to develop research programs which will provide the data necessary to evaluate the impacts of existing and potential deep-sea uses. This is relatively new thinking in ecological deep-sea research, and it is not an easy task to raise funds for such precautionary research – probably in the absence of definite time scales for the commencement of industrial or societal activities. Long-term commitments by funding agencies are rare, particularly if the perspective of some people in controlling positions is limited to the interval between elections. But the funding agencies must be made aware of the importance of deep-sea environments, and of their responsibilities in relation to them.

Precautionary and environmental science in the deep sea must not be neglected through falling between governmental and industrial funding agencies. Government agencies will tend to shift the responsibility to industry, but industrial funding would probably arrive too late for adequate action. Research and its funding, as well as industrial development, are conducted in the interest of human society, and a united path must be found to serve society.

An additional aspect, to be considered in this chapter, is the extent of the research deemed necessary to understand and evaluate potential impacts (Thiel et al., 1998). The various uses of the deep sea constitute large-scale intrusions, conducted for economic reasons. Technical developments and transport of material (wastes and ore) must be realized on a large scale to be commercially feasible. Therefore, the impacts to be expected are large, and scientific approaches need to be on an unusually large scale compared to usual oceanographic research (comp. pp. 443, 452). The efforts required for such large-scale research would be best provided by international cooperation.

Finally it must be stated explicitly that precautionary deep-sea research does not have the aim of promoting the disposal of wastes into the deep ocean. Deep-sea ecologists have their reservations about using the deep sea as a repository, but they realize the importance of gaining knowledge suitable for environmental impact assessments, for discussions on these matters must include materials already disposed of, and substances potentially to be dumped. Special emphasis must be laid on those actions which need large-scale experimentation for assessment of their environmental impact. Subsequent sections consider the material and its disposal, the actual or potential effects, and the research required to understand and evaluate the impacts.

Munitions

In 1994 the Secretariat of the London Convention received two notifications on the dumping of redundant ammunition. South Africa authorized the dumping of 77 863 kg and a further 14 000 tonnes of munitions such as bombs, shells, cartridges, mines, mortar bombs, grenades and smoke devices at two sites, one 150 nautical miles south-west of Cape Town at a depth of 3500 m, and the other 40 nautical miles south-east of Durban at an unidentified depth (London Convention, 1994). Also in 1994, Portugal scuttled a vessel loaded with nearly 2000 tonnes of various redundant munitions including grenades, chemical grenades, ammunition, fuses, pyrotechnics, depth charges, rockets, bombs, missiles and mines. During the Gulf War, this ship had been used as an ammunition transporter. Now it rests on or in the seafloor at a depth of more than 4000 m and a distance of 215 nautical miles from the Portuguese coast [Working Group on Seabed Activities (SEBA), 1995], but any substance transported away with the currents would arrive in international waters or those of neighbouring states.

For more than 200 years defective, obsolete and surplus munitions have been disposed of at sea. The largest dumping actions occurred after World War II, but most of the material remained in shallow waters where mustard gas, particularly, caused health problems to fishermen. Deep-water dumping of munitions is reported in a few further cases: a total of 137 000 tonnes of chemical weapons were dumped at several sites, the deepest at a depth of 4500 m and a distance of 350 nautical miles south-west of Britain, others at depths between 500 and 3000 m 55 nautical miles north-west of Northern Ireland, 45–90 nautical miles west of the Hebrides, and in and at the edge of the Rockall Trough. One of these operations included 17 000 tonnes of bombs filled with tabun[2], but other munitions contained sarin, phosgene and mustard gas (Advisory Committee on Pollution of the Sea, 1988; Hencke, 1995). Britain terminated the dumping of redundant munition and explosive stocks at the end of 1992. The last deep water dump site in use was located some 400 nautical miles off southwestern Britain at a depth of about 4500 m (Oslo Commission, 1992). According to Tornes et al. (1989), probably 38 ships with more than 150 000 tonnes of chemical munitions were scuttled, some in the North Sea, some in the Skagerrak at a depth of 600–700 m, and others in the Norwegian Sea at great depth.

This list of dumpings of munitions in deep waters could be extended. The examples are taken from European sources but include only part of Europe, and other countries may have dumped munitions similarly. Much of the material may have ended up in shelf regions, other parts of it on continental slopes or on abyssal plains. Although dumping has been regulated under the London Convention since 1975, military forces have generally been exempted under “sovereign immunity” provisions from these regulations. Not much can be found on military dumping in the open literature, since most information is confidential. The Contracting Parties of the London Convention in 1972 agreed to refrain from munition dumping at sea and to use alternative methods, such as controlled incineration in rotary kilns [Working Group on Seabed Activities (SEBA), 1996].

For marine scientists, it is difficult to understand how during the last decades, during which environmental consciousness has been well developed and has continued to grow, any country could have applied for exemption from environmental regulations. However, all international conventions exempt activities related to sovereign immunity, including military aspects, unless Contracting Parties declare otherwise. The London Convention and its 1996 Protocol impose responsibilities on the Governments of member states to ensure consistency with the object and purpose of the convention.

Additionally, it seems that dumping sites have rarely been investigated or monitored. Environmental impacts have never been studied, but it is to be expected that they may be both physical and chemical in nature. Upon the arrival of a munition-loaded ship on the seafloor, a large plume will be created, which will settle down-current from the wreck. The finer particles may drift away, but within a single event high concentrations in the plume may be of restricted duration. Impacts around the wreck may cover several square kilometres, but recolonization should proceed over many years, as was demonstrated by an experiment described below on disturbance and recolonization related to deep-sea mining (see p. 452) (Schriever et al., 1997; Borowski and Thiel, 1998).

No observations have been made on the disintegration of munitions in the deep sea. Whereas some agents of chemical warfare degrade completely in seawater (e.g., phosgene and Clark II[3]), others (such as Clark I, Adamsite and Lewisite) may release poisonous arsenical substances. They may become dissolved and transported by currents, or they may concentrate in current-quiet corners of the wrecks, while the bombs together may develop into a “time bomb” if they corrode and release poisons simultaneously. In deep water the wreck may disturb the community living on and probably around it. Mustard gas may occur in lumps and crusts owing to a thickening substance mixed with it in the bombs. It will kill or severely disturb organisms close by or in contact with this mass. Permanent storage of mustard gas in the deep ocean

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[2] The formal names of these agents of chemical warfare are: mustard gas, bis(2-chlorethyl)-sulfide; phosgene, carbonic dichloride; sarin, methylphosphorofluoric acid, (1-methylethyl)ester; tabun, dimethylphosphoramidocyanidic acid, ethylester.

[3] The formal names of these agents of chemical warfare are: Adamsite, diphenylaminochlorarsine; Clark I, diphenylarsinechloride; Clark II, diphenylarsinecyanide; Lewisite, dichlor-(2-chlorvinyl)-arsine.

should not, however, have any effects on man (Thiel et al., 1998).

No scuttled munition ship seems to have been monitored adequately. Had this been done, knowledge of impacts would not have remained merely hypothetical, and one would have been able to evaluate the effects of disposal of large structures such as are described in the next section. Probably more is known than is officially published; such information should be released and made available for science and the public worldwide.

Offshore installations

Large structures like oil rigs have not been dumped into the deep sea. During the summer of 1995, however, the *Brent Spar* affair taxed the minds of many people in Europe and world wide. The oil companies Shell and Esso intended to decommission the oil storage platform *Brent Spar* by disposal into the deep sea to the northwest of Britain. The "Greenpeace" organization demonstrated against this mode of decommissioning by occupying the platform while it was still in place, and later while it was being towed from the North Sea into the Northeast Atlantic. The oil companies and governmental agencies became aware that the deep sea is not just a remote storage place, and that the public can be mobilized to protect such little-known environments. Finally dumping was abandoned, and large compartments of the storage platform were used for other purposes, such as harbour construction.

Brent Spar was one of the few platforms in the North Sea which stored oil until it was transported ashore. During storage, residues of hydrocarbons and radioactive scale of low specific activity precipitated in the tanks and on the pipe linings. These materials are difficult to clean off. By contrast, all other offshore installations are used for drilling and extracting oil; they do not accumulate much residue and are easy to clean. However, they produce drilling muds which will contaminate the deep sea when oil extraction moves down the continental slope; depths of 3000 m are the target for the near future. Although in shallow waters of the Gulf of Mexico some offshore installations have been dismantled and used to create artificial reefs, in many regions this is not useful, and certainly not in the deep sea. According to recommendations of the International Maritime Organization, most of the platforms are to be totally removed and recycled, or deposited on land. All platforms to be installed from 1998 should be constructed for total removal from the sea. Thus, the number of large structures for which deep-sea disposal may be proposed is small, and should approach zero after one or two decades.

If an oil-storage structure like the *Brent Spar* had been dumped to the west of northern Britain at a depth of a few thousand metres, the impacts would have been similar to that of a sunken ship or a scuttled munition transporter: sediment disturbance around the platform, the development and distant resettlement of a plume, and chemical contamination, which might start immediately through dissolution if the storage tanks broke up on impact with the bottom, or might be delayed if they slowly disintegrated by corrosion. Dissolved substances would be carried downstream, and since the dumping would have been near the edge of the Exclusive Economic Zone, they would certainly not have remained inside this imaginary boundary but would have entered international waters. It is not important in whose Exclusive Economic Zone any material is dumped; the currents will mix it together with contaminants from other sources, and cumulatively over long periods of time effective concentrations may be reached.

There is little that can be done to understand and evaluate potential effects of the dumping of large structures. However, if impacts of similar events like sunken ships or scuttled munition transporters had been investigated, some deductions would have been possible. Since those opportunities have never been used, one must rely on imagination as to what may happen. To discuss the problems and controversial disputes which arose during the *Brent Spar* affair, the British Natural Environment Research Council (NERC) asked an international group of oceanographers and engineers to report on and evaluate the dumping of offshore installations (Natural Environment Research Council, 1996). Their recommendations included the study of impacts from shipwrecks of known sinking dates, from the dumping of radioactive wastes and sewage sludge, or natural events like sediment slides. Broad impact studies of known deep-sea uses and of natural events could have helped in evaluating dumping requests, and should do so in the future. A comprehensive description and evaluation of the *Brent Spar* event have been presented by Rice and Owen (1998). Finally it was decided that much of this storage platform should be recycled for various applications.

Radioactive wastes

Nuclear waste products were deposited in the deep sea of the Northeast Atlantic Ocean between 1949

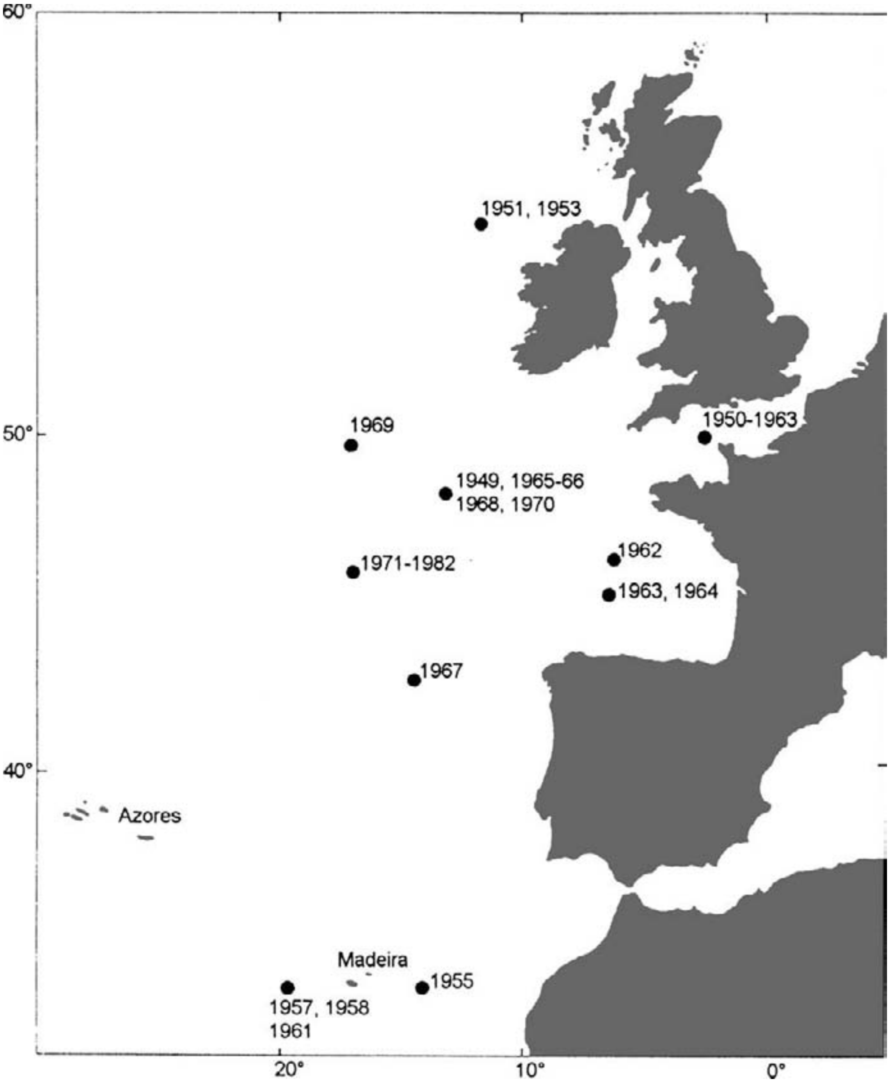

Fig. 13.1. Locations of sites used for disposal of radioactive waste in the Northeast Atlantic Ocean between 1949 and 1982 (from Nuclear Energy Agency, 1985).

and 1982 (Fig. 13.1) by eight European countries (Belgium, France, Germany, Italy, The Netherlands, Sweden, Switzerland and the United Kingdom) (International Atomic Energy Agency, 1991), from 1967 onwards under the supervision of the European Nuclear Energy Agency (ENEA), later the Nuclear Energy Agency (NEA). General overviews have been published by the Nuclear Energy Agency (Nuclear Energy Agency, 1982, 1995a,b) and Saunders (1992). In 1967 the disposal occurred in the northern Iberian Abyssal Plain at a depth of 5300 m. The level bottom of this plain seemed at that time to be suitable under the prevailing conditions of currents, disturbance and mixing. However, it was argued that the site was too close to the Iberian peninsula, and for subsequent disposals other sites were chosen to the northwest in the abyssal hill regions at depths of 4500–5300 m.

Iron drums were used as waste containers (Fig. 13.2). The low-level waste was homogeneously mixed, or packed as larger solid pieces within a matrix of bitumen or concrete. In some cases these drums were placed in a second metal or concrete container. Some of them were fitted with a pressure equalization device (Fig. 13.3a,b). The drums were dumped into the ocean surface, singly or several at a time, and sank to the

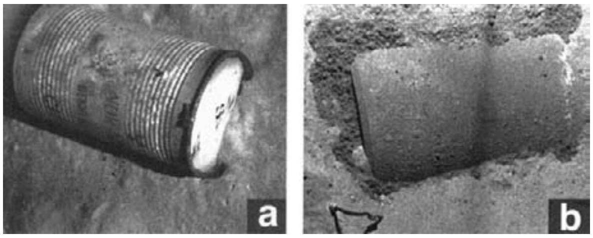

Fig. 13.2. (a) An iron drum about 1 m in length and (b) a concrete container of the same size with radioactive wastes on the seafloor at a depth of 4730 m in the Northeast Atlantic Ocean. Biogenic sediment structures around the upper left corner of the concrete container indicate biological activity close to the waste (Courtesy Dr. Myriam Sibuet, IFREMER, France).

seafloor. Radioactivity was calculated to be low, even if the drums broke open upon their arrival at the seafloor. Except for some seal failure, it was thought that drums would disintegrate as a result of corrosion, and their lifetimes were estimated to range from 15 to 150 years, though concrete caps may last only three years. Waste blocks embedded in concrete or bitumen were assumed to last for 1000 years (Holliday, 1984; Nuclear Energy Agency, 1985).

Between 1949 and 1970 a total of 50 201 metric tonnes (t), equivalent probably to 100 000 drums, were dumped in various deep-sea regions of the Northeast Atlantic (Table 13.1; Fig. 13.1). Between 1971 and 1982, gross mass ranged from 2265 t to 11 693 t per year, in total 64 525 t, and the number of drums amounted to 122 732 (Table 13.1). They were distributed over an area of about 5000 square kilometres in the outer Bay of Biscay, on average 24.5 per square kilometre, although clustering of the barrels can be assumed. No dumping occurred after 1982.

The United States disposed of 34 282 drums into the western Atlantic between 1949 and 1967, most of them in deep water, and between 1946 and 1970 another 56 261 containers were dumped in various places of the Pacific Ocean, mostly into the deep sea of the north-eastern part (Johnson et al., 1984; International Atomic Energy Agency, 1991). The Pacific Ocean received a further 3185 drums between 1954 and 1976 from the countries Japan, South Korea and New Zealand, all close to the countries of origin (International Atomic

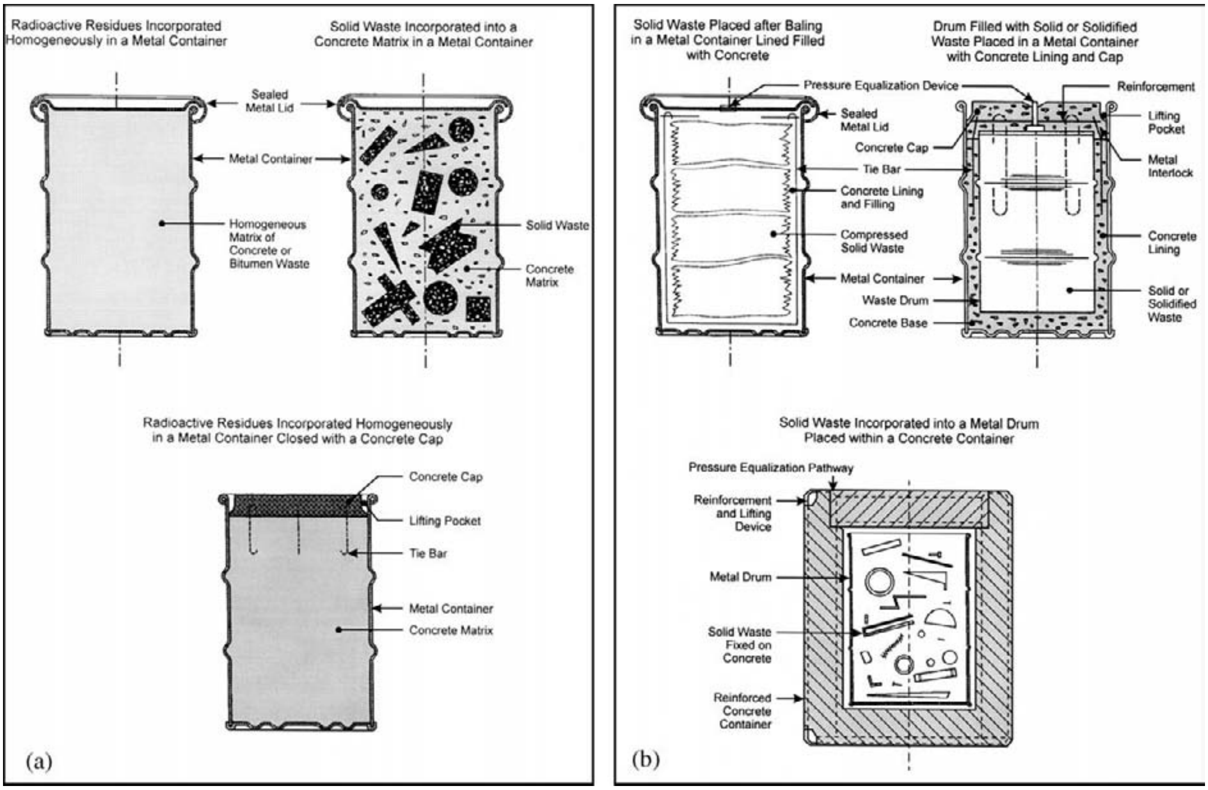

Fig. 13.3. (a) Types of monolithic packages (acceptable under guidelines of the Nuclear Energy Agency for sea dumping packages) (modified from Holliday, 1984). (b) Types of void-containing packages (acceptable under guidelines of the Nuclear Energy Agency for sea dumping packages) (modified from Holliday, 1984).

