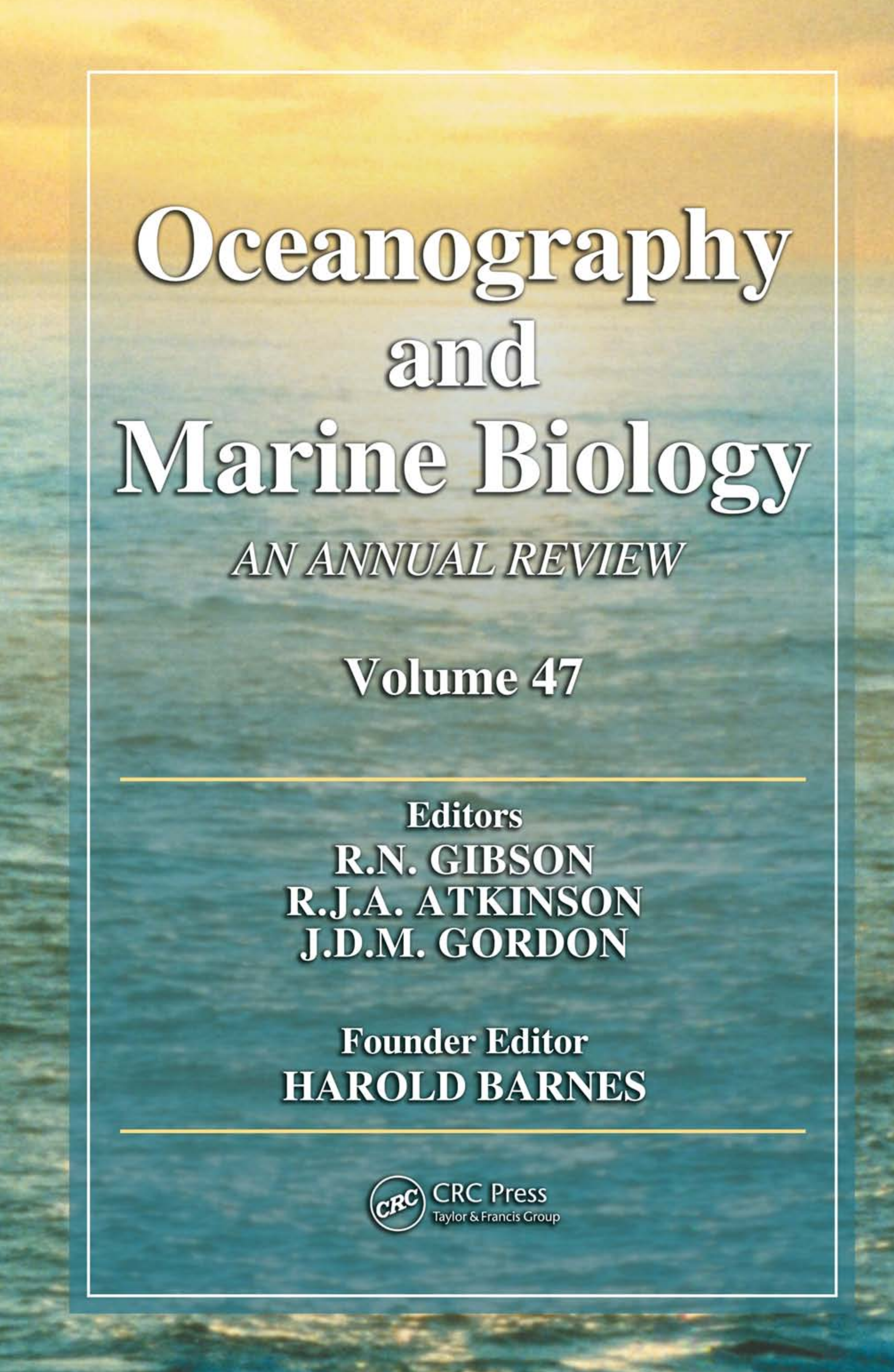

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AN ANNUAL REVIEW

Volume 47

Editors
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R.J.A. ATKINSON
J.D.M. GORDON

Founder Editor
HAROLD BARNES

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MARINE BIOLOGY

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Preface

The 47th volume of this series contains six reviews written by an international array of authors that, as usual, range widely in subject and taxonomic and geographic coverage. The editors welcome suggestions from potential authors for topics they consider could form the basis of future appropriate contributions. Because an annual publication schedule necessarily places constraints on the timetable for submission, evaluation and acceptance of manuscripts, potential contributors are advised to make contact with the editors at an early stage of preparation. Contact details are listed on the title page of this volume.

The editors gratefully acknowledge the willingness and speed with which authors complied with the editors' suggestions, requests and questions and the efficiency of CRC Press, especially Marsha Hecht, in ensuring the timely appearance of this volume.

Erratum to “Biology of the planktonic stages of benthic octopuses”

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Refers to: Villanueva, R. & Norman, M.D. 2008. Biology of the planktonic stages of benthic octopuses. *Oceanography and Marine Biology: An Annual Review* **46**, 105–202.

The publisher regrets the error introduced after proofreading in the scales of Figures 20 and 25 in the above paper. The corrected figures are reproduced as follows:

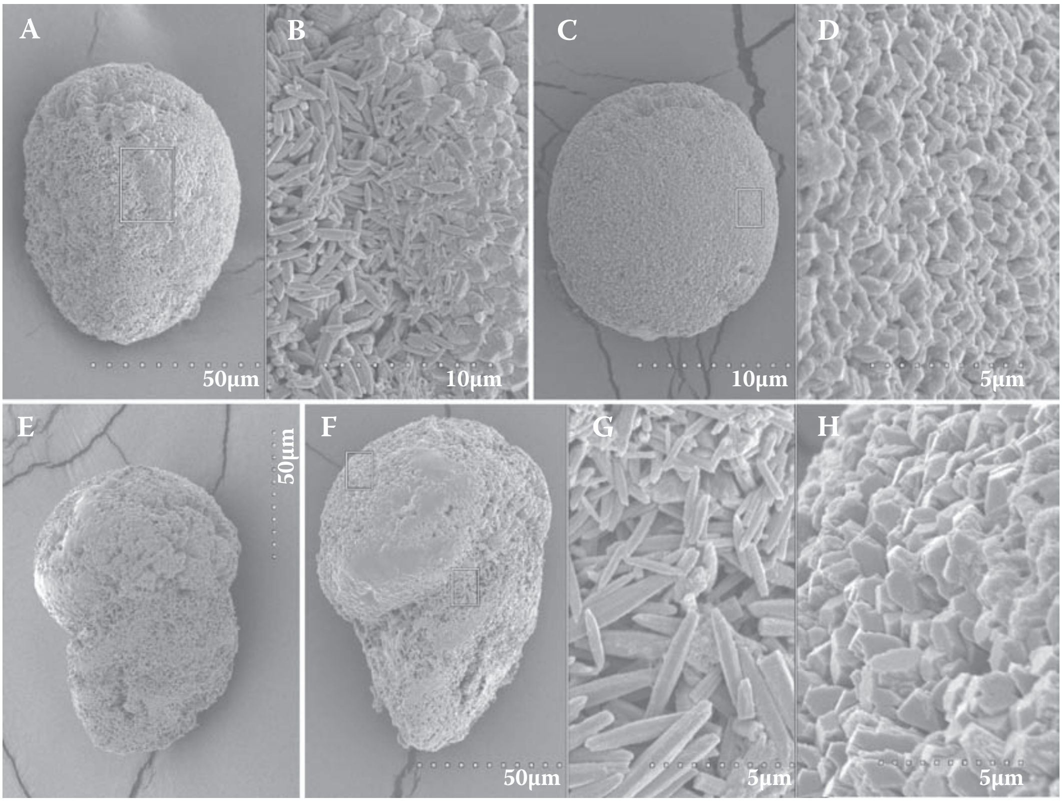

Figure 20 Statoliths of *Octopus vulgaris* paralarvae. Scanning electron micrographic images from antero-lateral (A) and posterior (C) views of hatchling statoliths with their respective crystalline surface structure presented inside the rectangles (B, D). In paralarvae aged 30 days, statolith growth is observed on the posterior side of the statolith (E, F). The crystalline structure of the surface observed inside the lower (G) and upper (H) rectangle of the image F is also indicated. Individuals obtained from rearing experiments described in Villanueva et al. (2004). Original.