Table 13.1
Approximate locations and annual quantities of low-level radioactive waste dumped in the Northeast Atlantic Ocean[1]

Year	Lat°N	Long°W	tonnes	Activity type			NEA[2]	Countries[3]
				α	β,γ	tritium		
1949	48°30′	13°00′	9	0.00	0.04	0.00	no	UK
1950	49°50′	02°18′	350	0.07	0.74	0.00	no	UK
1951	49°50′	02°18′	319	0.04	0.67	0.00	no	UK
	55°26′	11°20′	33	0.04	0.19	0.00	no	UK
1952	49°50′	02°18′	534	0.07	1.07	0.00	no	UK
1953	55°08′	12°10′	57	0.07	0.07	0.00	no	UK
	49°50′	02°18′	758	0.37	1.44	0.00	no	UK
1954	49°50′	02°18′	1145	0.85	2.04	0.00	no	UK
1955	49°50′	02°18′	1164	1.30	1.63	0.00	no	UK
	32°37′	14°05′	1453	0.44	1.22	0.00	no	UK
1956	49°50′	02°18′	1038	1.63	1.22	0.00	no	UK
1957	49°00′	02°18′	1537	4.03	5.96	0.00	no	UK
	32°42′	19°30′	4404	35.34	3.26	0.00	no	UK
1958	32°42′	19°30′	2715	25.72	40.15	0.00	no	UK
	49°50′	02°18′	1011	2.15	2.11	0.00	no	UK
1959	49°50′	02°18′	1197	0.15	2.74	0.00	no	UK
1960	49°50′	02°18′	2551	2.74	8.07	0.00	no	B, UK
1961	49°50′	02°18′	1967	0.74	11.40	0.00	no	UK
	32°38′	20°05′	4361	20.38	60.31	0.00	no	UK
1962	46°27′	06°10′	253	0.63	6.03	0.00	no	UK
	49°50′	02°18′	1444	0.19	2.81	0.00	no	B, UK
1963	49°50′	02°18′	1543	0.11	1.63	0.00	no	UK
	45°27′	06°16′	5809	13.65	263.85	0.00	no	B, UK
1964	45°27′	06°36′	4392	16.43	558.33	0.00	no	UK
1965	48°15′	13°15′	1760	4.22	508.90	0.00	no	UK
1966	48°15′	13°15′	1044	2.89	101.45	0.00	no	UK
1967	42°50′	14°30′	10 895	9.36	282.53	0.00	yes	B, D, F, NL, UK
1968	48°20′	13°16′	3164	27.05	2768.97	0.00	no	UK
1969	49°05′	17°05′	9178	17.95	816.44	0.00	yes	B, F, I, NL, S, CH, UK
1970	48°20′	13°16′	1674	8.62	748.29	0.00	no	UK
1971	46°15′	17°25′	3968	23.20	412.48	0.00	yes	B, NL, CH, UK
1972	46°15′	17°25′	4131	25.20	800.16	0.00	yes	B, NL, CH, UK
1973	46°15′	17°25′	4350	27.38	468.42	0.00	yes	B, NL, UK
1974	46°15′	17°25′	2265	15.39	3713.17	0.00	yes	NL, CH, UK
1975	46°15′	17°25′	4454	28.38	2122.84	1098.53	yes	B, NL, CH, UK
1976	46°15′	17°25′	6772	32.49	1980.17	766.01	yes	B, NL, CH, UK
1977	46°00′	16°45′	5605	35.45	2828.69	1179.78	yes	NL, CH, UK
1978	46°00′	16°45′	8046	40.74	2946.24	1354.68	yes	B, NL, CH, UK
1979	46°00′	16°45′	5416	52.32	3077.14	1562.88	yes	B, NL, CH, UK
1980	46°00′	16°45′	8391	68.64	6705.40	3631.00	yes	B, NL, CH, UK
1981	46°00′	16°45′	9434	80.55	5681.94	2751.76	yes	B, NL
1982	46°00′	16°45′	11 693	52.84	4698.56	2865.61	yes	B, NL, CH, UK
Total			142 284	680.21	41 638.73	15 210.26		

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[1] Based on Nuclear Energy Agency (1985). Quantities dumped in 10^{12} Becquerels per year.

[2] NEA, under NEA supervision.

[3] Countries which supplied waste: B, Belgium; CH, Switzerland; F, France; D, Germany; I, Italy; NL, Netherlands; S, Sweden; UK, United Kingdom.

Energy Agency, 1991). Yablokov et al. (1993) reported on the dumping of nuclear wastes by the former Soviet Union, though only a few items were deposited in the deep sea. An overview of nuclear-waste dumping is presented in Fig. 13.4, including the total radioactivity of low-level wastes in each general ocean region.

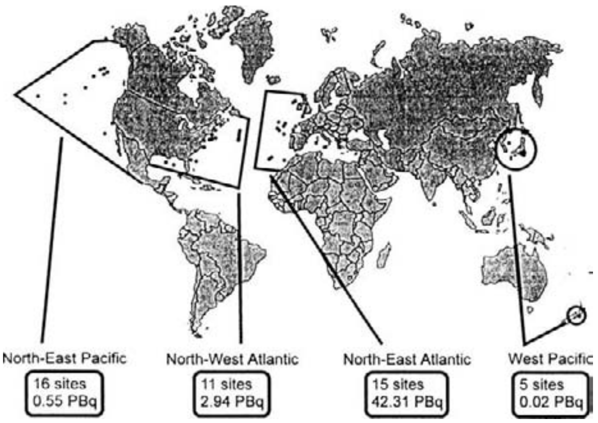

Fig. 13.4. Quantities of low-level radioactive wastes [given in PBq (Peta Becquerel = 10^{15} Bq)] disposed of in the Atlantic and Pacific Oceans (redrawn from International Atomic Energy Agency, 1991).

Based on preliminary regulations, the "Convention on the Prevention of Marine Pollution from Dumping of Wastes and other Matter", the so-called "London Convention" (LC) was adopted in 1972 and entered into force in 1975. Whereas dumping of low- and medium-level radioactive wastes was permitted under certain conditions, a voluntary moratorium on the dumping of low-level wastes at sea was introduced by the Contracting Parties in 1983. Dumping was banned through amendments adopted in 1993, taking effect in February 1995. These amendments also state that the Contracting Parties shall review the dumping of low-level radioactive wastes after 25 years, on the basis of scientific studies.

Various investigations have been carried out in the vicinity of the NEA dumping areas. No specific activity was found which could be traced back to the leaking of the drums. Nies (1988, 1989) investigated the concentrations of the radionuclides Cs-137, Sr-90, tritium and Pu-239/240 in the water column, and concluded that their origin was related to fallout, and Rutgers van der Loeff and Lavaleye (1986) studied the sediments and organisms. Feldt et al. (1985, 1989) analysed plankton and benthos samples. Although they initially assumed that some fauna close to a dump site might have been contaminated from leaking drums, they concluded in 1989 that Cs-137 in Actiniaria resulted from various biogeochemical processes. The Nuclear Energy Agency (1990) did not report any scientific evidence for pollution, and expressed the opinion that the dump site could continue to be used, with dumping rates already considered suitable earlier.

Together with dumping activities, the loss of nuclear-powered submarines must be considered. The *USS Thresher* sank in 1963 at a depth of 2590 m on the slope off Nova Scotia (Sheldon and Michne, 1993a), and the *USS Scorpion* was lost in 1968 southwest of the Azores at a depth of 3050 m, together with two torpedoes with nuclear warheads containing plutonium and uranium (Sheldon and Michne, 1993b). Radiological monitoring was conducted during several cruises around both wrecks following their loss, but no significant effect on the environment was detected.

The same is true for the USSR submarine *Komsomolets,* which sank with two nuclear warheads on the Barents Sea continental slope to the southwest of Bear Island in 1989 at a depth of 1685 m (Vinogradov et al., 1996). Corrosion of cooling systems released some Co-60 and Ni-63 in low concentrations. The total amount of radioactivity was small, and Vinogradov et al. considered that only very limited effects on the environment might result in the future.

Summarizing these data, it becomes evident that in the general dumping areas no increased levels of nuclear radiation have been detected, indicating no or very low leakage from the drums [see also Vartanov and Hollister (1997) and references therein]. However, studies were not conducted in the immediate proximity of the drums and their surroundings, except the photographic survey of Sibuet et al. (1985) and Sibuet and Coic (1989), who took images (Fig. 13.2) from an autonomous underwater vehicle gliding a few metres above the seafloor. No study has been undertaken to investigate the impact on the seabed, and on the community close to or on the drums. Such impacts may be expected to occur in concentric rings around the source, probably somewhat distorted by the direction of prevailing currents. Some of the drums may be leaking (Sibuet et al., 1985; Sibuet and Coic, 1989), and it would be of interest to learn about their effects on sediment and fauna, and whether specific types of drums show a higher leaking rate than others. Inspecting the various NEA dump sites, one would find drums which had been resting on the seafloor for 21–36 years; in the Northeast Atlantic the first drums were disposed of more than 50 years ago. These long-term introductions of hard substrata and obstacles for currents should be viewed as if they were "experimental" environmental changes, and their influence on the physico-biological system should be studied together with the distribution of anthropogenic radionuclides.

Essential for such investigations are close-up observations and narrowly spaced sampling in the vicinity of the sources, and this demands the use of manned submersibles and/or remotely operated vehicles (ROVs). It is important to obtain visual impressions of organism growth on the sunken submersibles and on the drums, and to observe corrosion and its influence on the sediments and animals.

Drums with radioactive wastes, lost nuclear submarines, munition dumping and shipwrecks in the deep sea together offer an arsenal of "experimental" facilities which should be used to answer basic questions on the ecology of the deep sea and to respond to questions on applied problems and societal needs.

All dumping activities included low-level wastes. The disposal of high-level wastes was discussed by various committees but abandoned. However, the option of burial below the seafloor may be reconsidered one day, and would need further research for environmental evaluation (Hollister and Nadis, 1998).

Sewage sludge and dredge spoil

As an example of deep-ocean dumping of sewage sludge, one may cite a case from the Northwest Atlantic. The Deepwater (Municipal) Dump site 106 (DWD 106) was established in 1986, some 106 nautical miles off the coasts of New York and New Jersey, at about 39°49′N, 72°08′W and 2500 m depth. This site received approximately 36 million tonnes of wet sewage sludge between March 1986 and July 1992 (Fry and Butman, 1991).

An interdisciplinary team of investigators studied the impact of DWD 106 while it was in use. Numerical models had predicted the area over which sludge would settle; and it was found that the material reached the seafloor in significant amounts somewhat west of the dump site. Clear faunal changes and higher concentrations of contaminants were discovered. The indicators used for the detection of sewage sludge were silver, originating from the photographic and electronic industries, linear alkylbenzenes, derived from wetting agents in detergents, the sterol coprostanol and spores from *Clostridium perfringens* originating from faecal material of mammals [see Bothner et al. (1994) and references therein].

As part of these studies, Van Dover et al. (1992) reported different ratios of stable-isotopes in the tissue of sea urchins and other large species after feeding on sludge material, and Grassle (1991) found numerical increases in several species of macrofauna in the zone impacted by sewage sludge, compared to more distant reference areas.

These impact studies aroused environmental concerns, and led to a reduction in dumping rate at DWD 106 from 1991; by late summer of 1992 measurable improvements of the environmental conditions had resulted. However, 50 nautical miles downstream pollutant indicators had increased.

Sewage sludge changes the seafloor community and may destroy it totally in areas of settlement. Examples from shallow waters have been given by Pearson et al. (1986) and Rees et al. (1992). This waste material derived from water purification plants and its composition depends on input materials and treatment. Basically it contains domestic discharges; but many drainage systems also receive rain water and the run-off from roads, enriched with hydrocarbons. Industrial waste water may add toxic substances like heavy metals, and anthropogenic contaminants like persistent organochloric materials (e.g., PCBs). Whereas coarser materials, organic matter and nutrient salts may be separated from the sludge in the purification plants, the content of organic matter remains high at about 5%, and contaminants cannot be separated before permanent storage. The thirteen European countries which are Contracting Parties to the Oslo Convention will produce nearly 10 million tonnes of dry sludge per year when the secondary-treatment step (to diminish the organic matter) is introduced in all plants. Many of them have already added the third step (to reduce plant nutrients).

The main components of a typical sludge are:

- inert materials predominantly consisting of extremely fine particles of silica, most of which are <100 μm in diameter; they tend to flocculate in seawater;
- reactive organic materials, which are predominantly cellulose fibres, higher fatty acids and oils;
- organic nitrogen compounds ranging from 6–10% and creating a chemical oxygen demand of 2000 ml O_2 g^{-1};
- persistent organic materials, such as polychlorinated biphenyls (PCBs);
- inorganic solutes, for example the liquid component contains about 1000 ppm of ammonia;

- bacteria dominated by methanogenic species, which continue to ferment the sludge, coliform bacteria and human pathogens;
- industrial contaminants, including heavy metals and hydrocarbons.

Dredge spoils may largely contain the same classes of anthropogenic contaminants as sludges: hydrocarbons, heavy metals and synthetic organic substances. However their origin is different. They are dredged from river, channel and harbour systems to keep the waterways open or deepen them for ship traffic. Uncontaminated dredge spoil may be used for building material, land reclamation or road construction, since particles of sand and gravel size may be abundant (GESAMP, 1990; OSPARCOM (Oslo/Paris Commission), 1993). Whereas contaminants may be higher in dredge spoil than in sewage sludge, the opposite is found for the content of organic matter.

Contaminated dredge spoils, specifically the fine-particulate-mud component, leaves the same problems for permanent storage as sewage sludge. Repositories on land are rare, dumping in coastal areas may contaminate shallow-water ecosystems, and in most countries this type of disposal is banned through national or international regulations. Although contaminants and pathogens may be returned to inshore waters and threaten the local human population (Collins et al., 1980), dumping of dredge spoils in shallow waters still occurs and may continue to be permitted (McIntyre, 1995). Certainly, the most important reaction of society would be the avoidance of sewage production and river pollution. Progress of waste-water treatment at industrial plants has led to reductions in the emission of contaminants. But deep-sea ecologists should be prepared to conduct environmental impact assessments comparing terrestrial and deep-sea disposal. Such evaluation may suggest that deep-sea disposal would be less of a threat both to human societies and to already impacted terrestrial communities (see also Valent and Young, eds, 1997; Young and Richardson, 1998).

The more knowledge deep-sea ecologists can accumulate, the more valuable will be their arguments in the decision process. Essential prerequisites for impact evaluations are acquaintance with disposal techniques, the composition of wastes, and the reactions of ecosystems and natural communities to the disposal. For all considerations it is of paramount importance to remember that the dumping of sewage sludge and dredge spoil are large-scale intrusions into the deep sea. The amount to be disposed of into an abyssal dump site may need to reach some 10^6 m^3 per year to ensure that the process is economically feasible. Since the general problems of disposal techniques and the environmental research requirements are similar, sewage sludge and dredge spoil are not further distinguished in this article and they are both referred to as mud or waste.

Basically, two types of techniques are considered, differing in their mode of waste delivery to the seafloor: uncontained discharge or contained dumping. Uncontained waste might be released at the ocean surface, as it was at DWD 106. Because of its low water content and high compactness it may sink as one large parcel, with more or less turbulent mixing and plume creation, and particulate transport by currents. Since great depth is preferable, the water column may be impacted over depths from 4000 m to 5000 m. For this reason, a riser technique would be preferable – carrying the muds in a pipe system down to about 100 m above the seafloor, where the material would be released for settlement. Such a riser system may be shipborne and deployed at the disposal site, or it may be an anchored floating system, at which the transport ships would dock to pump the mud down into the abyss (Fig. 13.5). On release from the pipe the slurry would spread out over the seafloor, and some light materials would drift for some distance with the current. The riser technique would avoid any contamination of the water column except in its deepest part.

Even better isolation from the environment would result from the disposal of muds contained in strong flexible plastic bags (De Bruin and Loos, 1995) with a capacity of 350 m^3. Properly sealed, these parcels would be released from the transport ship to sink to the seafloor as single units (Fig. 13.6), or they would be dropped close to the seafloor from some sort of autonomous underwater vehicle (AUV) (Fig. 13.7). Several of them could be carried to the dump site loaded on a transporter. Liberated from the mother ship, the AUVs would approach the seafloor, dump the bags, probably above a field marked by transponders, and return to the surface for recovery by the carrier (Valent and Young, 1995). If the bags were stable, the waste material would remain contained, if the synthetic geotextile is degradable, the waste material would be released after a longer or shorter lag time.

The results obtained by monitoring pollution indication at and around DWD 106 cannot be applied fully to an abyssal dump site, since the former is at about half the depth and governed by a more dynamic regime. However, several detrimental effects can be predicted,

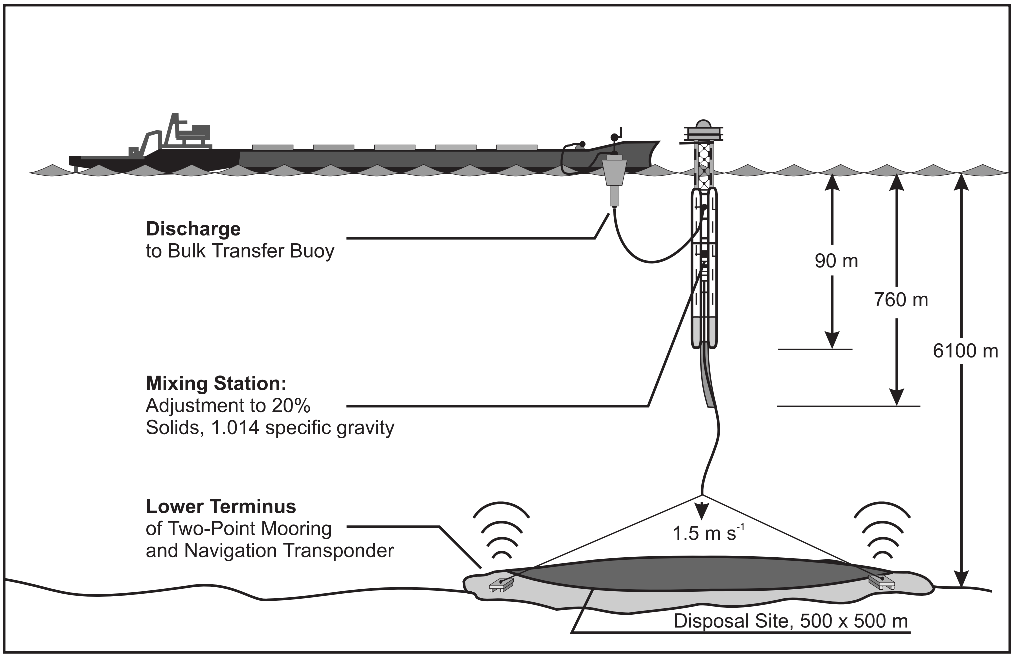

Fig. 13.5. The floating riser concept for sewage sludge and dredge spoil disposal (modified from Valent and Young, 1995).

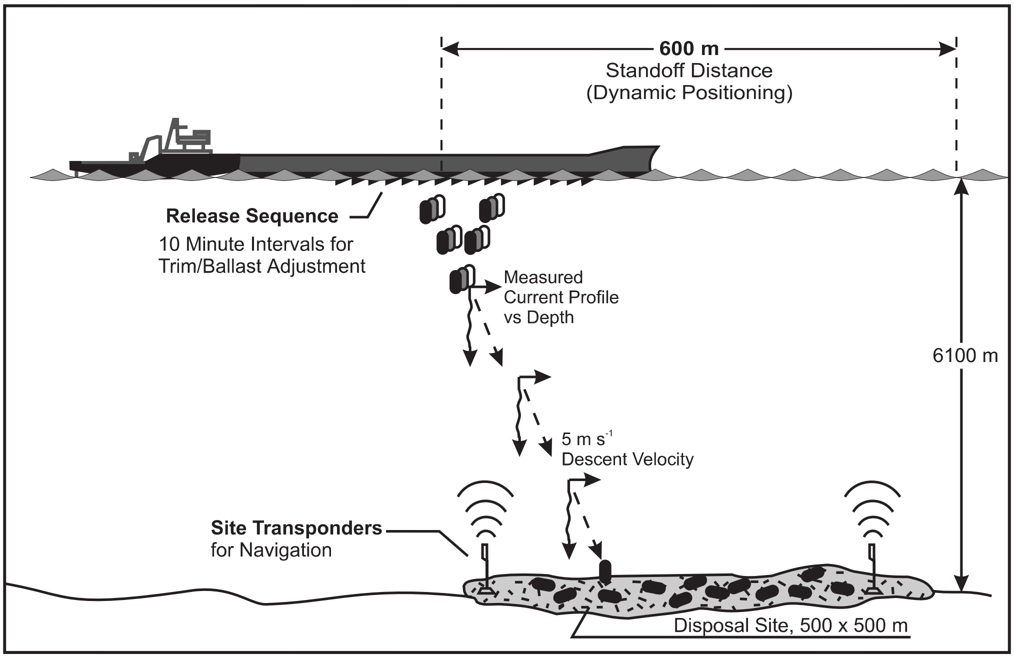

Fig. 13.6. Surface emplacement concept for contained sewage sludge and dredge spoil disposal (modified from Valent and Young, 1995).

particularly when the waste is dumped uncontained. The immediate effect would be the burial of the dump site, killing all epifauna and infauna except where the mud layer is less than a few millimetres thick, although even in this outer zone the sediment surface, containing the main food source, will be disturbed. At the same time plankton and benthos in the near-field of the dump may be affected through the particulate matter in the

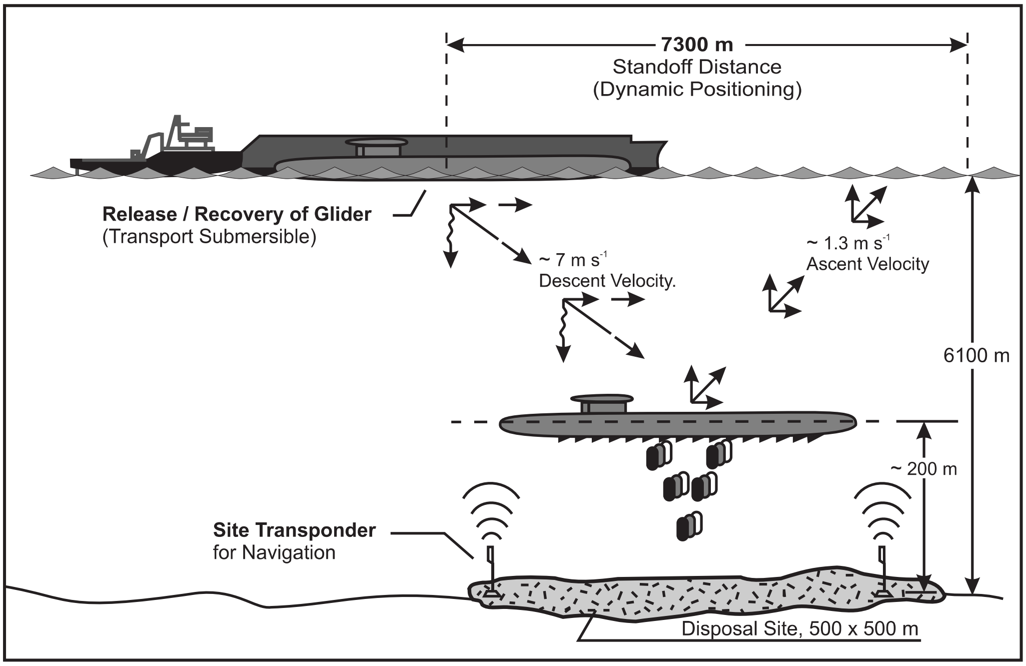

Fig. 13.7. The ROV (Remotely Operated Vehicle) concept for disposal of contained sewage sludge and dredge spoil (modified from Valent and Young, 1995).

plume clogging their gills and feeding mechanisms. Deep-sea bacteria may adjust to the introduced, rather refractory, matter. Although slow, its degradation may lead to reduced oxygen concentrations (e.g., Goldberg, 1995). Since deeper mud layers may not receive any oxygen supply, the organic matter may be attacked by sulphur bacteria and methanobacteria. The mud may be colonized by meiofauna and macrofauna, but the community composition is likely to be different from that of the abyssal plains. Opportunistic species will occur first, but it is difficult to predict the course of short-term or long-term community developments since little is known about the life histories and adaptational abilities of the species. A gradient in colonization from the periphery to the centre may develop, and a reverse gradient may build up for species numbers and diversity. Together with these changes, food-web relationships will be altered, and this will extend to the bentho-pelagic assemblage. Toxicity effects may be deduced from shallow-water studies. Recruitment stages are particularly susceptible to toxic substances, and this may limit the number of species living around and on the dumped material. Persistent organic compounds (e.g., organochlorines, PCBs) and some metals, (e.g., mercury, lead) may be stored in body tissues. Along food chains these substances may be accumulated, though the effects of most of the many thousands of chemicals known to be released to the environment have not been studied (Miller et al., 1987; Phillips and Rainbow, 1990).

A large body of information exists on the effects of the dumping of sludge and spoil on shallow-water species and on community structure (see McIntyre, 1995). Although basically the same general modifications can be expected, it is not possible to make firm predictions on the reactions of deep-sea species and communities. Species adaptations and tolerances are different, and under deep-sea conditions all processes are retarded. This illustrates the lack of knowledge available for environmental impact assessments. Laboratory experiments with deep-sea organisms are possible only with bacteria, and probably with flagellates or other protozoans, captured and cultured for bioassays under constant high pressure and low temperature.

There is only one approach for precautionary studies: the large-scale experiment. This category of deep-sea research was first developed for the evaluation of environmental disturbances through the mining of polymetallic nodules (see p. 452), but the methods developed may also be suitable for waste disposal, and required when no other techniques are available. Only *in situ* experimentation with waste material will allow the impacts to be predicted confidently, and such experiments must be conducted on a scale from which the results can be extrapolated to full-scale disposal actions. For mud dumping a set of integrated disposal experiments of increasing size has been proposed (Thiel et al., 1998). A large amount of mud, still small compared with an economically viable operation, should be deposited at a suitable site, already well studied in a baseline survey. Apart from topographical, biological and sedimentological descriptions, the current system must be analysed for at least one year, including measurements close to the seafloor and records of possible resuspension of sediment. After dumping, careful monitoring of the effects on the environment should include visual controls using a submersible or at least a remotely operated vehicle. If this step and its extrapolation to larger scales seem to be acceptable, a test disposal probably ten times larger should be arranged for, followed by an even larger one. Assuming an expected disposal of $10^6\,m^3$ per year, the experimental design for the steps could cover $10^5\,m^3$, $10^6\,m^3$ and in the pilot disposal operation (PDO) $10^6\,m^3$ for ten subsequent years. Careful monitoring of all effects must be conducted between the steps, with high technical and personal dedication. For financial reasons, such a test could be conducted only in cooperation with an industrial enterprise, and this would demand exact planning and implementation, with carefully chosen time schedules for the disposal and monitoring periods.

Carbon dioxide

One of the options to reduce atmospheric carbon dioxide (CO_2) is its storage in the deep sea (Ormerod and Angel, 1996). Carbon dioxide is well known as a "greenhouse gas" produced by society in excess of natural equilibrium. The content of carbon dioxide in the atmosphere has increased by about 50% during the last 200 years. Although technical and political efforts are being made to mitigate the emission of carbon dioxide, industrialization of "third-world" countries and increases in world population will probably cause the atmospheric concentration to double during the next century. All effective methods must therefore be mobilized against this development and related anthropogenic climate changes. Reductions of carbon dioxide production are still more than counterbalanced by enhanced energy consumption for the purpose of increasing food production (Pimentel et al., 1994). In order to increase agricultural areas deforestation will be called for, thus reducing the terrestrial uptake of carbon dioxide and, consequently increasing the atmospheric carbon dioxide (Keller et al., 1996). More energy will be demanded by expanding industry. Power-plants burning pulverized coal produce 23 kg of carbon dioxide per second to generate 100 megawatts; this output of carbon dioxide is equivalent to 7×10^5 tonnes of carbon per year. It is generally accepted that the increase in atmospheric carbon dioxide will cause a change in global radiation balance, even if some doubt is expressed about its influence on climate development. It may be difficult to counterbalance this change in radiation, but its global environmental and socio-economic implications may be so destructive that all possible measures must be taken to limit it. The situation is serious and requires urgent discussions and precautionary research on the various options to mitigate increase in atmospheric carbon dioxide and its potential impacts on the global ecosystem.

Whereas the avoidance of production of carbon dioxide and its release into the atmosphere should have priority in all developments, the gas may be discharged into geological formations deep below the seafloor, including saline aquifers, coal beds that cannot be mined, depleted oil and gas reservoirs, rock caverns, and mined salt domes in many localities of the world (Herzog et al., 2000). This is already happening, for instance, in the Sleipner oil and gas field 240 km off the Norwegian coast. In other situations sequestration in the deep ocean may be the best practical option. Certainly this would short-cut the natural passage of carbon dioxide from the atmosphere and the ocean surface into the deep sea by physical and biological processes, and later back to the surface, which may take many hundreds to thousands of years. Carbon dioxide pumped into the deep ocean may return to the surface and the atmosphere after 500 years; but this would be a long delay, and by that time one may hope that succeeding human generations will have found ways to reduce carbon dioxide emission greatly, or to dispose of it in other ways. There is little time left either for the present or for future generations.

Several options exist for the disposal of carbon dioxide into the oceans (Ohsumi, 1996). They are related to the thermophysical phases of this compound (Uchida et al., 1995), depending on temperature and on pressure, given as water depth:

- gaseous: surface – ~500 m;
- liquid: >~500 m, >11ºC;
- solid and gaseous: ~130–~350 m, <11ºC;

– solid and liquid: >~400 m, <11ºC.

The solid/liquid state occurs in the form of hydrates or clathrates, a crystallization of carbon dioxide and water where they have a common interface. At >600 m and deep-sea temperatures of 2–3ºC the carbon dioxide freezes to the solid form. Another important factor is the density of liquid carbon dioxide, which is higher than that of the ambient water at depths greater than 3700 m.

Ocean storage would use the liquid or the solid/liquid phase of the waste, through dispersion and dissolution in the bathyal or abyssal deep water column or on the abyssal sea floor as a liquid lake or in the solid form ("dry ice"). The time delay for the return of this carbon dioxide to the ocean surface and the atmosphere depends on the oceanographic conditions of the region and on the depth of disposal. Liquid and solid carbon dioxide will dissolve in the water mass, and the question of how long the isolation will be effective depends on the rate of dissolution. The disposal of carbon dioxide in liquid or solid form would therefore be equivalent to "delayed dissolution".

The discharge of liquid carbon dioxide could be achieved by a riser similar to those described for the delivery of muds to the seafloor (Adams et al., 1995; Kajishima et al., 1995), or by suspending a towed pipe and spraying mechanism for a wider distribution of droplets in the water column to aid dissolution. Solid carbon dioxide could be dropped in streamlined "dry ice" missiles, but during their descent much of the carbon dioxide might dissolve in the water column. This mode of disposal is unlikely to be employed, however, since the freezing process consumes a great deal of energy, and thus would lead to the generation of more greenhouse gas.

Carbon dioxide in the ocean is finely balanced with the carbonate system, and its introduction into the water column or onto the seafloor would lower the pH. Whereas production processes in the ocean surface are responsible for a certain variability of pH, with a seasonal amplitude of about 0.1 pH unit, the level in the deep sea is very stable and organisms are likely to be sensitive to minor changes. Ocean values of pH generally range between 7.7 and 8.2 (Brewer et al., 1995). A decrease would be detrimental to organisms, and below pH 6.5 organisms would be killed (Magnesen and Wahl, 1993; Pörtner and Reipschläger, 1996; Stenevik and Giske, 1997; Omori et al., 1998). Sublethal effects of a decrease in pH would be associated with the exchange and transport of respiratory gases, and would lead to modifications in community structure and ecological processes.

Creating a lake of carbon dioxide in a depression of the deep seafloor would certainly destroy all benthic life. Benthopelagic species would be impacted during the disposal, but there would be an additional long-term effect, since migratory species on their path to the seafloor might penetrate into the dissolution zone above the lake, or the lake itself, and would be trapped, unless they have the ability to swim up again and escape into the non-impacted neighbourhood. The dissolution of carbonates through the introduction of carbon dioxide would probably reduce the amount of carbon dioxide, but this would have little overall effect.

A similar fate for organisms can be expected if liquid carbon dioxide is allowed to flow down any slope into deeper regions; organisms would be killed, and carbonate components of the sediment might be dissolved along the track, eroding a channel into the seafloor. This could even lead to the destabilization of the slope sediments.

Liquid carbon dioxide released into the water column from a ship in passage would initially create a plume with a dissolution zone extending over a few hundred metres vertically and a few tens of metres horizontally at the current speed of $10\,\mathrm{cm\,s^{-1}}$ typically measured at great depths. A pH reduction of 2–3 may occur in the core of the plume, and again this may be lethal or sublethal for organisms. Mobile species may be able to escape such an impact on the water body. Dissolution away from the plume would gradually reduce the change in pH to tolerable levels.

As in the case of benthopelagic species, migration of plankton must also be considered. Vertical diel migration is intensive down to a depth of 1000 m, but in decapod Crustacea extends to 1200 m, and in lantern fish even to 1500 m. Seasonal and ontogenetic migrations may penetrate even greater depths, and it must be assumed that a layer of lowered pH might greatly disturb migrators of all age classes.

Carbon dioxide has been rarely considered as an ecological variable, and relatively little is known about the effects on organisms of higher concentrations of this gas in the natural environment (Pörtner and Reipschläger, 1996). Experimental research on different scales could be conceived, in order to learn about the effects of potential changes in the ocean system. Small-scale investigations may be conducted in the laboratory to test the reaction of single species in aquaria or communities in mesocosms. However, it may be difficult to extrapolate the results to natural systems, and large-scale experiments therefore seem to be unavoidable (Drange et al., 2002). These could be executed in well-defined more or less landlocked deep basins, such as a fjord, or in open ocean waters. A confined-basin experiment would allow the study of the reactions of the organisms and the system, and their restoration after natural flushing from the ocean. It would also help in the design of an open-ocean experiment, unless it demonstrates that the disposal of carbon dioxide into the ocean is unacceptable.

A few *in situ* experiments have been conducted recently, employing submersibles and remotely operated vehicles (Brewer et al., 1999; Tamburri et al., 2000). Unexpectedly, it was observed that animals on the seafloor may not necessarily avoid low pH and high concentrations of carbon dioxide, but actively move upstream, particularly when the current carries the odour of potential food (e.g., bait). Further tests are essential to understand the impact of carbon dioxide on life in the ocean.

Laying of submarine cables

Submarine communication cables have criss-crossed the oceans for almost 150 years, and their laying on or in the deep seafloor impacts the sediment surface, and life there. The cable may come to rest on hard bottom, may sink into soft ooze, or may be ploughed into deeper sediment layers. The local impact remains limited, and even the ploughing effects of sediment turnover and blanketing affects a path no more than a few metres wide. Animals from the neighbouring vast stretches of the abyssal plains and hills colonize the disturbed tracks relatively quickly, and sedentary species may settle on the cable mantle, using it as hard substrate (see p. 453). In fact, one of the early observations and proof for the existence of life in the deep sea was based on deep-water corals collected from a cable retrieved in 1860 from a depth below 2000 m in the Mediterranean Sea between Sicily and Africa (e.g., Menzies et al., 1973).

EXPLOITATION OF RESOURCES

The deep sea harbours living and non-living resources. The technology for their exploitation either is already available or is being developed. The use of living resources began some 20 years ago, but recent economic developments suggest that non-living resources could not be mined profitably for at least another 20 years. Oceanographers have assumed the obligations of environmental impact assessment for these existing and potential activities, and they need to channel their concerns into the industrial, administrative and political discussions.