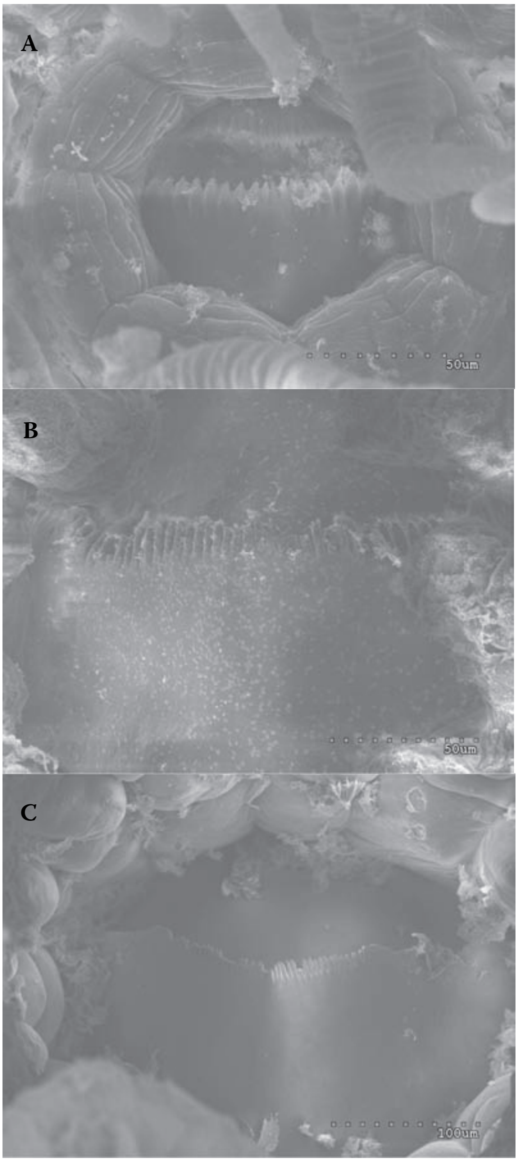

Figure 25 Denticulation of beaks in *Octopus vulgaris* paralarvae. Scanning electron micrographic images of (A) oral view of hatchling; (B) 50-day-old specimen in presettlement stage, 7.3 mm mantle length (ML) (fresh); and (C) 60-day-old recently settled individual of 9.3 mm ML (fresh). Note the broken denticles on the lower beaks of posthatching individuals and the rostral tip of the beak in the settled individual, in transition to the typical adult beak form. Individuals obtained from rearing experiments described in Villanueva (1995). Original.

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Villanueva, R. 1995. Experimental rearing and growth of planktonic *Octopus vulgaris* from hatching to settlement. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2639–2650.

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TRANSREGIONAL LINKAGES IN THE NORTH-EASTERN ATLANTIC — AN 'END-TO-END' ANALYSIS OF PELAGIC ECOSYSTEMS

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Abstract This review examines interregional linkages and gives an overview perspective on marine ecosystem functioning in the north-eastern Atlantic. It is based on three of the 'systems' considered by the European Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS was established in 2004 under the European Framework VI funding programme to promote integration of marine ecological research within Europe), the Arctic and Nordic Seas, North Atlantic shelf seas and North Atlantic. The three systems share common open boundaries and the transport of water, heat, nutrients and particulates across these boundaries modifies local processes. Consistent with the EUR-OCEANS concept of 'end-to-end' analyses of marine food webs, the review takes an integrated approach linking ocean physics, lower trophic levels and working up the food web to top predators such as marine mammals. We begin with an overview of the regions focusing on the major physical patterns and their implications for the microbial community, phytoplankton, zooplankton, fish and top predators. Human-induced links between the regional systems are then

considered and finally possible changes in the regional linkages over the next century are discussed. Because of the scale of potential impacts of climate change, this issue is considered in a separate section. The review demonstrates that the functioning of the ecosystems in each of the regions cannot be considered in isolation and the role of the atmosphere and ocean currents in linking the North Atlantic Ocean, North Atlantic shelf seas and the Arctic and Nordic Seas must be taken into account. Studying the North Atlantic and associated shelf seas as an integrated 'basin-scale' system will be a key challenge for the early twenty-first century. This requires a multinational approach that should lead to improved ecosystem-based approaches to conservation of natural resources, the maintenance of biodiversity, and a better understanding of the key role of the north-eastern Atlantic in the global carbon cycle.

Introduction

The European Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS) was established in 2004 under the European Framework VI funding programme to promote the integration of marine ecological research within Europe. The network includes around 140 researchers based in 69 research institutes from 26 countries and deals with research on pelagic ecosystems. When the network was founded in 2004, seven 'systems' were defined to give geographical scope to the project. These were the Arctic and Nordic Seas, Baltic, Mediterranean, North Atlantic Ocean, North Atlantic shelf seas, Southern Ocean and Upwelling regions. Since many aspects of marine ecosystem functioning are related to latitude, bathymetry, and distinct climate regions, these ecosystems do display some internally coherent features (e.g., productivity in the Arctic Seas is typified by strong seasonality). However, marine ecosystems do not exist in isolation and this is particularly true for those systems with relatively open boundaries. The Arctic and Nordic Seas, North Atlantic shelf seas and North Atlantic share common boundaries and the processes occurring across their boundaries act to modify local processes in important ways. This review examines these interlinkages and gives a regional perspective to marine ecosystem functioning in the north-eastern Atlantic (Figure 1). Because of EUR-OCEANS' focus on pelagic systems, the review does not deal

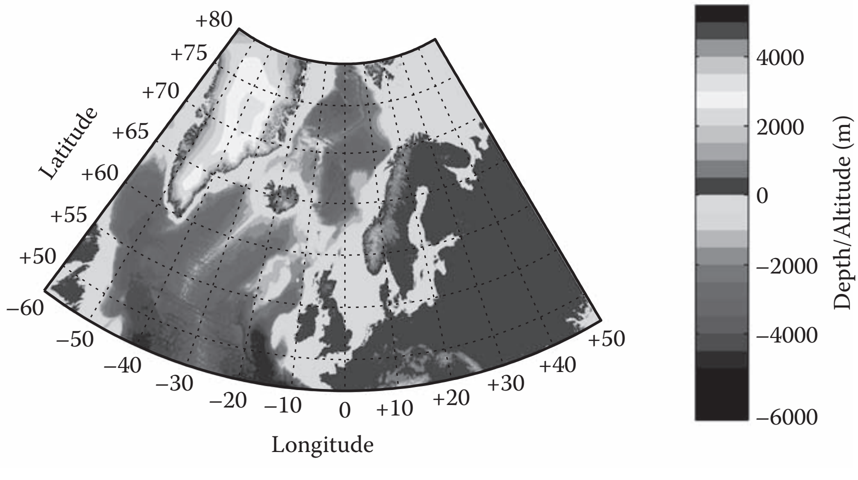

Figure 1 (See colour insert following page 52.) Overall topography of the north-eastern Atlantic, elevations in metres from mean sea level (MSL). (Prepared from ETOPO2v2 data.)

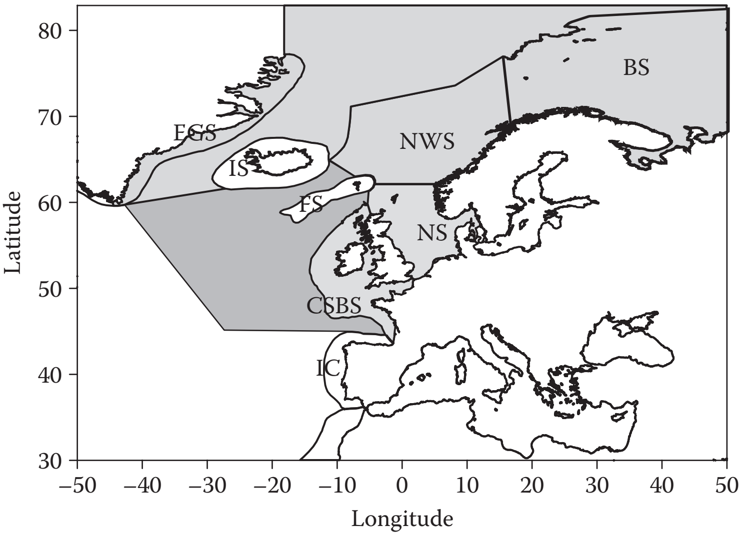

Figure 2 (See colour insert.) Large Marine Ecosystems (LME) boundaries within the north-eastern Atlantic. Colour coding refers to merging of LMEs and offshore regions to yield the three EUR-OCEANS systems: Nordic and Arctic Seas (blue), European shelf seas (yellow) and Atlantic Ocean (green). Processes occurring on the Icelandic Shelf and Faroes Shelf are not covered in this review. EGS = East Greenland Shelf; NWS = Norwegian Sea; BS = Barents Sea; IS = Icelandic Shelf; FS = Faroes Shelf; NS = North Sea; CSBS = Celtic Sea Biscay Shelf; IC = Iberian Coastal.

extensively with benthic ecology although the importance of benthic-pelagic coupling in nutrient recycling and the carbon cycle is acknowledged.

The system concept used in EUR-OCEANS is similar to the Large Marine Ecosystems (LME) introduced by Sherman et al. (1993). The aim of LME was to define sea areas on the basis of distinct bathymetry, hydrography, productivity and trophic interactions to promote coherent analyses of their functioning and health (Figure 2). The LME defined by Sherman did not extend into the deep oceans. However, as shown in this review, the linkages between the deep oceans and the LME cannot be ignored. Since then, reviews of ecosystem functioning in several defined areas within the north-eastern Atlantic have been undertaken (e.g., for the Nordic Seas; Skjoldal 2004) and the Regional Quality Status Reports produced under the auspices of OSPAR. However, all these approaches suffer from the delineation of somewhat artificial boundaries. Although some geographic features, such as the shelf break, do define genuine transition zones between areas where different physical and biological processes dominate (e.g., tidal mixing is dominant on the shelf seas but less important in the open Atlantic), other boundaries are more arbitrary and have been drawn in relation to national or management considerations. The aim of the present review is to consider the interlinkages in the north-eastern Atlantic, that is between the Arctic and Nordic Seas, European shelf seas and Atlantic Ocean.