Seafloor mineral resources and mining

In February 1873 the British HMS *Challenger* dredged the first manganese nodules (known also as ferromanganese or polymetallic nodules) in the Atlantic Ocean (Figs. 13.8, 13.9) (Murray and Renard, 1891). About 90 years later these nodules advanced from being an unutilized ore to become a resource for precious metals (Mero, 1965), and after 100 years they developed into tough units to be cracked during the negotiations from 1973 to 1982 for the new Law of the Seas, and until it entered into force in 1994 (see pp. 458–459).

Fig. 13.8. Manganese nodule field and coryphaenoid fish.

Fig. 13.9. Manganese nodules in the sediment surface of a box-corer sample.

During recent decades other potential resources have been discovered in the deep sea; some of them were found much earlier. Manganese crusts were also collected during the *Challenger* expedition from the top of seamounts (Murray and Renard, 1891; Hein et al., 1986), and phosphoritic nodules were dredged from the

Table 13.2
Characteristics of polymetallic nodules and crusts

Characteristic	Term	
	Polymetallic, ferromanganese or manganese nodules	Polymetallic, ferromanganese, manganese or cobalt-rich crusts
Form	Spheroidal, ellipsoidal, discoidal or asymmetrical; diameter up to 25 cm	Crusts up to 15 cm thick (rarely 20–40 cm)
Surface	Smooth or granular, botryoidal	Smooth to rough, knobbed, botryoidal
Growth rate	Few millimetres per million years, max. 18 mm	Few millimetres per million years
Accretion process	Hydrogenetic (in water), diagenetic (in sediment)	Hydrogenetic
Distribution	All oceans	All oceans
Habitat	(a) Sediment of abyssal plains and hills; (b) top and flanks of sea-mounts	Rock outcrops on slopes, and tops of seamounts
Depths (m), predominantly	(a) 4000–6000 (b) 1000–4000	Few hundred to 2000 m
Deposit	Two-dimensional, single units in sediment surface	Two-dimensional, continuous crust
Coverage	Up to 90% of sediment surface	100%
Abundance	Up to 60 kg m^{-2}	
Minimum mining	5000 metric tonnes per day	Same?
Valuable metals	Co, Cu, Mn, Ni	Co, Cu, Ni, Mn, Zn
Minor components	Ag, Au, Mb, Pt, Ti, Zn	Mo, Pt, V
Mining intensity	1 km^2 per day, 300 km^2 per year	Less?

South African continental shelf in 1874 (Murray and Renard, 1891). Polymetallic sulphides were discovered later; metalliferous muds were collected from the Atlantis II Deep in the central Red Sea during the International Indian Ocean Expedition (1959–1965) (Swallow and Crease, 1965; Miller et al., 1966; Degens and Ross, 1969; Schoell and Hartmann, 1978). In conjunction with the discoveries of seafloor spreading, consolidated massive sulphide deposits were found near the centres of crust genesis and hydrothermal vents (Francheteau et al., 1979; Hekinian et al., 1980; MacDonald et al., 1980; Spiess et al., 1980; Edmond, 1984; Lonsdale, 1984).

Some of these ores were already known on land, and mined to some extent. In 1861 Gümbel had collected manganese nodules in the Alps (Jenkyns, 1977); massive sulphides are well-known and mined from Cyprus (Scott, 1983; Oudin and Constantinou, 1984), in Canada (Malahoff, 1982), Oman and Japan (Ballard, 1984) and in Russia (Kusnetzov et al., 1993). Their marine origin was suggested by the presence of fossil vent animals, but a true understanding developed only after the discovery of active hydrothermal vents in the deep sea (Kusnetzov and Maslennikov, 2000).

Although five different ore types have been described from the deep sea, they have much in common and, in respect of aspects of mining, potential environmental impact, environmental risk assessment, and the need for precautionary research will be dealt with together.

Polymetallic nodules and crusts

These ores are so similar in their material accretion and their metal components that they can be considered as the same ore type precipitated under different conditions. Both show great variability. Their characteristics are summarized in Table 13.2. Important factors for economic mining are coverage, abundance, and the content of valuable metals (Lonsdale et al., 1982; Claque et al., 1984; Commeau et al., 1984; Halbach and Manheim, 1984; Halbach et al., 1988, 1989a). From the environmental point of view the seafloor area and the water-column volume impacted are important (see below, pp. 450–452).

Metalliferous muds and consolidated massive sulphide

These types of ore constitute another twin pair as they are of rather similar origin, but differ in consolidation. Together they may be termed “polymetallic sulphides”. Their metal source is the earth’s crust from which heated water, penetrating through fissures and cracks in the rock, leaches various metal components.

In the hydrothermal process the water is recirculated to and expelled through vents into the ocean water mass, where, close to the seafloor, the metals precipitate with other components as mud. Their content of metals depends on the leached rocks and the temperature. If precipitation occurs in a trough, as in the central graben of the Red Sea (Degens and Ross, 1969; Amann et al., 1973; Bignell, 1978; Bäcker, 1980; Rona, 1985), the ore is a watery mud, somewhat drier and stiffer in the deeper layers. When hydrothermal activity ceases, the mud may be covered with other sediment layers; if then it comes under pressure through tectonic shifts, rock-forming processes convert the metalliferous mud into consolidated massive sulphides. Direct precipitation of hard material also occurs at vents, in the formation of black and white smoker chimneys (Rona, 1982, 1985; Scott, 1992).

Thus, polymetallic sulphides are related to the processes at hydrothermal vents. Polymetallic sulphide deposits have been discovered in active formation at various localities around spreading centres (Hekinian et al., 1983; Halbach et al., 1989b), but very little is known about their resource possibilities that is, their ore mass and their metal content. Scott (1992) listed a few sites on the mid-Atlantic Ridge estimated to amount to 5 million tonnes of sulphides. The Ocean Drilling Programme discovered a sulphide source 94 m thick (Duckworth et al., 1994), but its horizontal extent was not investigated. The only ore of this type which has known resource potential is the metalliferous mud in the Atlantis II Deep in the central Red Sea. This deep is one of about a dozen located in the narrow central graben system. Below a hot brine pool [some 20 years ago, the water layer was about 200 m thick, with a temperature of 64ºC, and salinity about 320 (Karbe, 1987)], the "sediment" starts at a depth of about 2200 m. However, because the brine prevents the particles sinking and consolidating, there is no clearly demarcated seafloor (a multiple corer never collected any sort of boundary layer, but always penetrated totally into the fluid mud). The Atlantis II Deep covers an area of 60 km^2 and the ore has an average depth of 11 m (Karbe, 1987). The deeper sediments have strongly coloured layers reflecting varying ore composition. Mining at a rate of 100 000 metric tonnes of mud per day would yield 2×10^6 tonnes of Zn, 0.4×10^6 t Cu, 5.7×10^3 t Co, 3.6×10^3 t Ag and 47 t Au (Guney et al., 1984). The Atlantis II Deep resource could support at least a 16-years' mining operation (Mustafa et al., 1984).

Phosphorites

For completeness one must list phosphoritic deposits, although many land resources exist; most marine phosphorites occur on continental shelves, but other deposits have been found on the upper reaches of the deep sea, on continental slopes and seamounts [see Burnett et al. (1987) for a review].

Phosphorites occur as nodules, grains, conglomerates and crusts. They penetrate several decimetres into the sediment, so that the deposit must be classified as three-dimensional. They develop by authigenic precipitation or by the replacement of carbonates, mainly carbonate-fluoroapatite or francolite. The phosphoritic material is typically associated with terrigenous, calcareous or siliceous sediments.

Most phosphoric deposits are relicts of former ages; active deposition is occurring only off Peru and Chile, off Namibia, off Baja California, and off eastern Australia. Many of the deposits seem to be related to intensive coastal upwelling with high production levels, as is the case for the first three modern deposits; however, the region off eastern Australia does not fall into this category [see Thiel et al. (1998) for more details and references].

Mining techniques

Deep-sea mining has been considered only for polymetallic nodules and metalliferous muds, and therefore techniques have been developed and tested only for these two resources. However, the basic designs with some modifications should be applicable also for the other resource types.

The mining systems include the functions of ore collection and transport to the ocean surface. The simplest procedure would be the adaptation of bottom trawling as used in fisheries by the application of rather sturdy trawls to lift 120 tonnes of nodules per haul. This is the latest proposal for application in the Cook Island region (Bechtel Corporation, 1996); however, it is difficult to imagine how such a mass of nodules should enter and fill the trawl. The continuous-line bucket system proposed by Masuda et al. (1971) applies the principle of a bucket dredger. The single buckets are attached to an endless wire, leaving the ship at the bow and returning to the stern, scraping up nodules where the wire loop touches the seafloor. This system has been tested with some success, but appeared insufficiently controllable under sea conditions. The down-going and the up-coming legs of the wire entangled and the exploitation was inefficient. However, the system is thought to be applicable for crust mining (Masuda, 1991), although the crusts need to be broken away from the rock beneath and must be available in small fragments. But the simplicity of the system may not outweigh the shortcomings.

More promising techniques have separated the functions of ore collection and transport to the surface. For nodule mining the proposed collector systems consist of a towed or self-propelled vehicle, carrying a collector at its leading edge. This may employ mechanical screening, bucket or scraper methods or hydraulic principles to lift the nodules from the seafloor; probably both may be combined in one hybrid system (Fig. 13.10) (Burns and Suh, 1979; Bath, 1989; Amann, 1990; Oyama and Ushijima, 1990). Whereas most of the mud would be rejected from the collector system close to the seafloor, the nodules would be transported through a pipe by pumping or an airlift system (Fig. 13.11). This would force air into the pipe string at a depth from 1000 m to 2000 m. The rising and expanding air bubbles would lift the water–nodule mixture in the pipe and expel the nodules onto the mining ship, from where they would be pumped through another pipe to the transport ship (Clauss, 1978; Engelmann, 1978; Bernard et al., 1987). The water from the deep sea, together with sediment sticking on the nodules, and nodule fines scraped from their surfaces during the transport through the pipe several kilometres long, would need to be discharged into the ocean. To be economic, 5000 metric tonnes of nodules would need to be mined per day by each single mining unit. A first succesful mining test was conducted in 1970 (Geminder and Lecourt, 1972) on the Blake Plateau in a depth of 762 m. Several collector systems, hydraulic pumping and airlift methods, have been tested during a pre-pilot mining test (PPMT) at a depth of over 5000 m in the Pacific Ocean (Fellerer, 1980). Another study proposed the use of autonomous robot submersible shuttles (Moreau, 1984; Marchal, 1984), gliding down to the seafloor and returning to the mining ship filled with nodules collected during active movements along the seafloor.

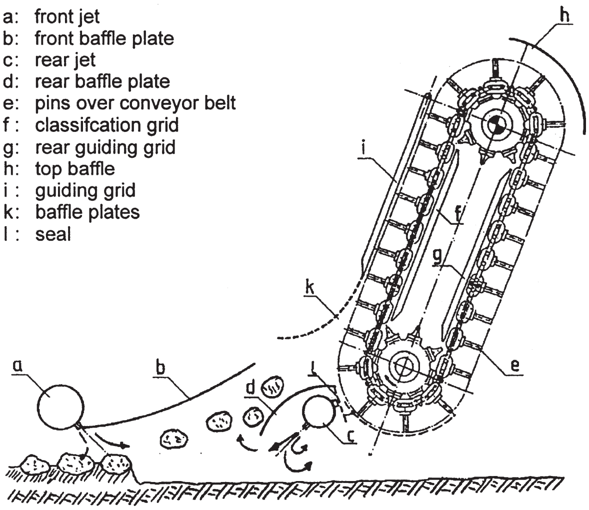

Fig. 13.10. Nodule collection with the help of water jets (modified from Oebius, 1997).

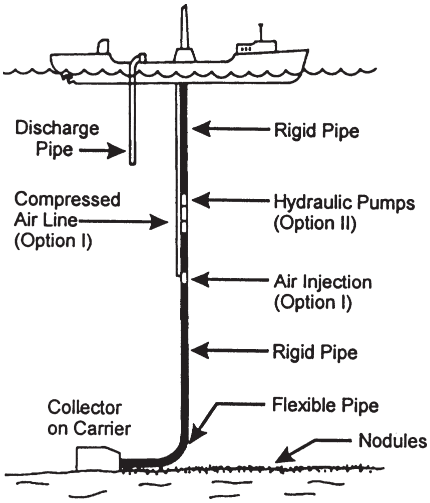

Fig. 13.11. Mining system in general outline, indicating the air-lift system (option 1) and the pump system (option 2). The carrier with the collector is towed along the seafloor.

For the mining of metalliferous muds a different collection head is required at the end of the pipe. A conical vibration system was developed which, together with water pumped into the mining pit, fluidized the consolidated mud before it was pumped to the mining ship. The economic mining rate is 100 000 metric tonnes of mud per day (Mustafa and Amann, 1980; Mustafa et al., 1984; Nawab, 1984; Amann, 1985), although this value may change with further development of the mining techniques.

Not much thought has been given to mining the other potential resources, but it is likely that technological developments after a few more decades will have produced new ideas. Phosphorite deposits may be too deep to apply shallow-water mining techniques. Gold mining was conducted off Alaska with a bucket-ladder dredge. Although the ladder was 88 m long, it could only work down to a water depth of 40 m, and the cut into the sediment was limited to 10 m (Garnett and

Ellis, 1995; Garnett, 1996). Where seafloor excavation is required for the mining of diamonds, two methods are employed. The drill system consists of a disc-like cutting wheel with hardened steel scrapers. The seabed crawler, carrying suction boxes at its front, is tracked along the seafloor, while water jets agitate loose sandbars and obstructing boulders. Both techniques are employed down to a water depth of 200 m, and their use may be extended to 1000 m. They can penetrate 5 m into the sediment. Airlift systems transport the sediment to the mining ship (Garnett, 1995; Environmental Evaluation Unit, 1996; P.K. Dixon-Savage, pers. comm., 1998). Whereas these shallow-water methods could be adapted to greater depths for mining of phosphorite nodules, the better choice might be the modification of approved deep-sea systems.

Environmental concerns

An essential characteristic of all mining activities in the ocean is their large scale. Economic feasibility determines all aspects: the amount of ore to be mined per unit time, the area of seafloor disturbed by mining, the extent of sediment plumes, and finally the scope of research. Although the figures available were calculated during the active exploration phases some 25 years ago, they are still valid; if they need to be corrected in the future, they seem more likely to increase than to decrease.

Economic calculations for the mining of metalliferous muds from the Red Sea Atlantis II Deep were based on the exploitation and ship-bound processing of 100 000 metric tonnes per day. Flotation of the strongly diluted mud would separate up to 3% of valuable material from inert overburden materials. All the “rest”, 97 000 t, at that stage diluted to nearly 400 000 t, needs to be discharged back into the sea (Thiel et al., 1986; Karbe, 1987). Environmental impacts are to be expected as a result of mining and discharge. Throughout the lifetime of the mine, 15–20 years, the sediment in the Atlantis II Deep would be excavated. A disturbed mass of mud and brine would remain in the depression of the seafloor, deep water at a temperature of 21.8ºC and 41 salinity, would be mixed into the brine with a temperature of >60ºC and 257 salinity (Karbe, 1987). The original sulphidic mud certainly contains bacteria adapted to high temperatures and salinity (Fiala et al., 1990), but their habitat would no longer exist. Whether there may be hydrothermal vents and communities above the brine, or whether special sulphide biomes occur in some boundary layer, is not known. The extent of the likely impacts is difficult to evaluate. It is also an open question whether the disturbance of this habitat of 60 km^2 will influence adjacent regions of the seafloor. The transport of mined material would have no effects on the environment unless a pipe failure occurs. If this happened, though, it would preclude further mud transport, and the impact would remain limited.

The most serious impact, the extent of which is not fully ascertained, would be from the discharge of the highly diluted mud. The fate of this material is not well understood. A gravity-flow model and a momentum-jet-flow model were calculated, but limited to a few hours (Thiel et al., 1986). The pre-pilot mining test (PPMT)[4] or technique test provided an opportunity for a small discharge experiment at 400 m depth as a compromise between surface discharge (industry aim) and a commercial discharge depth of 1000–1100 m within the central graben (science aim), accepted after initially severe resistance by industry. The results of this experiment showed plume development at a depth of 700–800 m, which falls between the two models (Thiel et al., 1986). Characteristics of the tailings generated during the pre-pilot mining test are: density 1.1 g cm^{-3}, temperature 35ºC, particulate matter 25 g ℓ^{-1}, salt content 150 g ℓ^{-1} and grain sizes 60% <0.002 mm (Abu Gideiri, 1984; Thiel et al., 1986). The original sulphidic mud will be oxidized at least partly following the strong dilution with deep and surface waters, resulting partially in altered chemical bonds. This process is promoted during the flotation process and after discharge into the deep water, the prevailing oxygen concentrations being about 2 ml ℓ^{-1} (Karbe et al., 1981; Karbe, 1987).

Dissolved trace metals including antimony, arsenic, cadmium, cobalt, lead, mercury, nickel, silver and vanadium were released. First toxicological tests with tailings demonstrated for standard test organisms a threshold level of approximately 10 mg solids per litre. If one applies a typical safety factor of 0.1% to exclude chronic effects, figures for solid content above 0.01 mg ℓ^{-1} would be unacceptable (Karbe et al., 1981). Although the environmental studies conducted during the commercial exploration period gathered results on the ecology of the central Red Sea (Thiel, 1979, 1987; Weikert, 1980, 1982, 1987; Karbe et al., 1981; Beckmann, 1984; Thiel et al., 1986; Karbe, 1987) it

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[4] For a list of acronyms see the appendix on p. 471.

remained impossible to evaluate the large-scale impacts to be expected from tailings discharge over a period of 15–20 years.

The lower economic limit for the mining of polymetallic nodules is estimated at 5000 metric tonnes (dry) per day. This would involve the total disturbance of 1 km^2 each day. The collector system, 6–15 m wide, is expected to move in close meanders. It will weigh several tens of tonnes and certainly strongly compress and mix the mud in its track, from which the nodules have been lifted up just before by the collector. The system is expected to create a large plume from ooze taken up with and separated from the nodules by the collector system. Much of the sediment, aggregated in lumps of various sizes, will resettle immediately but the lighter material will drift away for uncertain distances (Thiel et al., 1991; Zielke et al., 1995; Jankowski et al., 1996). Conservatively calculated (based on a sediment layer of only 2–3 cm), 20 000 metric tonnes would be mobilized per day, but it remains unknown what proportion of this would constitute the near-bottom plume, and for what distance it would drift. The effects of these near-bottom and seafloor impacts still cannot be evaluated correctly, and this is also true for the discharge plume (see also Thiel, ed., 2001).