This review is also structured using EUR-OCEANS' concept of 'end-to-end' analyses, which starts with a consideration of the physics and works up the food web to top predators such as marine mammals. For brevity, the review is also largely constrained to looking at those mechanisms 'linking' EUR-OCEANS' regions and not the internal processes occurring within them. Ocean currents, particularly downstream branches of the North Atlantic current, form the main physical link between the systems. Heat, dissolved nutrients and particulates are all transported by these currents. This has significant impacts within the regions themselves (e.g., the transport of heat by the North Atlantic current (NAC) is the reason why ice cover is more limited in the Nordic Seas compared to other areas at the same latitude). For pelagic biota, life-cycle duration tends to increase moving from lower to higher trophic levels. For example, individual phytoplankton cells, once in

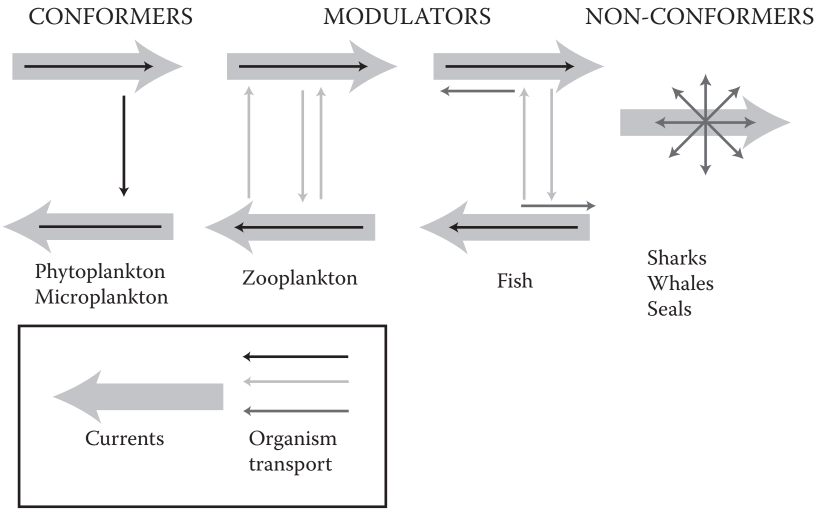

Figure 3 (See colour insert.) Role of water currents for individual dispersal options. *Conforming species* have insufficient motility to be anything other than passive to the general water flow. *Modulators* are primarily transported by water flow but can move vertically between flows to influence their trajectory. *Non-conformers* have sufficient mobility to overcome water flow. Some species, particularly fish, switch between conforming, modulating and non-conforming at different life stages.

a productive phase, can complete growth and division in a few days whilst many zooplankton take months to complete their life cycles. Consequently, longer-lived planktonic organisms can be dispersed over much larger distances compared with shorter-lived species. Although larger organisms such as fish are less directly affected by ocean currents, many have a planktonic larval phase. These can often exploit vertical differences in currents to influence their dispersal (Figure 3). In contrast, marine mammals can overcome flow velocities at all their life stages. Their life strategies and behaviour are therefore linked to the distribution patterns of their prey and predators. Moving from end-to-end we see that there is a transition from direct effects of oceanography on the dispersal of organisms to indirect effects via predator and prey distributions.

As well as direct oceanographic linkages between the regions, human activities are also increasing the exchange of materials between the regions. The most obvious example is the introduction of alien species ('alien species' refers to a species, subspecies or lower taxon introduced outside its natural past or present distribution whilst 'invasive alien species' means an alien species whose introduction or spread threaten biological diversity (Convention on Biological Diversity COP6 Decision VI/23), either via ships' ballast water, hull fouling or through aquaculture. Because of the regional connections many pollutants, introduced into one region, will spread through the north-eastern Atlantic. Finally, through industrial activities, humans are altering the concentrations of 'greenhouse' gases in the atmosphere and it is now almost certain that this is causing changes in climate that will persist over the rest of this century and beyond. In addition to affecting local temperatures, winds and precipitation/evaporation, this will lead to changes in some ocean currents, again affecting the whole north-eastern Atlantic. As our understanding of marine ecosystems improves we are beginning to appreciate how local-scale ecology is linked to the complete range of spatial and temporal scales ranging from regional to global, short term to long term and from the underlying physics to top predators. Appreciation of these interconnections by wider society is vital if we are to manage our activities in ways that promote the sustainable use and development of European marine resources.

Overview of the regions

The Nordic and Arctic Seas: general geography, size, bathymetry

The 'Nordic Seas' is used as a common name for the waters to the north of the Greenland-Scotland Ridge and between Greenland, Norway and Spitsbergen. This region forms the main connection between the North Atlantic and the Arctic Oceans. This area also includes wide shelf areas bordering the Arctic land masses. The International Hydrographic Bureau defines the Norwegian Sea as bounded to the east by the coast of Norway, on the north-east a line from North Cape over Bear Island to the south-west point of Spitsbergen (one of the Svalbard Islands). The western limit extends from this point along a line to Jan Mayen and further to the eastern tip of Iceland. The southern limit extends from there to the Faroe Islands and follows the 61st parallel to the coast of Norway. More recently, the oil industry has found it more practical to apply the 62°N parallel as the southern border of the Norwegian Sea. From an oceanographic point of view, it would be more correct to place the border to the north-east coincident with the shelf edge. The Barents Sea itself extends eastwards to Novaya Zemlya and northwards to the shelf edge between Franz Josef Land and Spitsbergen.

The main bathymetric features of the Nordic Seas are depicted in Figure 4. The Fram Strait, with a sill depth of about 2500 m, forms the main connection with the Arctic Ocean. To the south,

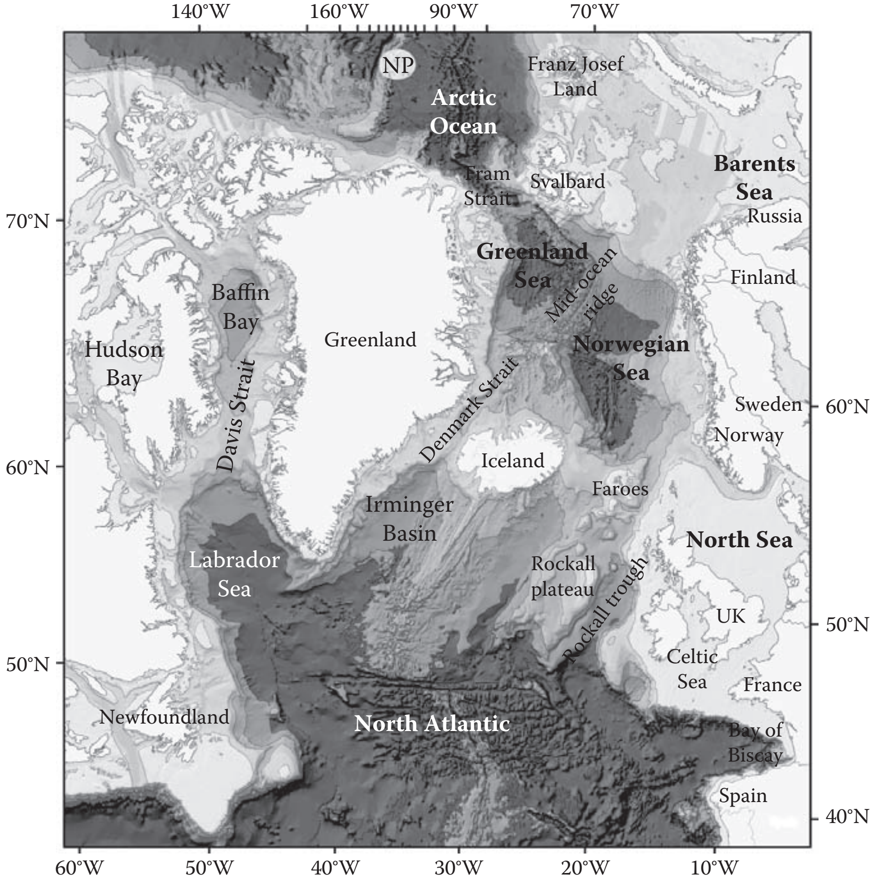

Figure 4 (See colour insert.) General bathymetry of the north-eastern Atlantic. NP indicates North Pole.

the Greenland-Scotland Ridge, with the deepest sills located in the Faroe Bank Channel (~850 m) and in the Denmark Strait (~620 m), forms the border towards the North Atlantic. Topographic features within the Nordic Seas divide the area into the Greenland, Iceland and Norwegian Seas. The most prominent of these features is the midocean ridge. Three main parts of this ridge system can be identified as the Kolbeinsey Ridge, Mohns Ridge and the Knipovich Ridge. The Kolbeinsey Ridge extends northwards from the North Icelandic shelf to the latitude of Jan Mayen where the Jan Mayen Fracture Zone cuts through it. Generally this ridge ranges in depth between roughly 400 and 1500 m, but to the west of Jan Mayen, some seamount-like features are shallower than 300 m, the shallowest only 25 m deep. The Mohns Ridge, between Jan Mayen and approximately 73.5°N, 8°E, has depths ranging between 1000 and 2000 m. Its rather complex topography is characterised by many isolated elevations. The shallowest peaks, the Myrseth and Boyd banks, are both about 600 m deep. The Knipovich Ridge stretches from Mohns Ridge to the Fram Strait, its shallower crests being at about 1000 m depth. Along the centre of both these ridges there is a rift valley with depths mainly greater than 3000 m. The topography along the southern side of the Jan Mayen Fracture Zone, between about 68°N, to the west of the Vøring Plateau, and 72°N off the East Greenland coast form a less-well-defined ridge system. Farther to the west, the area between Jan Mayen and Greenland is mostly shallower than 1500 m. Between 66.5°N and 68°N off the Norwegian shelf the Vøring Plateau has depths mainly between 1200 and 1400 m.