Ozturgut (1981) estimated that 25 000 m^3 of bottom water containing 1600 tonnes of sediment and 250 tonnes of nodule fines would need to be discharged from the mining ship or the nodule carrier per day. These figures may change in the future. They are based on a daily mining rate of 5000 tonnes which may increase, and the amount of nodule fines and sediment will depend on the sediment and nodule types. Comparing North and South Pacific mining areas, the small and rather smooth nodules of the North Pacific may be mined with less sediment, and they may lose less nodule fines during their transport to the surface. In contrast, mining the larger nodules of the South Pacific, lying partly buried in the stiff deeper sediments and having a rather loose, gritty surface, would result in a larger volume of particulate discharge into the water column.

Industry should be aware of these problems, and should minimize the different discharge volumes. But the need for discharge will inevitably exist, and a plume will certainly be created. For each mine site the appropriate discharge depth needs to be determined in relation to the local oceanographic conditions. Ecological factors to be taken into account include the depth zones of primary production, vertical migration depth of zooplankton and fish, the prevailing currents and vertical mixing of the water mass. Also, discharge above or into the oxygen minimum zone must be avoided, because manganese oxide and other metal components may go into solution following chemical reduction. Therefore, discharge into surface waters is certainly not acceptable for commercial mining, even though it was practised without detectable adverse ecological effects during the pre-pilot mining test (Ozturgut et al., 1981a; Hirota, 1981) in the North Pacific, because of the limited volumes mined and discharged. For commercial mining a discharge depth of at least 1000 m is recommended.

These considerations are valid for closed transport pipes between the mining system and the ship. Open systems like moving buckets and trawls would minimize the amount of nodule fines, because the nodules will be closely packed. Based on scientific trawling in the Peru Basin nodule area, sediment would be washed out of the containers or the trawl all the way to the surface, and much sediment caught between the nodules would be released onto the ship. No experimental results are available to estimate the amounts of mud arriving on the mining ship, but it is assumed that there would be too much for release into the ocean surface.

Mining of polymetallic crusts, massive sulphide and phosphorite are not further considered, since exploration and technique development have not proceeded far enough (Thiel et al., 1998). However, economic pressures for a large-scale intrusion into the deep sea would be the same as for polymetallic nodules or for metalliferous muds. Large amounts of ore must be excavated and transported to the ship, and overburden material or rather fluid tailings must be discharged into the sea. The general problems seem to be the same, though in particular situations it would be necessary to consider, for example, the specific fauna of a seamount or of hydrothermal vent communities in the neighbourhood.

In the mining of phosphorites the situation differs because of the relatively shallow depths at which they occur. Though mining would probably be technically less complicated and costly, environmental care would call for even more expenditure. Recolonization of the area mined out would probably be faster, but the plumes above the seafloor and from discharge in the water column may be more disturbing to the ecosystem. All the action would occur close to the euphotic zone, and upwelling conditions would carry the turbidity up into higher water levels, where the particulate matter could interfere with many organisms. Primary production and larval development could be affected. Generally, other interests in the use of the sea, like fisheries and recreation, would need to be evaluated in advance to avoid adverse interactions.

Past and future research

Evaluation of the environmental impact of mining in the deep sea is a major challenge to ecological research. The potential large-scale intrusions demand answers on acceptability. Ecological knowledge is not sufficient (Thiel, 1992), and precautionary research must specifically consider the scale of impact.

Since polymetallic nodules have been seriously considered as a mining resource, the environment has been taken into account. Already in 1970, the first pre-pilot mining test on the Blake Plateau of the Atlantic Ocean was monitored to evaluate the consequences of potential commercial mining (Amos et al., 1972, 1973; Roels et al., 1972, 1973; Roels, 1974; Amos and Roels, 1977).

Two extensive environmental programs were conducted in the seventies in conjunction with pre-pilot mining tests. The first accompanied the pre-pilot mining tests of Ocean Management, Inc. (Burns et al., 1980) and Ocean Mining Associates (Ozturgut et al., 1980, 1981b) in a programme named DOMES (Deep Ocean Mining Environmental Study) conducted in the Clarion–Clipperton Fracture Zone of the northeastern Pacific Ocean. This broad oceanographic programme concluded that mining would not result in harmful effects on the environment, but some of the authors (Lavelle et al., 1981; Lavelle and Ozturgut, 1981; Jumars, 1981; Ozturgut et al., 1981a) expressed concern about the discrepancy of scale between the test and commercial mining [see also Thiel (1991)]. A second large study was conducted in the years 1977–1981, and included some monitoring of the 1979 pre-pilot mining test for testing the equipment for mining of metalliferous mud in the Red Sea. The total programme, including commercial, technical and environmental assessment, was termed MESEDA (Metalliferous Sediments Atlantis II Deep). Plankton and benthos were studied, as well as primary production, toxicity of tailings, water chemistry, physical oceanography including the determination of water transport at great depths, and sedimentology (Thiel, 1979; Weikert, 1980, 1982, 1987; Karbe et al., 1981; Abu Gideiri, 1984; Beckmann, 1984; Thiel et al., 1986). The successful mining was completed with a small discharge test (see above, p. 450), and a tracer (radioactive iridium) was added to the mud released. The plume was investigated with an echo-sounder; two different types of models predicted the short-term spread of the plume, and sediment samples showed the distribution of the iridium on the seafloor (Fanger and Pepelnik, 1979).

The general approaches of DOMES and MESEDA applied standard methods of oceanography and obtained valuable sets of data on the Pacific Ocean and the Red Sea, respectively, but the main result of these studies was the realization that the data sets did not allow predictions of impact. The studies conducted and the results achieved are not appropriate to the large-scale intrusions anticipated by the mining industry (Thiel, 1991).

A new approach had to be developed to predict large-scale impacts of mining. This new step was successfully commenced when, in the years 1986–1988, the German Bundesministerium für Bildung und Wissenschaft agreed upon a long-term and large-scale *in situ* experimental study close to a national claim for the mining of polymetallic nodules in the South Pacific (Thiel, 1991). This project, known under the acronym DISCOL (DISturbance and reCOLonization of a manganese nodule area in the South Pacific), was launched in 1988 and had its first cruise from January to March 1989 (Thiel and Schriever, 1990). A large-scale disturbance of nearly 11 km^2 was achieved by ploughing the nodules into the sediment and turning its upper layer upside down. A programme for sampling before and after impact and for video/photo observations provided a basis for comparisons after 0.5, 3 and 7 years. After three years sedimentologists, geochemists and modellers joined the project (Thiel and Forschungsverbund Tiefsee-Umweltschutz, 1995), which terminated at the end of 1998. Early results indicate that after seven years the ploughing tracks are still visible, marked by the grey sediment ploughed up from deeper layers and resting on the surface alongside the dark brown upper sediment. The upper sediment layer became a three-dimensional mosaic of very soft, watery fillings between hard lumps of various sizes. This situation is expected after the passage of the collector system in the mining process, but the disturbance may reach deeper into the sediment. The relatively food-rich surface layer is mixed with deeper food-poor sediment, and the oxygen distribution may be changed [compare König et al. (1997)]. In addition to the disturbance by the collector system, resedimentation of the plume created by the mining occurs in the near-field. Lumps and aggregates sink back to the seafloor most probably in the mined area, as shown by modelling the sediment plume, and some fine-particulate matter will drift for longer distances (Zielke et al., 1995; Jankowski et al., 1996; Segschneider and Sündermann, 1997; Thiel, ed., 2001).

The faunal composition of all size classes remained permanently altered, because the manganese nodules, constituting a patchy hard substrate, were ploughed into the sediment. The megafauna, after an initial strong disturbance in the ploughing tracks, showed a slow recovery. After seven years even some of the less mobile species had returned. Outside the physically disturbed tracks the megafauna survived the drifting plumes from ploughing and resettlement of the sediment; after three years a strong increase in numbers was observed, whereas undisturbed regions outside the experimental area showed rather constant megafauna densities throughout this period (Bluhm, 1993; Bluhm et al., 1995; Schriever et al., 1997).

The macrofauna recovered slowly after a rapid increase in abundance in the initial post-impact phase (0.5 years), but the various dominant taxa behaved differently. While the isopods and tanaids recovered very rapidly, the polychaete abundance in disturbed sediments was affected significantly even after three years. The abundance of the subsurface deposit feeding polychaetes in disturbed samples were still significantly reduced, as is typical for recolonization stages (Rhoads and Boyer, 1982; Probert, 1984), and the distribution of the macrofauna in the sediment column extended deeper in the depressions refilled with sediment than in undisturbed layers (Borowski and Thiel, 1998). The "species diversity" (calculated from 78 selected polychaete species) in disturbed samples after three years was significantly different from that in undisturbed sediments, and reflected the artificially introduced heterogeneity of the habitat (Borowski, 1996; Borowski and Thiel, 1998). A similar result could even be demonstrated at the taxonomic level of polychaete families (Borowski and Thiel, 1996). While after seven years the densities of most taxa in the disturbed samples had increased to the levels in undisturbed sediments, those of bivalves behaved differently; their abundance also increased initially, but in the later phase decreased again, following medium densities after 0.5 and 3 years (Borowski, unpublished data).

The meiofauna exhibited a slight increase above baseline values from the post-impact study to half a year later. The immediate loss from disturbance amounted to 8% and 16% for nematodes and harpacticoids, respectively. Both these taxa, and also the Foraminifera, had already increased after three years – the nematodes and the harpacticoids to above pre-impact levels. Whether this is an effect of variation in faunal density, as has often been observed during community re-establishment (e.g., Pearson and Rosenberg, 1978), or an indication of higher organic-matter sedimentation, as the meiofauna had also increased at an upcurrent reference station, must remain open. After seven years, figures for nematode abundance are near the baseline values (Schriever et al., 1997). Changes in faunal composition were still detectable, but are expected to normalize in the future.

In general, it is assumed that a balanced community will develop in heavily disturbed mining regions, but with the removal of the nodules it will consist purely of a soft-bottom fauna, so that a reduction in species diversity is to be expected as a result of the overall reduction in habitat diversity. The nodule surface and its meiofauna differ from those of the sediment (Bussau et al., 1995). Thiel et al. (1993) and Maybury (1996) described a specific manganese-nodule crevice fauna inhabiting a mud-filled canal system in the large nodules of the Peru Basin. Nematodes, polychaetes, a sipunculid, harpacticoids and tanaids were discovered in this special habitat, and the nematode species *Acantholaimus maks* has never been found elsewhere.

The DISCOL large-scale *in situ* experiment was followed by a series of other large-scale *in situ* experiments (Table 13.3), studying the reaction of the benthos to various rates of resedimentation from an artificially created plume. These four experiments were conducted with the same disturber, slightly modified between experiments, designed to suck up sediment from the seafloor and eject the material several metres above, thus creating a plume which would settle downstream, blanketing the sediment surface and burying the fauna. The experiment simulated plume resettlement behind a collector system employed in the mining of polymetallic nodules.

The results of these experiments are so far limited. Trueblood and Ozturgut (1997) reported on the United States Benthic Impact Experiment (BIE). Nine months after the disturbance, nematodes were significantly reduced in the sediment redeposition area. Macrofauna diversity remained the same, but two families (one polychaete and one isopod) were strongly affected

Table 13.3
Benthic impact experiments

Acronym	Name of experiment	Organization	Year of disturbance	Tracks (*n*)
BIE	Benthic Impact Experiment	National Oceanographic and Atmospheric Administration (NOAA) (USA)	1993	49
JET	Japan Deep-Sea Impact Experiment	Metal Mining Agency of Japan	1994	19
IOM-BIE	Interoceanmetal Benthic Impact Experiment	Interoceanmetal Joint Organization, Poland	1995	14
INDEX	Indian Deep-sea Environment Experiment	National Institute of Oceanography, Goa, India	1997	26

(Trueblood and Ozturgut, 1997). In the Japan Deep-sea Impact Experiment (JET) the metazoan meiofauna was strongly reduced by the disturbance, and this reduction persisted one year later. The dominant nematodes seemed to be responsible for this decrease; the harpacticoids, on the other hand, did not show any effect immediately after disturbance, and had increased in abundance twelve months later. Bacterial numbers also increased [see Kaneko and Maejima (1997); Kajitani (1997) and references therein]. Some preliminary results from the benthic impact experiment conducted by the Interoceanmetal Joint Organization (IOM-BIE) were presented by Radziejewska (1997) and Radziejewska et al. (2001a,b). No significant change was detected in meiofauna abundance following the disturbance, but the absence of a short-term effect may mask a later reaction [compare Schriever (1995) and Foell et al. (1997)], probably because of the disrupted sediment surface layer, where feeding of the fauna is concentrated. In the IOM-BIE experiment a seemingly increased feeding activity of fish and shrimps was observed shortly after the disturbance. This mobile fauna may have been attracted to the site by increased food availability, but this would have been a short-term stimulation effect (Radziejewska, 1997).

These large-scale experiments (see also Sharma, 2001 and references therein) seem to result in faster re-establishment of a balanced community than was indicated by the observations from the DISCOL study. Sediment blanketing certainly has a less severe impact on the fauna than ploughing and strong mixing of the sediment. The resettled sediment, constituting a thin layer with a high water content and low shear strength, is easily penetrated by the fauna that have been smothered. However, the effect of disrupting the sediment surface as a food source cannot easily be guessed.

Although some effort has been spent on large-scale experiments, the results remain limited. The effort required has generally been underestimated and the studies have therefore been under-funded. The results of DISCOL and related projects were published by Thiel and Forschungsverbund Tiefsee-Umweltschutz (2001) (see also Thiel, ed, 2001). Oceanographers, pioneer investors, other contractors and the International Seabed Authority must decide in which direction precautionary research should be orientated. Several approaches may be suggested.

Baseline studies: All impact studies need a sound basis against which impacts originating from experiments or commercial actions may be assessed. Collecting such information demands considerable effort, which must therefore be concentrated on the most important questions. The DISCOL project confined itself to what was termed “indicator taxa” (Thiel et al., 1992). But which groups are likely to produce the most pertinent results? For this project Foraminifera, Nematoda, and Harpacticoidea were chosen from the meiofauna, Polychaeta from the macrofauna, and Holothuroidea from the megafauna. Each group is sufficiently abundant to be collected or photographed with the frequency needed enough to reveal any changes in a community. For large-scale overviews a simpler recording approach may be suitable: charting the megafauna and sediment structures on the seafloor as described by Bluhm (1993) and Bluhm et al. (1995) within the DISCOL project. Standardized methods for recording and image evaluation could result in a wealth of information gained with moderate effort.

Plankton investigations and hydrographic measurements should also be included in the baseline studies, specifically to assess the effects of tailings discharge. Plankton community structure at different depths, vertical migration patterns, and the depth of the oxygen minimum layer should determine the depth of mud release. The resulting plume should be modelled and evaluated. The same is necessary for the plume of resuspended sediment above the seafloor created by the mining vehicle during nodule uptake (see p. 451).

Impact experiments: This approach attempts to learn about impacts by creating an experimental disturbance. This should not be mistaken for simulation of full-scale disturbance by mining activities, since future techniques and activity levels may not be known. However, since such experiments cannot be undertaken in the laboratory, small-scale field experiments should be designed to demonstrate certain aspects of disturbances. Such small-scale impact experiments can be envisaged as blanketing an area of several square metres by using a submersible for exact deposition of sediment in layers and its subsequent sampling. Similarly, plume experiments could be conducted by employing a submersible for disturbance at different scales and for observations on sediment resettlement, transport and plume sampling. Further large-scale impact experiments may be conducted, after the results of the benthic impact experiments and DISCOL are made available (see also Thiel, ed., 2001).

Pre-pilot mining tests (PPMT): To be termed "technique tests" in future documents of the International Seabed Authority. Industrial pre-pilot mining tests can be expected to be conducted for testing newly developed techniques. As in the DOMES and MESEDA projects, disturbance would remain limited and would rarely allow extrapolation to full-scale activities. But accompanying those tests with an environmental programme would help one to imagine impacts and to ask the right questions in subsequent work. Early discussions of experimental needs with engineers may make it possible to design effective environmental studies concurrently with technical tests. Depending on the particular test, such experiments may be concerned with the impact on the water column or on the seafloor.

Pilot mining operations (PMO): To be termed "mining tests" in future documents of the International Seabed Authority. Industrial pilot mining operations follow the pre-pilot mining tests, and can be defined as pre-full-scale tests. Pilot mining operations are duration tests for the techniques to be employed in commercial exploitation. Technically a pilot mining operation system may be somewhat scaled down, but it will remain in operation for several months and the disturbances caused at and above the seafloor and in the water column will simulate the full-scale operation correctly. Pilot mining operations provide the only chance to extrapolate reliably to full-scale exploitation. These opportunities should be exploited by oceanographers of all disciplines in an interdisciplinary and well coordinated study.

International cooperation: The costs for a complete environmental pilot mining operation have been roughly estimated already by Thiel et al. (1991) and by Thiel and Foell (1993), who pointed out that no single country, consortium or company would be able to carry these costs, although they represent only a minor part of the total technical development and exploration phase. The only solution to the problem is international partnership for the environment (Thiel and Schriever, 1993).

An environmental pilot mining operation represents the final and most important step in environmental impact assessment, but cooperative partnership should be prepared and trained much earlier. It is essential for the different disciplines to adopt the same methods, to generate comparable results in baseline studies and experimental approaches, to discuss the results, and to know each other. Cooperation needs administrative effort and communication, but the profit for all parties will more than compensate for these efforts.

Below-seafloor resources and exploitation

The hydrocarbons, oil and gas, and in the future probably methane hydrates, are important resources for most human societies. Although in the narrow sense they should not be regarded as marine resources, their exploitation may nevertheless pollute the sea. Oil and gas, for example, are located from a few hundred to more than one thousand metres below the seafloor, but their extraction from various geological facies requires transport through the sea. This occurs in hermetically enclosing systems, unless leakages or accidents allow the oil to disturb the environment. Methane hydrates may be located less deep in the sediment, even rather close to the sediment surface; but most of this frozen material is found deep under sediment layers.

Oil and gas

Regular impacts by drilling are introduced into the sea by the discharges of (1) drill-cuttings, and (2) production water. Discharged drill-cuttings consist of material separated from the drilling fluids which have been pumped through the drill-string to lubricate the drilling bit, to carry drillings to the surface and to control the reservoir pressure. This drilling fluid contains water, bentonite, barium sulphate, cellulose compounds and occasionally salt and biocides. In the past, drilling fluids also contained oil. This fluid is recycled after separating out the drill-cuttings, to minimize the escape of pollutants.

Kingston (1992) studied the benthos around drilling platforms in the North Sea (to a depth of about 150 m), after surveying sampling transects of 5 km length following the prevailing bottom currents. The results may be summarized by characterizing four zones at increasing distances from the platform:

(1) 0–750 m: oil level 1000 times background value, disrupted community, low diversity;
(2) 750–1500 m: oil level 20–100 times background value, transition from low to background diversity;
(3) 1500–3000 m: oil levels 5–20 times background value, diversity appears normal, effects on indicator species may be detected;
(4) >3000 m: oil level elevated above background value at distances up to 10 km, no confirmed evidence of any effect on the benthos.