These bathymetric features divide the Nordic Seas into four major basins. To the west of the midocean ridge lie two deep basins in the Greenland Sea. The Greenland Basin is the largest of these, reaching depths from 3400 to 3600 m. To the north, the Greenland Fracture Zone separates it from the smaller and shallower Boreas Basin. Along its margins there are several shallower structures and seamounts, for example the Vesteris Bank (73°N, 9°W), which rises from the basin floor at approximately 3000 m to a depth of 130 m. Two deep basins are found in the Norwegian Sea, the Norwegian and Lofoten Basins, the former being the largest and deepest basin in the Nordic Seas. Its floor lies mainly between 3200 and 3600 m, but depths exceed 3800 m in a narrow trough around 65°N, 5°W. The shallower and somewhat smaller Lofoten Basin to the north of the Norwegian Basin reaches about 3200 m. The Iceland Plateau is the area between Iceland and Jan Mayen to the east of the Kolbeinsey Ridge. Along its eastern margin, which slopes into the Norwegian Basin, the Jan Mayen Ridge extends southwards from Jan Mayen. West of this ridge lies a small basin that is more than 2200 m deep but elsewhere, depths are mainly in the range 1200 to 2000 m. West of the Kolbeinsey Ridge the narrow Scoresby and Blosseville Basins (to the south) extend from the Jan Mayen Fracture Zone towards the Denmark Strait.

The Nordic Seas have been the subject of numerous national and international research programmes. Although many originated with a fisheries focus, they have now broadened to include studies on most aspects of the ecosystem (Skjoldal 2004). Since the Nordic Seas are experiencing particularly rapid changes linked with global climate, there has been a renewed emphasis on how these changes may affect biological productivity in the coming decades (Arctic Climate Impact Assessment [ACIA] 2004). There has also been a strong emphasis on the development of international programmes to measure the strength of ocean fluxes in the region because of their fundamental importance in climate control (Dickson et al. 2008).

The Atlantic: general geography, size, bathymetry

The Atlantic Ocean is the second largest of the world's oceanic divisions. It has a total area of about 106 million km^2 (41 million mi^2) and covers approximately one-fifth of the Earth's surface but this includes the southern Atlantic. The North Atlantic, which is the largest oceanic water mass associated with Europe, was not included in the original LME definitions as it is less productive than the adjacent shelf seas, but is included as a EUR-OCEANS' system. The North Atlantic Ocean is bounded on the west by North and South America whilst in the north and north-east, it is separated from the Arctic Ocean by the Canadian Arctic Archipelago, Greenland, Iceland, Jan Mayen, Svalbard, and mainland Europe. It connects to the Nordic Seas and Arctic Ocean through the Denmark Strait, Greenland Sea, Norwegian Sea and Barents Sea. To the east, the boundaries of the ocean proper are Europe and the Straits of Gibraltar (where it connects with the Mediterranean Sea). The average depth of the Atlantic is 3926 m but it reaches 8605 m in the Puerto Rico Trench. The principle bathymetric feature is a submarine mountain range, the Mid-Atlantic Ridge, which extends from Iceland in the north to around 58°S. The ridge has a maximum width of about 1600 km and a great rift valley extends along most of its length. The depth of water over the ridge is generally less than 2700 m.

The North Atlantic has been the subject of a number of major coordinated programmes at both the international (Joint Global Oceans Flux Study, World Ocean Circulation Experiment, Global Ocean Ecosystem Dynamics) and the European (Trans-Atlantic Study on *Calanus*) levels. Current relevant international programmes include the International Council for the Exploration of the Sea (ICES)/Global Ocean Ecosystem Dynamics (GLOBEC) Cod and Climate Change (CCC) programme, which is a North Atlantic regional component of GLOBEC. GLOBEC is a part of the International Geosphere Biosphere Program (IGBP) suite intended to evaluate the causes and consequences of global change. Another relevant IGBP programme is IMBER (Integrated Marine Biogeochemistry and Ecosystem Research), which is currently under development. Other international projects such as Climate Variability and Predictability (CLIVAR) and the Global Ocean Observing System (GOOS) are also relevant.

The European shelf seas: general geography, size, bathymetry

The European shelf seas within the EUR-OCEANS' context comprise the North Sea and the Celtic Sea/Biscay Shelf LMEs (Figure 2). The North Sea (including its estuaries and fjords) has a surface area of about 750,000 km^2 and a volume of about 94,000 km^3. It is relatively shallow in the south (including the Southern Bight and the German Bight) but becomes progressively deeper moving into the northern North Sea and the Norwegian Trench (Figure 5). The shallow Kattegat forms a transition zone between the North Sea and the Baltic. In the south, the North Sea is subject to strong tidal mixing, which prevents thermal stratification. However, significant freshwater run-off generates a series of salinity fronts and transient haloclines in this region. Water column structure in the central and northern North Sea is strongly affected not only by localised heating but also by significant inflows of Atlantic water, mainly through the Faroe-Shetland Channel and by outflow of freshwater through the Jutland Current, the Kattegat and the Norwegian Coastal Current. The English Channel is relatively shallow, and from a depth of about 30 m in the Strait of Dover deepens gradually to about 100 m in the west. The seabed topography shows extensive evidence of river valley systems that were carved during glacial periods when the sea level was lower (OSPAR 2000).

The Celtic Sea/Biscay Shelf LME covers 760,000 km^2. In the north it consists of the waters to the west of Scotland, including the Minch, between Scotland and the Hebridean islands. At this point the Rockall Trough separates the Rockall Bank from the western Scotland shelf with three significant seamounts, the Hebridean, Anton Dhorn and Rosemary Seamounts. The Rockall Trough follows northwards over the Wyville-Thompson Ridge into the Faroe-Shetland Channel and this topography is an important feature for interconnections between the Atlantic and North Sea (Baxter et al. 2008). Moving south, the shelf broadens forming the Malin Shelf and then follows the west coast of Ireland. The Irish Sea itself is semi-enclosed and relatively shallow (<60 m) in the east but with a deep channel (down to 200 m) in the west. The shelf continues as the Celtic Sea and narrows adjacent to the French coast forming one side of the Bay of Biscay.

The North Atlantic shelf seas are amongst the most productive in the world with respect to higher trophic levels. Despite overexploitation, this region still supports some of the world's major

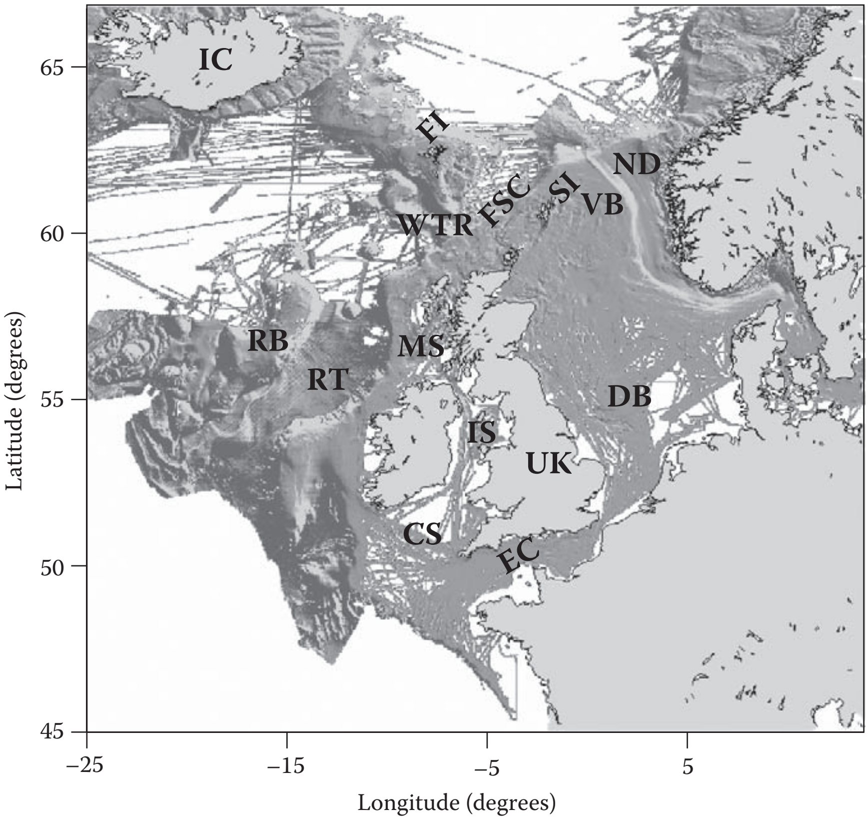

Figure 5 Many of the features of the shelf seas are revealed in this bathymetry compiled, processed and managed by Olex DS. Data are contributed voluntarily and merged into the central database; hence coverage is incomplete. IC, Iceland,; FI, Faroe Islands; WTR, Wyville-Thompson Ridge; FSC, Faroe-Shetland Channel; SI, Shetland Islands; VB, Viking Bank; ND, Norwegian Deeps; DB, Dogger Bank; EC, English Channel; CS, Celtic Sea; RT, Rockall Trough; RB, Rockall Bank; MS, Malin Shelf. (Reproduced with permission from Olex DTm, Edinburgh.)

fish stocks (e.g., herring and mackerel) whilst efforts are being made to rebuild other historically important stocks, such as cod (Horwood et al. 2006). Although the biological components of the shelf seas and the general physical conditions are fairly well described, the mechanisms responsible for interannual and longer-term variability in biological production are still poorly understood, and capturing the relative impacts of local and transregional processes is proving challenging. Nevertheless, understanding these couplings is crucial for sustainable resource exploitation in the North Atlantic shelf seas.

Over recent decades there have been many national research programmes in these shelf seas (e.g., the UK Natural Environment Research Council [NERC] North Sea programme and German GLOBEC). These have provided rich datasets for process understanding and for model development and testing. Since the 1960s, annual fisheries resource surveys have been coordinated through ICES and these provide some of the best multinational long-term datasets for evaluating the effects of environmental change and exploitation. The region is also generally well covered by Continuous Plankton Recorder (CPR) routes (www.sahfos.ac.uk), which extend over the last 70 years. However, in the context of understanding the impacts of long-term environmental change on the complete regional ecosystem, data availability and consistency over time remain problematic.

The major patterns across the wider region

The large-scale atmospheric and oceanic forcing that influences the north-eastern Atlantic

Overall environmental conditions in the north-eastern Atlantic are strongly influenced by three large-scale forcings: the global thermohaline circulation (THC), the freshwater balance in the north-eastern Atlantic and large-scale wind forcing which is strongly influenced by the North Atlantic Oscillation (NAO). In addition, the Atlantic Multidecadal Oscillation (AMO) exhibits as a long-term periodicity in sea temperatures covering the entire North Atlantic but the forcing mechanisms behind this phenomenon are poorly understood (Sutton & Hodson 2005). The global THC is driven by fluxes of heat and freshwater at the ocean surface driving density changes in the seawater, which in turn drives convective overturning (Rahmstorf 2006). Measurements of parts of the global THC have been made whilst the complete global picture is supported by theoretical and modelling results. The THC circulation arm in the Atlantic is relatively well observed and is alternatively termed the meridional overturning circulation (MOC). Changes in the THC have strong consequences for global climate; for example, a partial shutdown of the global overturning has accompanied abrupt shifts of the global ocean-atmosphere towards glaciation (Broeker & Denton 1989). The MOC helps to maintain the relatively warm climate of the North Atlantic compared with similar latitudes in the Pacific (Rahmstorf 2003) and in combination with wind-forcing and ice formation maintains the relative warmth of the north-eastern, compared to the north-western, Atlantic. Model experiments suggest that the impact of a hypothetical collapsed MOC would be an average cooling in the north-eastern Atlantic of around 1.7°C but with localised cooling of more than 15°C in the Norwegian and Barents Seas (Wood et al. 2003). Although it is now thought that a total shut-down of the THC is extremely unlikely, the results from Wood et al. (2003) do demonstrate the importance of the ocean circulation for regional climate in the north-eastern Atlantic. Precipitation and sea level would also be affected by a weakened MOC (Vellinga & Wood 2008). The impact of variations in the strength of the MOC on pelagic ecosystems are however relatively unstudied although see the work of Kuhlbrodt et al. (2009).

The large-scale balance of freshwater flux is important because of its impact on the MOC and because riverine inputs can strongly affect productivity in coastal areas (through water column stratification and nutrient supply). The major input of freshwater to the north-eastern Atlantic comes from rivers emptying into the Baltic and the eastern North Sea. The majority of this freshwater is carried into the Arctic by the Norwegian Coastal Current. On an annual timescale the whole of the north-eastern Atlantic benefits from an excess of precipitation over evaporation. This positive balance is particularly high to the south and west of Norway and over Iceland and south-east Greenland (Serreze et al. 2008) and is balanced by the southwards oceanic transport of ice and freshened seawater to regions where evaporation predominates.

The NAO is the dominant mode of atmospheric variability in the North Atlantic, accounting for 44% of the variance in winter (December–March) atmospheric sea-level pressure (SLP) in the last century (Hurrell 1995, Hurrell & Dickson 2004). The mode of SLP is manifest through changes in the relative strength of the Icelandic low and the Azores high pressure systems. Hurrell (1995) constructed a time series of the winter NAO index of SLP differences between Lisbon and Stykkisholmur, whilst Jones et al. (1997) used the SLP difference between Gibraltar and Reykjavik. These indices have the benefit that they can be extended as far as the 1800s allowing investigation of climate at multidecadel timescales. By using paleoclimate proxies the time series can be extended even further back but relating local conditions, such as surface temperature, to the NAO over these extended time-periods has proven problematic (Jones et al. 2001). These indices remain measures of SLP difference between two particular land stations and this may not account for long-term shifts in the centres of pressure. The oceans response to the NAO has been reviewed in detail by Visbeck et al. (2003) with changes identified including sea-surface temperature (SST), mixed-layer depth, heat content, extent of sea ice and currents. When the index is positive, winter westerly airflow of warm, humid air across the North Atlantic is enhanced and the shelf seas become warmer (Ottersen & Stenseth 2001, Hurrell & Dickson 2004). SST in the subpolar gyre is generally cooler through the enhanced heat flux generated by stronger winds and also northerly airflow at the western edge of the Iceland low. Positive NAO winters are also associated with a north-eastwards shift in storm activity and increased precipitation that is particularly evident along the Atlantic inflow pathway to the Nordic Seas.

The state of the NAO can also be linked to wider changes. Sundby & Drinkwater (2007) showed that the NAO influences the volume flux of water between the North Atlantic and the Arctic Oceans. A high NAO increases the flux of warm Atlantic water from the north-eastern Atlantic through the Nordic Seas to the Arctic Ocean. This increase is balanced by an increased flux of cold Arctic water from the Arctic Ocean into the north-western Atlantic. In contrast, a low NAO decreases the flux of warm Atlantic water in the north-eastern Atlantic, and again, this is balanced by less outflow of cold Arctic water. Hence the NAO forcing causes opposite decadal-scale ocean climate signals in the north-eastern and the north-western Atlantic. Moreover, it was demonstrated that these dynamics could explain the propagation of the great salinity anomalies in an alternative way (Dickson et al. 1988, Belkin et al. 1998, Belkin 2004).

During the last decades, it has become obvious that large-scale changes in atmospheric conditions over the open North Atlantic can be related to biological processes on both land and sea (Hurrell et al. 2003). For example patterns in phytoplankton (Irigoien et al. 2000), zooplankton (Piontkovski et al. 2006) and fish production (Stige et al. 2006) have all been correlated with the NAO index (but see Kimmel & Hameed 2008 for a counter-example). This suggests that atmospheric processes over the North Atlantic during winter–spring have an influence that extends over the whole region (Ottersen et al. 2001).