Rather similar results were obtained by Olsgard and Gray (1995), reporting on studies around 14 oil and gas fields; but in some fields contamination was much less. After 6–9 years, contamination had spread to distances of 2 to 6 km from the platform. The relationship between fauna and environmental variables indicated that the main components of drill cuttings impacting the benthic fauna were total hydrocarbons, barium and strontium, and also metals such as zinc, copper, cadmium and lead. Impacts by water-based mud clearly indicated less effect on the environment and on organisms than those of oil-based fluids. The replacement of larger epifauna by smaller infauna may have had an influence on food for fishes.

Drilling in deeper waters would probably produce similar effects to those observed around these relatively shallow (<400 m) North Sea platforms. Discharged drilling muds would immediately sink to the seafloor, although currents may separate out clay and silt components, and they may settle at greater distances from the platfom, presumably at lower concentrations. If a riser tube were used, resulting in the mud being released close to the seafloor, impacts could be restricted to a smaller field. Whereas water-based drilling fluids are allowed to be released into the sea, oil-based materials should be disposed of on the land.

Oil companies are aware of the environmental problems introduced into the ocean by drilling actvities, and a more responsible approach has developed during the decades of drilling in shallow seas. Clean drilling and exploitation are possible, as demonstrated by the Deutsche Erdöl-Aktiengesellschft with their platform in the tidal area of the German Wadden Sea. There is no contamination, and drilling muds are transported back to the coast for terrestrial disposal (Mittelplate Konsortium, 1999).

Methane hydrate

This gas was discovered only recently, and it may become an important resource. Methane occurs in the oceans as a compound with water, and in the deep sea, due to the high pressure and low temperature, this compound exists in the form of a solid “ice”. Techniques for the extraction of methane hydrates have not yet been developed, but potential environmental hazards have been suggested. Extraction of methane “ice” may destabilize sloping areas and trigger mud slides down into greater depth, similar to those occurring naturally (see Gas Technology Information, 2000).

Living resources and fishing

Some deep-water fish stocks have been exploited for many years, and the long-line technique employed for catching black scabbardfish (*Aphanopus carbo*) off Madeira and the Azores is a positive example of the sustainable use of deep-living fish species. However, during recent decades industrial fishing activities have shifted to greater depth, following the construction of more powerful trawlers, the development of highly sophisticated methods for the detection of and trawling for aggregated fish schools, and also because of the decline of many fish stocks in shelf areas due to overfishing. In recent publications, deep-water fishing is defined as occurring below 400 m or 500 m, and fishing activities have been recorded to a depth of nearly 2000 m.

The inherent problems of deep-water fishery are basically understood, and are well summarized in a number of review papers [e.g., those of Merrett and Haedrich (1997) and Jennings and Kaiser (1998), and the very recent one of Koslow et al. (2000)]. The life-history characteristics of the species are described as typical for their deep, cold and energy-poor environment, reflecting mostly extreme K-selection: slow growth, low natural mortality, late maturity (25 years in the orange roughy, *Hoplostethus atlanticus*), high longevity (>100 years in the same species), large eggs and low specific fecundity, all resulting in exceptionally low productivity. Additionally, recruitment seems to be an episodic process, with many years of low recruitment to the adult stock and rare ones in which it is high. Generally, species with these features are highly vulnerable to exploitation and disturbance. Nearly all exploited deep-water populations suffer from overfishing within a few years. According to Clark (1995), the sustainable yield for orange roughy in New Zealand waters has been estimated at only 1–2% of the population, and even this figure may be too high.

Various impacts on fish populations as a result of fishing activities may be predicted, but life-history characteristics may hide changes in community structure. Individual sizes in fished populations were found to decrease (Large et al., 1998) but no alteration of species composition in the community was observed. A shift in community structure to a larger proportion of species or size classes with faster turnover, and the consumption of smaller prey, had been hypothesized by Merrett and Haedrich (1997) as results of fishing and described by Jackson et al. (2001). The few observations available demonstrate the discrepancy between the development of deep-water fisheries and the lack of basic knowledge on the ecology of fish species, and on the functional relationships of species in deep-water ecosystems.

Deep-water fisheries impact not only the fish stocks but also the benthos and their habitat. The depth range at which fish occur and fishing takes place includes the zone of the continental slope in which the coldwater coral *Lophelia pertusa* builds up its large reef structures in European waters (Freiwald and Wilson, 1998; Rogers, 1999). Trawling with heavy fishing gear destroys those reefs upon contact, their community-structuring functions are lost, and the unique deep-water ecosystem dramatically changes, losing its high biodiversty. This has been well demonstrated by Probert et al. (1997), Koslow and Gowlett-Holmes (1998), Richer de Forges et al. (2000) and Koslow et al. (2001), who have described fishery impacts on the benthos off New Zealand and Australia, with decreases of biomass by 83% and number of species by 59% on the tops of Tasmanian seamounts. Thus, deep-water trawl fisheries not only overexploit fish stocks, but also over-disturb deep-water habitats and the benthos, particularly the epibenthic species.

Truly sustainable yields for fish species are unknown, and therefore cannot inform discussions on fishery management. Only precautionary measures can be emphasized, and catch limits should be regulated at a level low enough to ensure recovery of fish stocks, benthos and environment. By such regulations sustainable fishing may become economically unfeasible. Fisheries for deep-water fish stocks are virtually guaranteed to be unsustainable if they are developed without the support of scientific knowledge and expertise. Fishing News (2000) reported a rush of trawlers from Namibia, New Zealand and South Africa to seamounts in the southern Indian Ocean to fish for orange roughy, and others from Russia and China were expected to join the fishing fleet. Such an action will most probably lead to short-term profit for a few people, but at the same time to the loss of the fish stocks on isolated seamounts through overfishing. For seamounts and other deep-water habitats beyond the national jurisdiction of states no regulations exist for the conservation of species, species diversity and habitats (see pp. 459–461).

LEGAL REGULATIONS

Three legal instruments exist for the protection of the deep sea from environmental harm: the London Convention, 1972; the Convention for the Prevention of Pollution from Ships, 1973/1978; and the UN Convention on the Law of the Sea, 1982 (Sand, 1992). Their memberships are not identical.

The "Convention on the Prevention of Marine Pollution by Dumping of Wastes and other Matter", the so-called "London Convention" (LC[5], originally LDC: London Dumping Convention) was adopted on 29th December 1972. Article 1 gives as the main objectives to

> prevent the pollution of the sea by dumping of waste and other matter that is liable to create hazards to human health, to harm living resources and marine life, to damage amenities or to interfere with other legitimate uses of the sea.

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[5] For a list of acronyms see the appendix on p. 471.

The ratification of this Convention is open to any state (Art. 18), but as of December 2002 it had been ratified by only 78 states. According to the International Maritime Organization (IMO), the Secretariat for the LC, this international agreement developed into an effective instrument for the protection of the marine environment (International Maritime Organization, 1991). Consultative Meetings of the Contracting Parties receive multidisciplinary advice from the Group of Experts on Scientific Aspects of Marine Environmental Protection (GESAMP), a scientific consortium of independent experts, from an intergovernmental panel of Experts on Radioactive Waste Disposal at Sea, and from a specially established Scientific Group as an advisory body.

Thus, basically, the LC is well established, although it would seem advantageous if the number of Contracting Parties would increase, and if they were induced to reflect the LC in their national legislation and to reduce the potential for uncontrolled dumping. However, the LC and a Protocol adopted in 1996 but still not in force, specifically exclude in Article III, 1c of the LC and Article 1, 4.3 of the Protocol (protocol additions and changes in brackets):

> The disposal [or storage] of wastes or other matter directly arising from, or related to exploration, exploitation and associated off-shore processing of seabed mineral resources is not covered by the provisions of this Convention [of this Protocol] (International Maritime Organization, 1997)

This is an adverse decision, dictated by commercial self-interest.

The International Convention for the Prevention of Pollution from Ships (MARPOL – MARine POLlution) was adopted on 2 November 1973 and amended by a Protocol in 1978. Several Amendments to the Convention and its Annexes have been made subsequently. It has currently 102 members. MARPOL does not exclude mining activities in the Area (that is, the seafloor of the high seas outside the national Exclusive Economic Zones); its objectives are restricted to preventing pollution from ships. The various possible impacts of mining are not covered by this Convention.

The United Nations Convention on the Law of the Sea (UNCLOS) (United Nations, 1997) was adopted on 10 December 1982 after ten years of negotiations, and came into force on 16 November 1994 one year after the sixtieth instrument of ratification was deposited with the United Nations. As with the LC and MARPOL, UNCLOS is global in scope. By December 2002 the European Union and 137 states had ratified this convention. The main objectives are presented in paragraph 4 of the Preamble, which states that the Convention shall establish

> a legal order for the seas and oceans which will facilitate international communication, and will promote the peaceful uses of the seas and oceans, the equitable and efficient utilization of their resources, the conservation of their living resources, and the study, protection and preservation of the marine environment

Thus, already in this prominent position “study, protection and preservation of the marine environment” are emphasized, which is of significance in the context of this Chapter. There are further important statements in various parts of the Convention, such as Article 192 in Part XII:

> States have the obligation to protect and preserve the marine environment,

and in Article 193 of this part in relation to Exclusive Economic Zones (EEZs):

> States have the sovereign right to exploit their natural resources persuant to their environmental policies and in accordance with their duty to protect and preserve the marine environment.

Provisions regarding “pollution by dumping” are set out in Article 210 (Part XII). These require that

> national laws, regulations and measures shall be no less effective in preventing, reducing and controlling such pollution than the global rules and standards.

It is generally understood that “global rules and standards” means provisions set out in the 1972 LC. This will be replaced by the 1996 Protocol to the Convention, after its entry into force.

Part XI of UNCLOS is concerned with mining in most deep-sea regions – that is, all parts outside the Exclusive Economic Zones. This part of the Convention was very controversial during the negotiations and was the reason for the long delay between the Convention’s adoption and its entry into force. Problems arose because of the very high returns expected from the mining of polymetallic nodules, which were declared the “common heritage of mankind”, and because there was an attempt to translate principles of the highly controversial New International Economic Order into legally binding provisions related to deep-sea mining. However, these controversies, solved by the 1994 Agreement relating to the Implementation of Part XI, did not affect the environmental provisions laid down in the various articles.

UNCLOS articles 145 in Part XI and 209 in Part XII provide the necessary measures related to all activities in the Area to give effective protection from harmful effects (145) and to develop interrelationships between international and national laws (209). Article 145

> further provides that … the [International Seabed] Authority shall adopt appropriate rules, regulations and procedures for the prevention, reduction and control of pollution and other hazards to the marine environment, and the protection and conservation of the natural resources of the Area. … the Convention does not impose measures which would prohibit deep-seabed mining activities. It does, however, recognize that deep-seabed mining cannot be carried out without due regard to its impact on the marine environment.
> Nandan (1999)

In addition to the UNCLOS provisions, the Preparatory Committee for the International Seabed Authority (ISA) and the International Tribunal for the Law of the Sea (PrepCom) dealt with a Draft Mining Code, which contained a paragraph on the protection of the environment from activities in the Area (cf. document LOS/PCN/SCN.3/WP.6/Add.5 of 8th February 1990). The draft describes "serious harm to the marine environment" as

> effects from activities in the Area on the living and non-living components of the marine environment and associated ecosystems beyond that which is negligible or which has been assessed and judged to be acceptable by the Authority pursuant to these regulations and the relevant rules and regulations adopted by the Authority and which represent:
>
> a) significant adverse changes in the living or non-living components of the marine and atmospheric environment;
>
> b) significant adverse changes in the ecosystem diversity, productivity and stability of the biological communities within the environment; or
>
> c) loss of scientific or economic values which is unreasonable in relation to the benefit derived from the activity in question.

Although this definition is broader in scope than the phrase "serious harm", it remains rather unspecific.

Nevertheless, the provisions under the UNCLOS and the draft of the Mining Code are encouraging. The marine environment is broadly considered under the aspects of "study, protection and preservation of the marine environment" and "… sustainable development… "

However, the relevant statements, particularly in the Mining Code, are weak and do not constitute objective measures for the protection of the deep sea. Phrases like "serious harm" are not sufficiently precise to ensure environmentally sustainable mining, or more generally for the sustainable use of the deep sea.

Before UNCLOS entered into force in 1994, at which time the PrepCom was automatically dissolved, the commission transmitted the Draft Mining Code together with its final report to the International Seabed Authority (ISA). The ISA Secretariat then had to review the draft in order to adjust it to the provisions of the 1994 Agreement. The new draft, which became restricted only to the preparatory phases of mining, prospecting and exploration, was presented to the Legal and Technical Commission of the ISA in March 1997. With regard to the protection of the marine environment it contains only general principles and no concrete standards. This is because insufficient knowledge is currently available for the deep sea and its environment. However, in 1998/1999 the ISA developed environmental and monitoring guidelines for mining contractors engaged in exploration of the deep seabed for polymetallic nodules (International Seabed Authority, 1999). The principles for the sustainable development of deep-sea mining will have to be amplified at a later stage, but well before deep seabed mining starts. As exploitation of polymetallic nodules is still many years away, some time remains to acquire the necessary knowledge on the deep sea and the potential impacts of deep seabed mining on the environment. This period should be used by deep-sea scientists to undertake relevant research and to provide the results to the ISA, in order to enable it to elaborate and adopt sufficiently concrete provisions for effective protection of the marine environment against serious harm from activities in the Area. Without this information the ISA will not be in a position to discharge its relevant functions effectively, and to fill in the gaps in the LC, its 1996 Protocol and MARPOL as they relate to deep-sea mining. It is the responsibility of scientists and of industrial and governmental funding agencies that these obligations are met in due time. Various workshops related to the environmental problems of deep-sea mining were organized by the ISA during the last years. Scientists developed research programmes and are conducting investigations to learn about the impact of polymetallic nodule mining on seafloor species diversity (International Seabed Authority, 2002).

PROTECTED AREAS FOR THE HIGH SEA

The increasing use of the deep sea and the necessity (for economic reasons) of large interventions in this environment have led to consideration of the conservation of species, communities and habitats. Already in 1978 the concept of a stable reference area (SRA) had first been suggested at a meeting of the International Union for the Conservation of Nature and Natural Resources (IUCNNR) at Ashkhabad (USSR), later discussed by the National Research Council of the United States National Academy of Sciences (National Research Council, 1984). This concept involves the establishment of two types of protected areas, the preservational reference area (PRA) and the impact reference area (IRA). Both these areas should be characteristic for a wide region proposed for mining, and they should be ecologically similar. The PRA should remain unmined and far removed from any mining impacts, so that unimpacted community development can be studied after mining activities are in progress in other areas. In contrast, the IRA should have been established after mining to observe the reconstitution of a new community. Since mining did not commence, and discussions on the mining code and environmental regulations in the International Seabed Authority (ISA) were restricted to the mining exploration phase in the deep sea, the SRA concept has remained dormant for many years.

The need for nature conservation of deep-water species and communities again came under review with the development of deep-sea fisheries by trawling. The traditional long-line fisheries off Madeira and the Azores are sustainable uses of deep-water resources, but trawling for deep-living species has led to overfishing after a few years (see pp. 456–457), and conservation measures are essential to ensure sustainability for exploited fish stocks and ecosystems. Conservation is not only of importance for the target fish species but also for the benthos of fished areas. Epifauna, structuring habitats and communities (see p. 457) deserve the same protection.

To a large extent deep-water fisheries are executed in waters under national jurisdiction – that is, within the EEZ of states. According to UNCLOS such states not only have the right of exploitation, but they also have an obligation of nature conservation in these extended national sea areas. Most countries have not declared their EEZs, and national jurisdiction may not provide for conservational regulations. But at least three positive examples exist: Australia has established a deep-water marine reserve. It covers an area of 370 km^2 on the continental slope south of Tasmania, enclosing 14 seamounts in the vicinity of a fishing ground for orange roughy (Koslow et al., 2000). In 1999 Norway set aside two Sula Reef areas, in its EEZ northwest of Trondheim, at a depth of 300 m, where large reefs of the deep-water coral *Lophelia pertusa* exist. Rare and highly diverse communities are structured by its presence (Fossa et al., 2000). Portugal protects two hydrothermal-vent sites since 2002 (World Wide Fund for Nature, 2001).

Thus, deep-water conservational areas can be successfully established under national jurisdiction, but difficulties in the lobbying of fishery authorities must be overcome. Positive response to well-founded scientific arguments can be expected. However, for the high seas beyond EEZs, no regulations exist for the isolation of marine protected areas (MPAs). UNCLOS provides a number of general statements for the protection of species and communities, but this is not sufficient legal background for the establishment of MPAs. This general jurisdictional problem for the high seas may be somewhat different in European waters, and may reach beyond areas of national influence. The Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR Convention, which combined the OSlo and PARis conventions) covers an area far beyond national jurisdiction, west to the Mid-Atlantic Ridge (46ºW) – that is, including the high seas of the North-East Atlantic. According to Czybulka and Kersandt (2000, p. 16), most authors agree on

> the applicability of [the European] Community law beyond the territorial sea.

Consequently, an OSPAR working group discussing the establishment of MPAs is also considering protected areas for the high seas.

Deep-sea environmental science has always had a strong foreseeing and forecasting character. Environmental studies have been conducted already during the exploration phases for the mining of manganese nodules in the Pacific Ocean (e.g., Ozturgut et al., 1980; Foell et al., 1997; Thiel and Forschungsverbund Tiefsee-Umweltschutz, 1995) and for metalliferous sediments in the Red Sea (Thiel et al., 1986; Karbe, 1987). These studies were not postponed until the commencement of mining. Thiel et al. (1998) presented an overview on risks of exploiting the deep sea, and recommended further predictive studies to avoid over-exploitation of this space. In this context of foresight, high-seas MPAs should be established independently of any actual threat to species and communities (Thiel and Koslow, 1999). It is not possible to predict all uses of the deep sea, their extent and their adverse impacts. Therefore, regions of high scientific relevance should be demarcated and protected from any use, except for further scientific investigations. A few regions exist in the North-East Atlantic which have been target areas for long-term scientific studies (e.g., the Porcupine Seabight and the Rockall Trough region predominantly studied by British scientists, and the BIOTRANS / BIO-C-FLUX region around 47ºN, 20ºW studied by German and international research groups). A large number of expeditions have been conducted to study these areas, many results have been obtained and funding agencies have invested tremendous amounts of resources in them. These areas are of potentially high importance in the future, when comparative studies should provide evidence for stability, or for changes in species composition and community structure. They are of high value for science and for society; the funds already invested could rarely be mobilized again if such potential reference areas were disturbed. It is therefore of utmost importance and urgently emphasized that legal regulations should be provided and high-seas unique science priority areas established (Thiel, 2002, 2003).

An interdisciplinary workshop involving legal experts, administrators and ecologists was held at the Internationale Naturschutzakademie Insel Vilm (on the tiny German island of Vilm) early in 2001 to discuss legal and scientific aspects of marine protected areas on the high seas (Thiel and Koslow, 2001). The conclusions of this conference were submitted through political channels for further negotiations to the United Nations Informal Consultative Process on Oceans and the Law of the Sea (UNICPOLOS).

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APPENDIX 1: List of acronyms used in this chapter

Area (the)	seafloor of the High Seas, i.e. beyond national jurisdiction
ACOPS	Advisory Committee on Polluton of the Sea
AMAP	Arctic Monotoring and Assessment Programme
AUV	Autonomous Underwater Vehicle
BIE	Benthic Impact Experiment (USA–Russia, Japan, IOM, India)
BIO-C-FLUX	Biological Carbon Flux in the Near-bottom Water Layer in the Deep Sea of the Northeast Atlantic (Germany)
BIOTRANS	Biological Vertical Transport and Energetics in the Benthic Boundary Layer of the Deep Sea (Germany)
CFC	Chlorofluorocarbon
DISCOL	Disturbance and Recolonisation of a Manganese Nodule Area in the South Pacific (Germany)
DDT	Dichlorodiphenyltrichlorethane
DOMES	Deep Ocean Mining Experimental Study (USA)
DWD 106	Deepwater Municipal Dumpsite 106 (USA)
EEZ	Exclusive Economic Zone
ENEA	European Nuclear Energy Agency
GESAMP	Group of Experts on the Scientific Aspects of Marine Pollution
GTI	Gas Technology Information
HCH	Hexachlorocyclohexane
IAEA	International Atomic Energy Agency
IMO	International Maritime Organization
INDEX	Indian Deep-sea Experiment
IOM	Interoceanmetal Joint Organization
IRA	Impact Reference Area
ISA	International Seabed Authority
IUCNNR	International Union for the Conservation of Nature and Natural Resources
JET	Japan Deep-sea Impact Experiment
LC (London Convention)	Convention on the Prevention of Marine Pollution by Dumping of Wastes and other Matters
MARPOL	International Convention for the Prevention of Pollution from Ships
MESEDA	Metalliferous Sediments Atlantis II Deep (Germany)
MPA	Marine Protected Area
NEA	Nuclear Energy Agency
NERC	Natural Environment Research Council (UK)
NOAA	National Oceanic and Atmospheric Administration (USA)
NRC	National Research Council (USA)
OSCOM (Oslo Commission)	Oslo Convention for the Prevention of Marine Pollution by Dumping from Ships and Aircraft
OSPAR	Convention for the Protection of the Marine Environment of the North-East Atlantic
OSPARCOM (Oslo and Paris Commission)	Oslo and Paris Conventions for the Prevention of Marine Pollution
PCB	Poly-chlorinated biphenyls
PCC	Poly-chlorinated camphenes
PDO	Pilot Disposal Operation
PMO	Pilot Mining Operation (mining test)
PPMT	Pre-pilot Mining Test (technique test)
PRA	Preservational Reference Area
PrepCom	Preparatory Commission for the International Seabed Authority and for the International Tribunal for the Law of the Sea
SEBA	Working Group on Sea-based Activities (of OSPARCOM)
SRA	Stable Reference Area
UNCLOS	United Nations Convention on the Law of the Sea

Chapter 14

EPILOGUE:
EXPLORATION, OBSERVATION AND EXPERIMENTATION

Paul A. TYLER

Where does deep-sea biology go from here? As with all science there are many stages in the intellectual and practical development of the subject. Firstly there is *exploration* and the discovery of the phenomena. This is followed by *observation* that leads to a better understanding of the subject and finally there is *experimentation* that allows one to fully dissect the processes that contribute to the cause and function of the subject. The fourth, and essentially non-scientific aspect, is the economic *exploitation* of an environment. Deep-sea biology is one of the few areas of science, especially natural science, where the scientific community is involved in the first three aspects but should not ignore the last.

EXPLORATION

The 'heroic' age of deep-sea exploration started with the *Porcupine* and *Challenger* expeditions and culminated in the *Galathea* expedition of 1950–1952. This era demonstrated that there was a fauna at all depths in the sea. Since the 'heroic' age exploration has continued, so that many of the major discoveries in the deep-sea have been as much serendipitous as planned. The discovery of hydrothermal vents along the Galapagos Rift in 1977 showed there were major ecosystems on earth independent of sunlight, and parallel chemosynthetic communities are now known from cold seeps along both active and passive continental margins. Very recently, the 'Lost City' along the mid-Atlantic ridge has been discovered, in which hydrothermal chimneys are located on crust 1.5 My old, ~15 km off the ridge axis. The chimneys are formed of carbonates rather than sulphides, and hydrothermal fluid is relatively low in temperature (40 to 75ºC) and high in pH (9 to 9.8) (Kelly et al., 2001).

Once discovered, such phenomena as vents and seeps have become foci for observation and experimentation; but still vast areas of the deep ocean remain to be explored. With the exception of the North Atlantic, the fauna of the great abyssal plains under the oligotrophic waters of the great subtropical gyres of the oceans remains poorly known. Very little is known of the vast sedimentary siliceous oozes of the open deep circumpolar Southern Ocean or the fauna under the ice-covered areas of the Arctic and Antarctic (see Chapter 8), although interest in both non-vent and vent environments in the ice-covered Arctic is accelerating (Kröncke et al., 2000; Edwards et al., 2001).

Little is known about the global distribution of hydrothermal vents, or even whether they exist at higher latitudes (Van Dover, 2000). Cold seeps would appear to be the most commonly discovered new sites at present, the latest reports of cold seeps being in the Norwegian Sea (Gebruk et al., 2002) and off Angola. Vents have been point centres for research along the mid-ocean ridges, but very little is known of the faunas inhabiting the rocky substrata on the flanks of the ridges, or along the steep rocky regions of the continental margin. Exploration of the deep sea has been limited by technology, and it is only recently that the technology has become available to sample in difficult areas within otherwise well-sampled regions such as the northeast Atlantic (Tyler and Zibrowius, 1992). Such distributional and taxonomic knowledge is imperative before one can start addressing some of the fundamental biogeographic questions of the deep-sea faunas.

A last problem for modern-day exploration of the deep sea, as with other remote environments, as well as outer space, is that such exploration costs money and there is never a guarantee that there will be a return, either intellectually, commercially, or in publicity, for the investment of taxpayers' money. It is the very dramatic images from hydrothermal vents that have kept these ecosystems in the public eye and, indirectly, aided the public funding of research in such environments. To maintain the momentum for exploration and discovery in the deep sea it is necessary for the deep-sea research community to emphasise the importance of all aspects of their chosen ecosystem.

OBSERVATION

If there are 'ages' in science, the deep-sea biological community is in the later stages of the age of observation. At hydrothermal vents the age of observation has passed quickly. This may be a function of the relatively low species diversity there; the dominant species were described and aspects of their basic ecology were studied within a few years of their discovery. Only the more obscure taxa at vents still await identification, although with a new phase of exploration new species of even the dominant groups are sure to be found. Observation of the ecology of vents has also proceeded with the development of technology such as high-temperature probes, long-term temperature probes and increasing sophistication of the chemical analysis of the environment (Luther et al., 2001). These observations have shown that the ecology of vent organisms is much more refined than originally thought.

Studies of the non-vent deep marine environment are still largely limited to observation. Most of the major programmes over the last twenty years or so have sampled the deep-sea with a specific aim in mind. One of the main drives in deep-sea biology has been to determine the level of biodiversity. Results from the 'heroic' age suggested that species diversity in the deep sea was low, but the pioneering work of Howard Sanders and Bob Hessler (Hessler and Sanders, 1967) with improved sampling apparatus demonstrated that species diversity was made up mainly of small infaunal species. As a result of a carefully designed sampling programme, Grassle and Maciolek (1992) predicted that there may be up to ten million species in the deep sea. This conclusion led to much debate with lower (May, 1992) or higher values (Lambshead, 1993) being suggested. In addition, there are indications that dysoxic environments at cold seeps, such as *Beggiatoa* mats, harbour a novel diverse protistan and meiofaunal community which may give insights into the origin of eucaryotes in the sea (Bernhard et al., 2000).

The debate on species diversity is sure to continue (see Levin et al., 2001 and Chapter 10). Sampling of the remoter areas of the ocean is important. This will enable the remarkable estimate of 10^7 [which Grassle and Maciolek (1992, p. 333) based on the tacit assumption of a linear increase in species number with size of sample – an assumption clearly at variance with all the small-scale evidence which they presented] to be replaced with a more realistic figure.

Observational deep-sea ecology has led to detailed understanding of seasonal processes in the deep-sea bed and how energy from surface production fuels the deep-sea ecosystem (Billett, 2001). This aspect of deep-sea understanding is now moving into the phase of experimentation.

EXPERIMENTATION

The testing of hypotheses and their falsification or acceptance underpin modern science. Experimentation, especially manipulative experimentation, makes it possible to obtain a real detailed insight into the mechanisms that drive an ecosystem. Deep-sea experimentation varies in scale, and there have been a variety of approaches from observational experimentation at relatively large scales to detailed experimental protocols on the sub-metre scale.

One of the earliest great experiments in the deep sea was the HEBBLE (High Energy Benthic Boundary Layer Experiment) programme in which the cause and effects of the transmission of mesoscale eddies to the seabed and the subsequent benthic storms on the fauna in their path were studied. Hypotheses were tested, but the data were essentially observational (see Chapter 2). A more recent large-scale experiment has been the DISCOL (Disturbance/Colonization Experiment) in the deep southeast Pacific Ocean in which the seabed was 'ploughed' up (the disturbance) and observed over the subsequent ten years to see how the perturbation was overcome by the local fauna (the colonization). As this volume is written the fauna has yet to reach pre-disturbance equilibrium (see Chapter 13).

One of the most difficult aspects of the deep sea for experimentation is temporal phenomena. Because of the necessity to collect data over a period of time, 'landers' have been developed which can be free-floated to the seabed, left for the duration of the experiment and released to the surface on command from a surface ship. This technology has developed rapidly over the last ten years, and is used extensively – for instance, to study scavenging by deep-sea crustacea and fish, or to measure temporal variables such as the oxygen consumption of the sediment community (see Chapter 11). The use of landers will continue to provide a valuable platform for deep-sea experimentation.

Possibly the greatest advance for deep-sea experimental biology has been the development of the manned submersible. In its traditional form this is a vehicle that will take pilots and observers to the deep-sea bed, where they can conduct *in situ* experiments as well as making observations. Even more recent is the development of Remote Operated Vehicles in which the vehicle is operated by a pilot and observer on the mother vessel, obviating the potential dangers of subjecting them to pressures of several hundred atmospheres in the ocean. ROVs have developed so far in the last five years that they have almost the same capability as manned submersibles. Last of the new batch of engineering technologies is the 'Autonomous Underwater Vehicle', which is able *inter alia* to map and photograph the seafloor. Such vehicles may well herald a new era of deep-sea exploration.

Submersibles have been critical to the success of observation and experimentation at hydrothermal vents. Without the ability to work at a scale of less than one metre, considerably less would have been achieved at hydrothermal vents. The physiology of the unique organisms at vents is now well understood (Van Dover, 2000), while the microenvironment (Luther et al., 2001) and the most intractable of processes, dispersal, are now being unravelled (Marsh et al., 2001; Pradillon et al., 2001). Vents are even known to emit light (White et al., 2000), leading to speculation on the origins of photosynthesis, and even life itself.

It is always possible to plan and execute experiments, but it is often the serendipitous observation that leads to some of the most exciting science. The deep sea has provided many examples, but one stands out: the effect of whale falls on the deep-sea bed. Large food falls entering the deep sea initially provide a food focus for scavengers; but it is now realized that the food fall and the scavengers structure the seabed and cause a variation in the local fauna. Subsequently, Smith et al. (1989) showed that the whale skeleton became a cold seep, and there was the suggestion that such whale falls may be the stepping stones for the dispersal of hydrothermal-vent faunas. Thus, a feature that appeared originally to have a short time-scale is now known to structure the deep-sea community over a period of decades.

A tool that is fast becoming an essential part of the armoury of the deep-sea biologist is molecular technology. The use of molecular techniques in deep-sea research has been pioneered particularly by those working at hydrothermal vents (Vrijenhoek, 1997); but the technology has massive applications in all aspects of deep-sea biology, particularly *inter alia* in the field of population biology, the identification of cryptic species (Etter et al., 1999), and the analysis of experimental studies on the invasion of the deep sea (Tyler and Young, 1998).

EXPLOITATION

The deep sea is one of the least exploited environments on earth. Challenges to it in terms of harvesting natural resources or disposing of anthropogenic waste have been essentially minimal, owing to the huge assimilative capacity of the ocean. However, the deep sea is now being seen much more to contain harvestable resources. Oil exploration is moving into deeper and deeper water. It should, however, be noted that most exploration oil companies have a positive environmental attitude to the deep sea and will not exploit if there is likely to be an environmental penalty. Of more concern is fishing activity as it moves into deeper water. Already the populations of orange roughy (*Hoplostethus atlanticus*) have declined disastrously before any useful management strategy could be put in place. Is there enough productivity along the continental margins to sustain a profitable fishing industry without the over-exploitation seen in many shelf fisheries in the North Atlantic? Fishing at bathyal depths in the northeast Atlantic is both actively and passively resulting in the destruction of colonies of the deep-water coral *Lophelia pertusa* and of the large hexactinellid sponges that are found on soft sediments and rock. Remarkably little is known about these magnificent organisms or the associated faunas. Such knowledge should be gained before exploitation continues. These are specific challenges for the deep-sea biologist.

Disposal in the deep sea is nowhere near the scale on which it has occurred in coastal waters. Environmental legislation is resulting in the clean-up of coastal waters, and may limit any disposal in the deep sea. Since the 1980s, official action has been taken to limit waste disposal in the deep sea; previously it was more or less unrestricted (see Chapter 13). Subsequently, there has been interest in the disposal of certain types of waste. The 1980s saw great interest in the potential disposal of high-level radioactive waste, and the 1990s saw the publicity disaster (for those involved) of trying to dispose of large structures such as the Brent Spar (Rice and Owen, 1998; Rice, 2001). The late 1990s and early 21st century have seen interest in the disposal of excess carbon dioxide as gas hydrates in the deep ocean. None of these proposals has yet passed the 'ideas and practicalities' stage, although some experiments in carbon dioxide disposal have already taken place on a small scale (Brewer et al., 2000; Tamburri et al., 2000).

CONCLUSIONS

The deep sea provides one of the most challenging environments on the planet. One knows that the ocean in total is an important buffer for the world's climate and for the transport of heat and oxygen. However, remarkably little is actually known about it; it is thus imperative, before there is any further major exploitation, that a full range of studies be mounted of the systems and processes driving this, the largest ecosystem on earth – potentially the most biologically diverse, and in the opinion of the authors in this book the most interesting!

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GLOSSARY

Abyssal. Between 3000 and 6000 m deep; the abyssal plain.

Aleurites. A term used primarily in the Russian literature referring to silt-sized particles.

Authigenic. Minerals formed where they are now found; the products of chemical and biochemical action.

Barophilic. Those organisms that can only live at high pressure and do not survive at low pressure; literally, "lover of pressure".

Bathyal. Between ~200 and 3000 m deep; the continental slope.

Benthic lander. Any piece of apparatus that is free-floated to the seabed, carries out observations or analysis, and floats to the surface on weight release.

Benthopelagic. The zone in the water column immediately above the sea bed. It often has its own distinct fauna.

Box corer. A piece of equipment for taking a square core from the seabed with an area of 0.25 m^2. The main apparatus used for quantitative deep-sea benthic ecology.

Calcium carbonate compensation depth. The depth at which calcium carbonate goes into solution.

Depocentre. An area or site of maximum deposition.

Diagenetic process. The compression and hardening of sediment into rock.

Diapir. A salt dome in sediment, often associated with oil deposits.

Diatreme. A volcanic vent or pipe drilled through enclosing rocks by the explosive energy of gas-charged magma.

Ekman layer. A layer in which water is moved to the right (northern hemisphere) or left (southern hemisphere) of the wind direction.

Epibenthic sledge. A sampling apparatus towed over the seabed using a fine mesh as a filter.

Epibenthos. Those animals living on the surface of the seabed.

Eurybathic. Having a wide depth range.

Hadal. Deeper than 6000 m; the oceanic trenches.

Hemipelagic. Silt-sized fraction of sediment found on or near continental margins composed of plankton flux and terrigenously derived material.

Hyperbenthic. Those animals living in the water column immediately above the seabed; cf. benthopelagic, suprabenthos.

Ladder of migration. term for the overlapping vertical distribution of pelagic species down through the water column.

Macrobenthos. Animals retained by an 0.5 mm sieve but not visible in bottom photographs; cf. macrofauna.

Macrofauna. Animals retained by an 0.5 mm sieve.

Macroinfauna. Macrofauna living in the sediment.

Macroplankton. Zooplankton with dimensions between 200 μm and 2 mm.

Macrophyte. Large plant material in the sea, usually algae but occasionally flowering plants.

Marine snow. Aggregates of organic and inorganic particles sinking through the water column.

Mass wasting. The slippage of large amounts of sediment down the continental slope.

Megafauna. Those animals on the seabed visible to the camera.

Mega-infauna. Large animals burrowed in the sediment.

Megaturbidite. A very large turbidite.

Meiofauna. Those animals that pass through a 0.5 mm sieve.

Mesopelagic. The zone in the water column between ~400 and 1000 m depth.

Microbiota. Microorganisms, usually unicellular, especially bacteria.

Micronekton. Small swimming organisms in the water column.

Nekton. Organisms that swim in the water column, e.g. fish, cetaceans, squid.

Nepheloid. A turbid layer of water immediately above the seabed or associated with a physical discontinuity such as a thermocline.

Neuston. Organisms living at the immediate water/air interface; often blue in colour.

Opal flux. The flux of silica to the seabed.

Pelagic. Within the water column.

Phytoplankton. Plants floating in the water column.

Phytodetritus. Organic aggregates in the water column and on the deep-sea bed formed from phytoplankton debris.

Picoplankton. Plankton with dimensions from 0.2 to 2.0 μm.

Potential temperature (θ). The temperature of deep water once the heating effect of high pressure is removed.

Plankton. Organisms floating in the water column, mainly bacteria.

Sled or Sledge. A piece of apparatus towed over the seabed.

Stenobathic. Having a narrow depth range.

Stepper motor. A very controllable form of motor working on a series of pulses.

Suprabenthos. Those animals living in the water column immediately above the seabed.

Surficial. At the very surface of the sediment.

Sverdrup (Sv). A measure of water flow (10^6 m^3 s^{-1}).

Trawl. A net for catching fish and large invertebrates.

Turbidite. A graded sequence of sediment, both horizontally and vertically, laid down by a turbidity current.

Zooplankton. Animals floating in the water column.