The role of atmospheric circulation for the transport of materials between the four systems: aerosol effects, iron particles, pollutants

North of about 60°N, the prevailing winds are westerly but in summer airflow can switch to easterly. This will transport Asian dust and smoke from boreal fires, and the area can suffer from the persistent presence of 'Arctic haze'—aerosol derived from pollutants originating from anthropogenic emissions at lower latitudes (Tomasi et al. 2007). South of about 60°N the prevailing winds are the Westerlies. At the western boundary of the Atlantic Ocean, anthropogenic nitrogen sources have increased dramatically over the last 150 years and North American industry and agriculture contribute a major source of reactive (or fixed) nitrogen to the Atlantic atmosphere (Duce et al. 2008). This probably represents a considerable increase in flux of reactive nitrogen to the oceans compared with the 1860 baseline. The atmospheric nitrogen contributes to new production in the Atlantic and has an impact on primary production in areas that are nitrogen depleted (Moore et al. 2006, 2008). Concentrations of atmospheric nitrogen are reduced considerably by the time the air reaches the north-eastern Atlantic, but nevertheless concentrations in 'clean' background air in the eastern north Atlantic are approximately 4-fold higher than in background air over the South Atlantic (Baker et al. 2006). Although the prevailing Atlantic wind direction between about 60°N and about 40°N is from west to east, long-range aeolian transport also brings iron-bearing mineral dust to the Atlantic from the Sahara Desert, the largest global source of such dust. This is important for biological production as iron can be a limiting nutrient for phytoplankton (Jickells et al. 2005) due to the high iron requirements by these organisms in electron transport machinery and enzymes such as nitrate reductase and nitrogenase (Geider & LaRoche 1994). Although the major transport pathway from the Sahara is the north-easterly equatorial trade wind, which carries material westwards towards the Amazon and Florida, a less-frequent pathway sporadically ejects dust over the north-eastern Atlantic Ocean (Prospero et al. 2002). The supply of iron from Saharan dust is considered to control the distribution of nitrogen-fixing organisms in the (sub)tropical North Atlantic Ocean (Falkowski et al. 1998). Atmospheric concentrations of Saharan dust decrease with distance from the source (Mahowald et al. 2005), and consequently concentrations of dissolved iron in surface waters also decrease moving northwards in the Atlantic (Measures et al. 2007). Since the majority of dust found in the Greenland ice cap appears to originate from Asia (Grousset & Biscaye 2005) it seems likely that the waters of the north-eastern Atlantic also receive small inputs of dust from Asian sources.

Less-frequent transport events from sources in Europe can also be significant for the north-eastern Atlantic. For example, a brief episode of south-easterly flow from the United Kingdom and northern Europe contributed most of the atmospheric nitrogen, lead and zinc input into waters off the west coast of Ireland in May 1997 (Spokes et al. 2001, 2006). Similar high concentrations of nitrogen in European-origin air have been reported over other areas of the north-eastern Atlantic (Baker et al. 2006, Spokes et al. 2006) and might be important for local enrichment of iron (Choel et al. 2007, Jickells et al. 2008) and other pollutants. Back trajectory analyses have indicated that Saharan dust plumes moving into the North Atlantic have European airmasses mixed in, resulting in an enhancement of an anthropogenic signature (e.g., with nickel, lead, copper, zinc) of such plumes (Baker et al. 2007).

The oceanographic flows

The general circulation of the northern North Atlantic is heavily influenced by the complex topography of the region (Figure 6). The most obvious feature is the NAC, which brings warm Atlantic water from the south-west. The NAC splits south of Iceland, one branch heading north before splitting again at the Denmark Strait. The flow of Atlantic water along the west coast of Iceland, through the Denmark Strait and into the Nordic Seas has the weakest, although highly variable, volume flux of the NAC branches. However, this current is of great importance to the regional marine climate of North Icelandic waters. The average volume flux of Atlantic water in this curent is around 0.75 Sv[*] with little seasonal variation.

The other main branch of the NAC flows north-east around the Faroe Plateau carrying warmer water over the ridge between Iceland and the Faroes. North-east of this ridge, the water meets the colder and less-saline waters of the East Icelandic Current and becomes confined into a fairly narrow current flowing eastwards over the northern slope of the Faroe Plateau. On average, the Faroe branch transports volume flux of around 3.5 Sv of Atlantic water. The Shetland branch carries Atlantic water through the Faroe-Shetland Channel in addition to water recirculated from the Faroe branch. On average the Atlantic water flux has been estimated at 3.2 Sv with only a small seasonal amplitude of 0.2 Sv and maximum flow in November. The remaining warm Atlantic waters of the NAC flow through the Faroe-Shetland Channel thence northwards parallel to the Norwegian coast. The warm waters then split into a gyre-like circulation in the Barents and Greenland Seas. Some of its waters may deflect westwards into the northern Greenland Basin and the Boreas Basin, but most recirculation occurs in the Fram Strait. A smaller part of the West Spitsbergen Current eventually enters the Arctic Ocean where it flows eastwards along the Eurasian continental slope. The boundary current continues around the Arctic Ocean, although some of its water advects into the interior basins and forms the Atlantic Intermediate Layer. During this time, the Atlantic waters are subjected to seasonal cooling and mixing with cold, dense Arctic waters. The water of Atlantic origin is known as recirculating Atlantic water, and flows parallel with and partly underneath the cold and fresh polar surface waters, including sea

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[*] 1 Sverdrup = water volume transport 10^6 m^3s^{-1}.

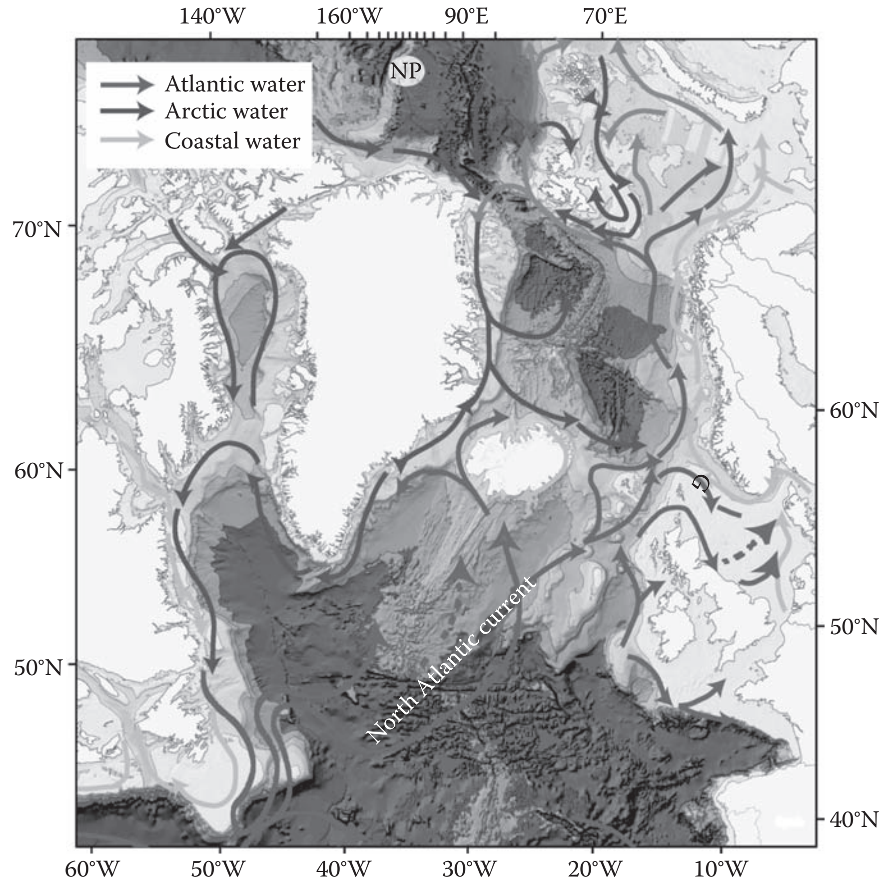


Figure 6 (See colour insert.) The general pattern of oceanographic flows in the north-eastern Atlantic.

ice. This generates the return flow via the East Greenland current. Just north of Iceland, a portion of the upper water masses and probably most of the bottom water in the East Greenland Current turns eastwards into the Iceland Sea. The remaining part flows out of the Nordic Seas through the Denmark Strait. It is important to note that Pacific water also enters the Arctic Seas through the Bering Strait and becomes mixed into the waters flowing south to the Atlantic.

Further south the most striking oceanographic feature is the strong northwards-flowing shelf-edge current, which acts to limit exchange between the Atlantic and the continental shelf. There are very few measurements of cross shelf-edge flows which tend to be episodic and mostly wind driven, either due to local forcing or large-scale pressure effects. Flows on to the shelves are particularly important for the influx of nutrients but because of their large-scale and episodic nature, the best estimates of direct transport come from modelling. Proctor et al. (2003) estimated that 0.7 Mt of nitrate entering the Celtic Sea region originated from across shelf-edge. Internal waves generated at the shelf edge can mix nutrients vertically and if coupled with surface wind flow can be responsible for transport on to the shelves. In reverse, cascading occurs when shelf waters cool and become more dense than adjacent waters over the slope and this is a potentially important mechanism for exporting biogenic material to the deep sea. Evidence of individual cascading events has been found during various studies including Shapiro & Hill (1997).

The mean currents of the North Sea form a cyclonic circulation (Figure 7). The bulk of this circulation is concentrated to the northern part of the North Sea due to major water exchange with

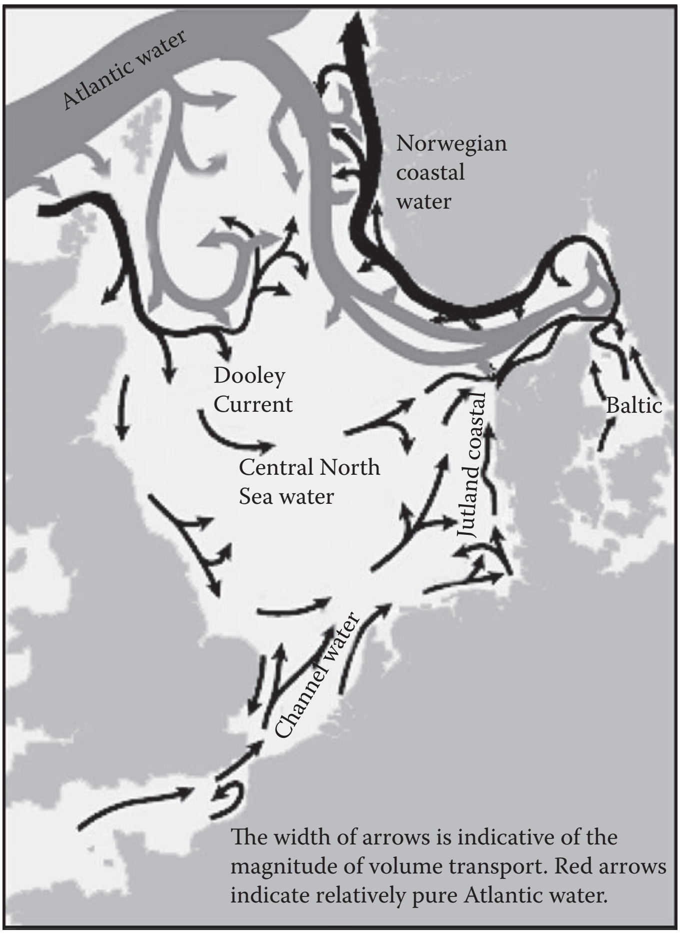


Figure 7 (See colour insert.) Schematic diagram of general circulation in the North Sea. (After Turrell 1992. Reproduced with Crown permission.)

the Norwegian Sea. The circulation in the northern North Sea can occasionally reverse into an anticyclonic pattern under persistent wind forcing (Dooley & Furnes 1981). The main inflow occurs along the western slope of the Norwegian Trench but significant inflows are also found around the Shetland Islands (Turrell 1992). Less than 10% of total inflow to the North Sea comes through the English Channel. All of these inflows are compensated by the northwards Norwegian coastal current. Because the western and southern regions of the North Sea are strongly mixed by the tides, vertical shear values are relatively low. However, the movement of North Sea bottom water has a strong seasonal signal in other parts of the North Sea, with large areas becoming almost motionless during the summer. These areas are usually marked by depressed oxygen levels (to a minimum of about 65% saturation) and by temperatures similar to those of the preceding winter. This typically occurs in large areas of the central and northern North Sea at depths greater than about 70 m. The situation is usually temporary as renewal of these deep waters occurs in the autumn. Areas permanently stratified by salinity have a generally slow bottom water exchange. In the Kattegat, the bottom water is renewed in 1–4 mo, the longest periods of stagnation occurring during summer. This slow renewal, in combination with eutrophication, frequently leads to periods of low oxygen content. The slowest movement of bottom water occurs in central parts of the Skagerrak where depths exceed 700 m. Here, waters are normally replaced at a much slower rate (every 2–3 yr), but rapid changes can occur in winter if bottom water cascades into the Norwegian Trench.

Major biological patterns across the wider region: primary production

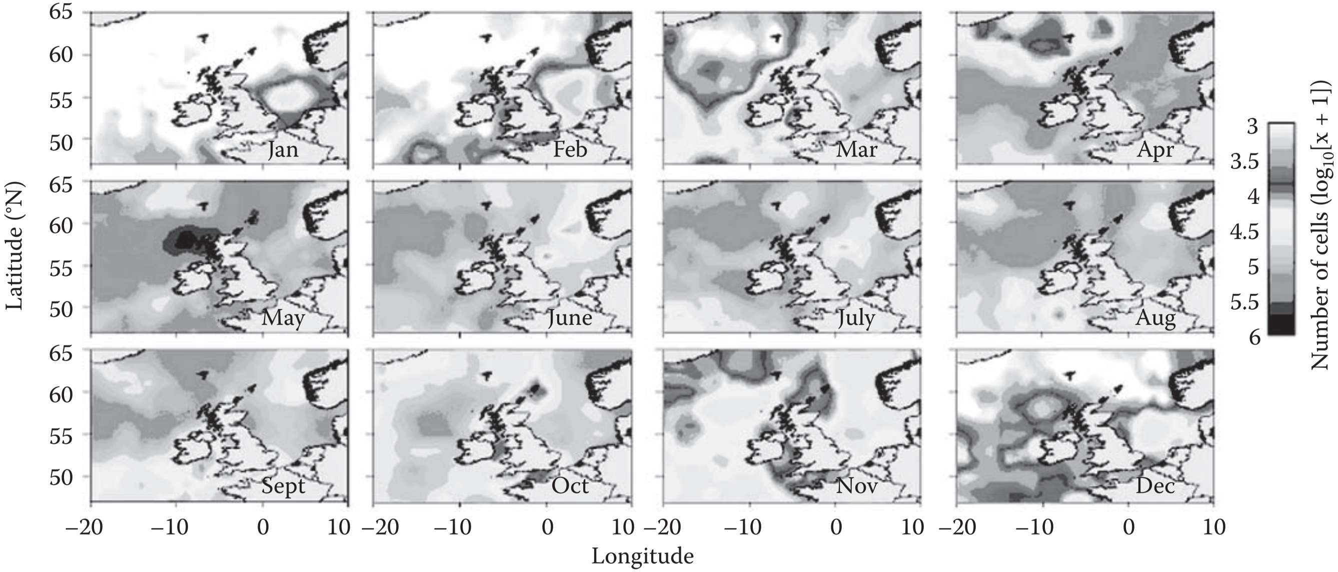
Primary production by phytoplankton fuels the majority of marine food chains and overall sets upper limits to both the activity of the pelagic food web and the quantity of organic carbon exported to the benthos (Mann & Lazier 2005). Phytoplankton community structure is strongly influenced by physical and chemical factors whilst the main losses are due to grazing (mostly by zooplanktonic organisms), sinking (Nielsen & Richardson 1989, Turner 2002) and viral infection (Suttle 2007, Brussaard et al. 2008). In the north-eastern Atlantic the growing season is strongly seasonal due to the annual light cycle and is accompanied by community successions as changing nutrient ratios favour particular phytoplankton groups (Colebrook 1979, 1982, Dippner 1998, McQuatters-Gollop et al. 2007a).

In midlatitude waters the classical picture is of a strong spring bloom dominated by diatoms, followed by a summer decline to a flagellate-rich community, followed by a smaller autumnal bloom as increasing winds mix nutrients back into the euphotic zone (Figure 8). This view has largely come from samples collected by the Continuous Plankton Sampler and latterly from satellite observations (Colebrook 1979, McQuatters-Gollop et al. 2007b). For those parts of the shelf seas subject to thermal stratification, the situation in summer is more complex as significant levels of primary production, not detected by surface sampling, take place just above the thermocline (Richardson et al. 2000, Weston et al. 2005).

However, despite the transient spring period of high biomass and hence productivity and export, in many regions of the open North Atlantic, including the Iceland and Irminger Basins, residual nitrate ($>2\ \mu M\ NO_3^-$) and phosphate ($>0.15\ \mu M\ PO_4^{3-}$) concentrations have been observed during the post-bloom summer period (Sanders et al. 2005). In addition these areas are characterised by consistently low chlorophyll concentrations during summer periods (Henson et al. 2003). The atmospheric supply of iron and the surface water iron concentrations in these regions are very low and recent biophysical and experimental observations have now shown that iron limitation of the phytoplankton community occurs in northern Atlantic waters (e.g., in the Iceland Basin following the spring bloom) (Moore et al. 2006). As a consequence there can be incomplete removal of nitrate and hence a reduced efficiency of the biological carbon pump in this region.