SYSTEMATIC LIST OF GENERA

All taxa mentioned in the text are included in their taxonomic position. Taxa have been included down to either order or family level. Taxa appear in alphabetical order. Where possible, higher taxon levels are primarily based on Barnes, R.S.K. (Editor), *The Diversity of Living Organisms* (1998, Blackwell Science, Oxford). A large number of colleagues have offered advice and guidance on the classification of particular taxa. I thank them sincerely but retain responsibility for any errors.

BACTERIA
(= Monera or Procaryota)

ARCHAEA
EUBACTERIA
PROTEOBACTERIA
Beggiatoa
Desulphovibrio
Thioploca

ENDOSPORA
Clostridium

CYANOBACTERIA

PROTOCTISTA
(= Protista)

HAPTOMONADA
(= coccolithophorids)
DINOMASTIGOTA
(= dinoflagellates)
BACILLARIOPHYTA
(= diatoms)
CHLOROPHYTA
GRANULORETICULOSA
FORAMINIFERA
Allogromida
Tinogullmia
Astrorhizida
Crithionina
Hyperammina
Lagenammina
Oryctoderma
Rhabdammina
Saccorhiza
Astrorhizida
(Superfamily Komokiacea)
Lagenida
Lagena
Lenticulina
Miliolida
Miliolinella
Pyrgo
Rotaliida
Alabaminella
Bathysiphon
Bolivinia
Bulimina
Cibicides
Cibicidoides
Ehrenbergina
Elphidium
Epistominella
Globobulimina
Hyalinea
Oridorsalis
Rupertina
Uvigerina
Textulariida
Cribrostomoides
Cyclammina
Leptohalysis
Reophax
Subreophax
Tritaxia
Trochammina

XENOPHYOPHORA
XENOPHYOPHOREA
Psamminida
Psamminidae
Reticulammina
Stannomidae
Stannophyllum
Syringamminidae
Syringammina

CILIOPHORA (= ciliates)
SPIROTRICHEA
Oligotrichida
Tintinnida (= tintinnids)

ACTINOPODA
(= radiolarians)
PHAEODARIA (= Sarcodina)

RHIZOPODA
ZOOMASTIGOTA
(= zooflagellates)

FUNGI

PLANTAE

PHAEOPHYTA
PHAEOPHYCEAE
Laminariales
Hydrocharitaceae
Macrocystis
Fucales
Sargassaceae
Sargassum

TRACHEOPHYTA
MAGNOLIOPSIDA
LILIOPHYTA
Thalassia
MAGNOLIOPHYTA
Quercus

ANIMALIA

PORIFERA
DEMOSPONGIAE
Astroporida
Ancorinidae
Stryphnus
Geodiidae
Isops
Lithistida
Poecilosclerida
Cladorhizidae
Asbestopluma
Myxillidae
Ectomyxilla

SYMPLASMA
HEXACTINELLIDA
Hyalonema
Pheronema

CNIDARIA
MEDUSOZOA
HYDROZOA
Conica
Campanulinidae
Lafoeina
Filifera
Stylasteridae
Crypthelia
Errina
Siphonophora
Physaliidae
Physalia
SCYPHOZOA
ANTHOZOA
ALCYONARIA
Alcyonacea
Anthomastus
Eunephthya
Gorgonacea
Corallium
Isidella
Muricea
Primnoa
Radicipes
Pennatulacea
Distichoptilum
Kophobelemnon
Pavonaria
Pennatula
Stylatula
Umbellula
ZOANTHARIA
(= Hexacorallia)
Ceriantharia
Cerianthus
Antipatharia
Antipathes
Actinaria
Actinoscyphia
Amphianthus
Bolocera
Halcurias
Hormathia
Kadosactis
Paracalliactis
Phelliactis
Sicyonis
Scleractinia
Caryophyllia
Desmophyllum
Desmosmilia
Lophelia
Madrepora
Thecopsammia
Zoanthinaria
Epizoanthus

ANNELIDA
OLIGOCHAETA
POLYCHAETA
Amphinomida
Amphinomidae
Benthoscolex
Paramphinome
Euphrosinidae
Euphrosine
Capitellida
Capitellidae
Capitella
Capitellides
Heteromastus

Notomastus
Maldanidae
Cossurida
Cossuridae
Cossura
Eunicida
Eunicidae
Eunice
Onuphidae
Hyalinoecia
Nothria
Onuphis
Paronuphis
Dorvilleidae
Ophryotrocha
Protodorvillea
Fauveliopsida
Fauveliopsidae
Fauveliopsis
Flabelligerida
Flabelligeridae
Brada
Opheliida
Opheliidae
Ophelina
Scalibregmidae
Scalibregma
Orbinida
Orbiniidae
Aricia
Methanoaricia
Microrbinia
Paraonidae
Aricidea
Cirrophorus
Oweniida
Oweniidae
Myriochele
Phyllodocida
Aphroditidae
Macellecephala
Macellecephaloides
Glyceriidae
Glycera
Hesionidae
Hesiocaeca
Lacydoniidae
Lacydonia
Nephthyiidae
Nephthys
Nereidae
Nicon
Phyllodocidae
Pilargiidae
Sigambra
Pisionidae
Polynoidea
Bathynoe
Branchipolynoe
Harmothoe
Opisthotrochopodus
Sigalionidae
Pholoe
Syllidae
Sabellida
Sabellidae
Euchone
Potamilla
Serpulidae
Omphalopomopsis
Placostegus
Spionida
Acrocirridae
Chaetopteriidae
Chaetopterus
Cirratulidae
Aphelochaeta
Chaetozone
Tharyx
Poecilochaetidae
Poecilochaetus
Spionidae
Aurospio
Minuspio
Paraprionospio
Prionospio
Terebellida
Alvinellidae
Alvinella
Paralvinella
Ampharetidae
Acanthicolepis
Ampharete
Amphisamytha
Eclyssipe
Lagisca
Paedampharete
Sabellariidae
Jasmineria
Terebellidae
Biremis
Frenulata
(= perviate Pogonophora)
Lamellisabellidae
Lamellisabella
Siboglinidae
Siboglinum
Monolifera
(= monoliferan Pogonophora)
Vestimentifera
Escarpiidae
Escarpia
Seepiophilia
Lamellibrachiidae
Lamellibrachia
Ridgeiidae
Ridgeia
Riftidae
Riftia
Tevniidae
Tevnia

NEMATODA

ADENOPHORA
Chromadorida
Axonolaimidae
Pararaeolaimus
Chromadoridae
Acantholaimus
Desmodoridae
Desmodora
Desmoscolecidae
Tricoma
Greeffielidae
Greeffiella
Leptolaimidae
Camaicolaimus
Leptolaimus
Plectidae
Setoplectus
Enoplida
Enoplidae
Enoplus
Ironidae
Syringolaimus
Oxystominidae
Halalaimus
Rhabdodemaniidae
Rhabdodemania
Thoracostomopsidae
Enoplolaimus
Monhysterida
Comesomatidae
Sabatieria
Sphaerolaimidae
Parasphaerolaimus
Sphaerolaimus
Subsphaerolaimus
Xyalidae
Theristus

PRIAPULIDA

NEMERTEA

Phallonemertes

ECHIURA

Bonellia

SIPUNCULA

Aspidosiphon
Golfingia
Onchnesoma

KINORHYNCHA
ROTIFERA
CHELICERATA

PYCNOGONIDA

CRUSTACEA

OSTRACODA
Myodocopia
Alacia
Archiconchoecia
Gigantocypris
Proceroecia
COPEPODA
Calanoida
Calanoides
Calanus
Harpacticoida
CIRRIPEDIA
Thoracica
Balanus
Poecilasma
MALACOSTRACA
Leptostraca
Stomatopoda
Kempina
Peracarida
Isopoda
Asellota
Acanthaspiidae
Dendrotiidae
Eurycopidae
Eurycope
Storthyngura
Illyarachnidae
Ilyarachna
Ischnomesidae
Munnidae
Munnidopsidae
Nannoiscidae
Paramunnidae
Plerocopidae
Stenetriidae
Flabellifera
Bathynomidae
Bathynomus
Cirolanidae
Natatolana
Flabelligeridae
Serolidae
Gnathiidea
Gnathiidae
Valvifera
Arcturidae
Amphipoda
Ampeliscidae
Ampelisca
Eusiridae
Eusirus
Hyperiidae
Themisto
Lysianassidae
Alicella
Eurythenes
Glycerina
Hirondellea
Orchomene
Paralicella
Pseudamaryllis
Socarnes
Mellitidae
Eriopisa
Phoxocephalidae
Harpiniopsis
Pseudharpinia
Tanaidacea
Cumacea
Diastyllidae
Diastylis
Diastyloides
Leptostylis
Leuconidae
Leucon
Nannastacidae
Procampylaspis

Mysidacea
Gnathophausiidae
Gnathophausia
Mysidae
Boreomysis
Erythrops
Michthyops
Eucarida
Euphausiacea
Euphausiidae
Euphausia
Meganyctiphanes
Nyctiphanes
Decapoda
Dendrobranchiata
Aristeidae
Aristeus
Benthesicymidae
Benthesicymus
Penaeidae
Haliporus
Plesiopenaeus
Sergestidae
Sergestes
Sergia
Pleocyemata
Caridea
Bresiliidae
Alvinocaris
Chorocaris
Mirocaris
Rimicaris
Nematocarcinidae
Nematocarcinus
Oplophoridae
Acanthephyra
Oplophorus
Systellaspis
Pandalidae
Pandalina
Pandalopsis
Parapandalus
Plesionika
Thalassinidae
Calocaridae
Calocaris
Macrura
Polychelidae
Stereomastis
Willemoesia
Anomura
Chirostylidae
Chirostylus
Eumunida
Uroptychus
Galatheidae
Galathea
Munida
Munidopsis
Paralomis
Homolidae
Paromola
Lithodidae
Neolithodes
Paguridae
Parapaguridae
Parapagurus
Brachyura
Bythograeidae
Bythograea
Cancridae
Cancer
Dromiidae
Goneplacidae
Bathyplax
Geryonidae
Chaceon
Geryon
Leucosidae
Ebalia
Majidae
Achaeus
Anamathia
Chionoecetes
Dorhynchus
Encephaloides
Rochina
Portunidae
Charybdis

MOLLUSCA

APLACOPHORA

Prochaetodermatidae
Prochaetoderma

POLYPLACOPHORA

Hanleya

GASTROPODA

EOGASTROPODA
Docoglossa (= Patellogastropoda)
Neolepetopsidae
ORTHOGASTROPODA
CAENOGASTROPODA
Sorberoconcha
Buccinidae
Colus
Neptunea
Ianthinidae
Ianthina
Laubierinidae
Muricidae
Murex
Provannidae
Rissoidae
Alvania
Benthonella
Styliferidae
Pelseneeria
Neomphalina
Neritopsina
Neritoida
Neritidae
Bathynerita
Vetigastropoda
Pleurotomariidae
Entemnotrochus
Trochidae
Bathybembix
Calliotropis
Cocculiniformia
Pyropeltidae
Heterobranchia
Nudibranchia
Glaucidae
Glaucus
Gymnostomata
(= naked pteropods)
Thecostomata
(= shelled pteropods)

SCAPHOPODA

Dentalida
Cadulus

BIVALVIA

PROTOBRANCHIA
Nuculida
Nuculanidae
Deminucula
Ledella
Malletia
Nucula
Nuculana
Nuculoma
Yoldia
Solemyida
Solemyidae
Acharax
LAMELLIBRANCHIA
Pterioidea
Amussidae
Amussium
Arcida
Arcidae
Arca
Bathyarca
Mytilida
Bathymodiolidae
Bathymodiolus
Mytilidae
Amygdalum
Idas
Idasola
Pectinidae
Aceste
Chlamys
Pecten
Spondylus
Thyasiridae
Axinus
Thyasira
Tindariidae
Tindaria
Vesicomyidae
Calyptogena
Vesicomya
Xylophaginidae
Xyloredo
Xylophaga

CEPHALOPODA

Nautiloidea
Nautilus
Octopoda
Japetella
Spirulida
Spirula
Teuthoidea
Cranchidae
Vampyromorpha
Vampyroteuthis

PHORONIDA
BRYOZOA
BRACHIOPODA

Pelagodiscus

ECHINODERMATA

CRINOIDEA

Comatulida
Antenonidae
Thaumatometra
Isocrinida
Isocrinidae

ASTEROIDEA

Brisingida
Brisingidae
Brisinga
Brisingella
Freyellidae
Freyella
Forcipulata
Pedicellasteridae
Pedicellaster
Zoroasteridae
Zoroaster
Notomyida
Benthopectinidae
Benthopecten
Luidiaster
Pectinaster
Pontaster
Paxillosida
Astropectinidae
Bathybiaster
Dytaster
Plutonaster
Psilaster
Porcellanasteridae
Hyphalaster
Porcellanaster
Styracaster
Goniopectinidae
Ctenodiscus
Valvatida
Goniasteridae
Paragonaster
Pseudarchaster
Velatida
Pterastidae
Hymenaster

CONCENTRICYCLOIDEA

Peripodida
Xyloplax

OPHIUROIDEA

Phrynophiurida
Gorgonocephalidae
Astrophyton
Ophiurida
Amphiuridae
Amphilepis
Ophiacanthidae
Amphilimna

- *Ophiacantha*
- *Ophiolimna*
- *Ophiophthalmus*
- Ophioleucidae
  - *Ophiopyren*
- Ophiuridae
  - *Amphiophiura*
  - *Homalophiura*
  - *Ophiocten*
  - *Ophiomusium*
  - *Ophiura*

ECHINOIDEA

- **Cassiduloida**
  - Cassidulae
    - *Conolampas*
- **Cidaroida**
  - Cidaridae
    - *Cidaris*
    - *Poriocidaris*
    - *Stylocidaris*
- **Clypeasteroidea**
  - Scutellidae
    - *Echinarachnius*
- **Diadematoida**
  - Arbacidae
    - *Coelopleurus*
  - Aspidodiadematidae
    - *Aspidodiadema*
  - Echinidae
    - *Echinus*
    - *Lytechinus*
  - Echinothuridae
    - *Araeosoma*
    - *Calveriosoma*
    - *Hygrosoma*
    - *Phormosoma*
    - *Sperosoma*
  - Salenidae
    - *Salenia*
  - Strongylocentrotidae
    - *Allocentrotus*
- **Spatangoida**
  - Hemisateridae
    - *Brisaster*
  - Laganidae
    - *Laganum*
  - Palaeopneustidae
    - *Archaeopneustes*
    - *Linopneustes*
    - *Palaeobrissus*
    - *Phrissocystis*
  - Palaeostomidae
    - *Palaeostoma*
  - Pourtalesidae
    - *Pourtalesia*
  - Spatangidae
    - *Brissopsis*
    - *Echinocardium*
    - *Spatangus*

HOLOTHUROIDEA

- **Elasipodida**
  - Deimatidae
    - *Deima*
    - *Oneirophanta*
  - Elpidiidae
    - *Amperima*
    - *Ellipinion*
    - *Elpidia*
    - *Kolga*
    - *Peniagone*
    - *Scotoplanes*
  - Laetmogonidae
    - *Benthogone*
    - *Laetmogone*
    - *Pannychia*
  - Psychropotidae
    - *Benthodytes*
    - *Psychropotes*
- **Aspidochirotida**
  - Holothuridae
    - *Holothuria*
  - Synallactidae
    - *Bathyplotes*
    - *Hansenothuria*
    - *Mesothuria*
    - *Paelopatides*
    - *Paroriza*
    - *Pseudostichopus*
- **Dendrochirotida**
  - Cucumariidae
    - *Abyssocucumis*
- **Dactylochirotida**
  - Ypsilothuridae
    - *Ypsilothuria*
- **Molpadida**
  - Molpadidae
    - *Cherbonniera*
    - *Molpadia*
- **Apodida**
  - Chiridotidea
    - *Chirodota*

CHAETOGNATHA

HEMICHORDATA

ENTEROPNEUSTA

- *Planktosphaera*
- *Saxipendium*
- *Stereobalanus*

CHORDATA

UROCHORDATA

ASCIDIACEA

- **Phlebobranchia**
  - Ascidiidae
    - *Hypobythius*
- **Stolidabranchia**
  - Pyuridae
    - *Bathypera*
    - *Culeolus*
  - Styelidae
    - *Styela*

THALIACEA

- **Doliolida**
  - Doliolidae
- **Salpida**
  - Salpidae

LARVACEA

VERTEBRATA

AGNATHA

- **Hyperatreta**
  - Myxinidae
    - *Eptatretus*

CHONDRICHTHYES (= Selachii)

- **Pleurotremata**
  - Carcharhinidae
    - *Iago*
  - Chimaeridae
  - Hexanchidae
    - *Heptanchus*
    - *Hexanchus*
  - Rajidae
  - Scyliorhinidae
    - *Galeus*
  - Squalidae
    - *Centroscymnus*
    - *Etmopterus*
    - *Somniosus*

OSTEICHTHYES

- **Anguilliformes**
  - Muraenesocidae
    - *Muraenesox*
  - Synaphobranchidae
    - *Synaphobranchus*
- **Antheriniformes**
  - Antherinidae
    - *Paraliparis*
- **Beryciformes**
  - Trachichthyidae
    - *Hoplostethus*
- **Clupeiformes**
  - Alepocephalidae
  - Engraulidae
    - *Engraulis*
  - Gonostomatidae
    - *Cyclothone*
    - *Gonostoma*
  - Malacosteidae
    - *Aristostomias*
    - *Malacosteus*
  - Melanostomiidea
    - *Pachystomias*
  - Sternoptychidae
    - *Argyropelecus*
- **Gadiformes**
  - Gadidae
    - *Gadus*
    - *Lepidion*
    - *Phycis*
    - *Urophycis*
  - Macrouridae
    - *Coryphaenoides*
    - *Nezumia*
  - Merlucciidae
    - *Merluccius*
  - Moridae
  - Zoarcidae
    - *Lycenchelys*
    - *Pachycara*
    - *Typhlonus*
- **Lophiformes**
  - Lophiidea
    - *Lophiodes*
- **Perciformes**
  - Lumpenidae
  - Trichiuridae
    - *Aphanopus*
- **Pleuronectiformes**
  - Pleuronectidae
    - *Pleuronichthys*
- **Scopeliformes**
  - Ipnopidae
    - *Bathymicrops*
    - *Bathypterois*
  - Myctophidae
    - *Benthosema*
    - *Ceratoscopelus*
- **Scorpaeniformes**
  - Anoplopomatidae
    - *Anoplopoma*
  - Cottidae
  - Liparidae
  - Scorpaenidae
    - *Sebastes*
    - *Sebastolobus*

MAMMALIA

- **Cetacea**
  - Delphinidae
  - Balaenopteridae
    - *Balaenoptera*

AUTHOR INDEX[1]

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[1] Page references to text are in roman type, to bibliographical entries in italics.

SYSTEMATIC INDEX

GENERAL INDEX