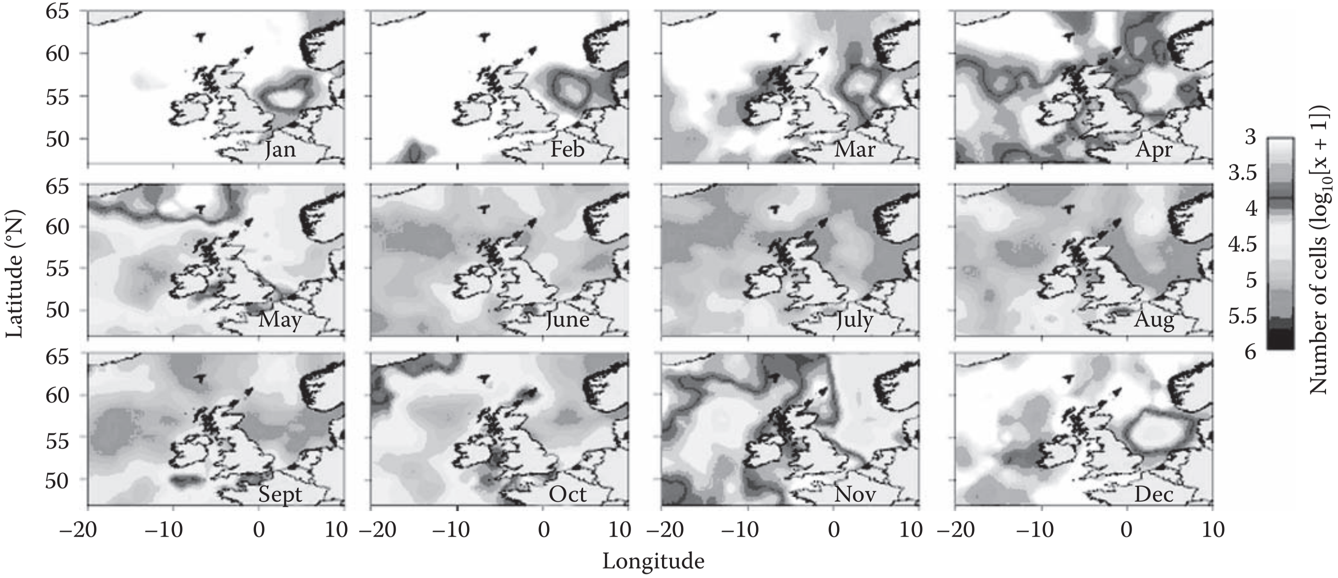
With increasing latitude, the growing season becomes progressively shorter due to changes in illumination (Mann & Lazier 2005). In the far north the bulk of production is concentrated into a single annual peak lasting only a few months. Again the spring bloom is diatom dominated (Hegseth & Sundfjord 2008) although in the Arctic Ocean proper, smaller flagellates are more common. Recent reductions in sea ice between 1998 and 2006 have led to increases in open water area at the rate of around 70,000 $km^2\ annum^{-1}$ with the greatest increases in the Barents, Kara and Siberian sectors. Although pan-Arctic primary production averaged 419 ± 33 Tg C $annum^{-1}$ during 1998–2006, recent increases in open water area have led to higher rates of annual production, which reached a 9-yr peak in 2006 (Pabi et al. 2008).

Throughout the north-eastern Atlantic, spring blooms tend to be diatom rich whereas in summer the picophytoplankton (<3 µm in diameter) dominate as described above (McQuatters-Gollop et al. 2007a). Several species of the colonial Prymnesiophyte *Phaeocystis* (e.g., *P. pouchetii*) in the colder Nordic Seas and *P. globosa* in the temperate Atlantic shelf seas, regularly dominate the phytoplankton community (Schoemann et al. 2005, Long et al. 2007, Nejstgaard et al. 2007). Another important organism in the north-eastern Atlantic is the coccolith *Emiliania huxleyi*. This species forms massive summer blooms in the temperate and subpolar north-eastern Atlantic and associated shelf seas and plays key roles in the global carbon cycle (Hays et al. 2005). As well as squestering atomospheric carbon dioxide, *Phaeocystis* and *E. huxleyi* also play key roles in climate regulation through the production of dimethylsulphide (Strom 2008).



(A) Spatial distribution of diatoms

Figure 8 (See colour insert.) Mean monthly spatial patterns of (A) diatoms and (B) dinoflagellates in the north-eastern Atlantic during the period 1958 to 2003. (From McQuatters-Gollop et al. 2007a. With permission of Inter-Research Science Center.)



(B) Spatial distribution of dinoflagellates

Figure 8 (continued).

Under the right circumstances the formation of phytoplankton blooms is common. Algal blooms are loosely defined phenomena, generally used to describe the accumulation of monospecific phytoplankton cell biomass through enhanced primary production. What constitutes an algal bloom is, however, not simply a biomass issue, as illustrated by blooms of toxic species (Smayda 1997). Phytoplankton species with relatively low *per capita* growth rates can still bloom if they escape grazing (Strom 2008). Reduced edibility is often linked with size (Long et al. 2007) or the production of phycotoxins (Turner & Tester 1997). Interestingly, *Phaeocystis globosa* appears to be able to modify its morphology in response to the dominant consumers present (ciliates or copepods), a strategy that may reduce the level of grazing it suffers (Long et al. 2007). Blooms of phytoplankton differ in their magnitude and frequency with latitude and closeness to land. Furthermore, the Atlantic shelf seas are enriched with inorganic nutrients from terrestrial run-off, leading to concern about eutrophication (Andersen et al. 2006) and stimulation of harmful algal blooms (HABs) in these areas (Smayda 1997). A broad classification of HABs distinguishes two groups of organisms: the toxin producers that can contaminate seafood or kill fish and the high-biomass producers that are considered 'nuisance' algae, causing anoxia, clogging fishing nets and affecting tourism. Some HABs have characteristics of both. Many of the toxin-producing HABs are dinoflagellates. There are also concerns that, particularly in the shallow shelf seas, multiple stressors of climate change and anthropogenically altered nutrient ratios will lead to increases in the occurrence of HAB events (Peperzak 2005).

Evidence has also emerged that a significant change in the primary production cycle in the central north-eastern Atlantic and North Sea took place in the mid-1980s with an extended growth season and loss of the classic double peak in production (Reid et al. 1998). This is associated with a 'regime change' spanning all trophic levels and may have been caused by recent warming and changes in turbidity, altering phytoplankton community structure (McQuatters-Gollop et al. 2007b).

Major biological patterns across the wider region: secondary production

Zooplankton includes a wide range of organisms (e.g., ciliates, chaetognaths, hydrozoa, copepods and egg and larval stages of fish, bryozoans, echinoderms). Zooplankton communities are often dominated by copepods (Williams et al. 1994), which act as the key link between primary producers and higher trophic levels and as a critical food resource for early-feeding larval fish (Banse 1995). The population dynamics of individual zooplankton species is a product of their rates of reproduction, growth and mortality. Reproduction and growth patterns of zooplankton vary not only between species but also within species, reflecting regional dissimilarities in production cycles and thermal regimes. The timing of the zooplankton production cycle is an important factor for controlling phytoplankton growth (Fileman et al. 2007), for larval fish survival (Cushing 1990) and for benthic-pelagic coupling (Townsend & Cammen 1988). Much of our knowledge of large-scale zooplankton patterns has come from the Continuous Plankton Sampler (Barnard et al. 2004, Warner & Hays 1994) and the north-eastern Atlantic is unique globally in the long-term and broad spatial coverage of zooplankton distribution by this survey.

The regional patterns of secondary production generally follow those of primary production, with highest levels in North Atlantic shelf seas and the Arctic and Nordic Seas; production levels in the open ocean North Atlantic are generally lower. As mentioned previously the primary production season becomes shorter with increasing latitude and this in turn affects secondary production (Mann & Lazier 2005). Local features particularly mixing and stratification of the water column will also affect secondary production through their influence on phytoplankton growth (Cushing 1989). Frontal systems in shelf seas have been shown to be particularly significant in influencing regional-scale distributions and productivity (Perry et al. 1993, Thibault et al. 1994, Albaina & Irigoien 2004, Wishner et al. 2006).

Zooplanktonic metabolic responses to climate change, in particular warming, can be assessed using ecological metabolic theory. This considers how metabolic rates vary with body size and temperature (Brown et al. 2004). Although mainly applied to terrestrial systems, this approach is emerging as a powerful tool in marine studies. For example, the metabolic theory can be used to predict variations in production and respiration and to evaluate how the primary production/respiration rate and implied changes in carbon flux will vary with different climatic scenarios (López-Urrutia et al. 2006).

Ocean currents as the major mechanism linking the regions in the north-eastern Atlantic

The role of ocean currents in the transport of nutrients

The traditional concept was that availability of nitrogen was the primary control on phytoplankton growth but for the North Atlantic, the general picture that is emerging is of a latitudinal gradient with nitrogen-deficient systems in northern parts and a shift towards phosphorus deficiency in the south. The present understanding is one of a biological control of the nitrogen/phosphorus balance in which the nitrogen content adjusts to the phosphorus content via the two opposing processes of nitrogen fixation and denitrification (Tyrrell 1999).

For the Arctic inflow around Greenland, the nitrogen deficiency seems at least partly to originate from the Bering Strait and Chukchi shelf regions, where high sedimentation rates combined with shallow depths produce low-oxygen environments that favour denitrification (Carmack & Wassmann 2006). Denitrification appears to function relatively efficiently at low temperatures, as illustrated by the detection of denitrification and an-ammox (anaerobic ammonium oxidation) activity in Arctic sea ice (Rysgaard et al. 2008). Adaptation to temperature appears to be a strong selective force among diazotrophs (nitrogen-fixing bacteria), as demonstrated by the distribution of different nifH phylotypes according to temperatures in the southern North Atlantic (Langlois et al. 2008). Despite evidence that low temperature *per se* is not inhibitory to nitrogen fixation (Karl et al. 2002), nitrogen fixers appear to be absent in cold marine waters (Staal et al. 2003). Presumably as a consequence of this, nitrogen deficiency is conserved in the Arctic and a low nitrogen/phosphorus signal is still a characteristic feature of water when it leaves the Arctic Ocean in the East Greenland current (Daly et al. 1999).

The first claims of phosphorus deficiency in the southern part of the North Atlantic came from the Sargasso Sea. Here, rapid turnover of orthophosphate leads to phosphate concentrations below 1 n*M* (Cotner et al. 1997, Wu et al. 2000). Iron is a critical cofactor for the nitrogenase enzyme (Karl et al. 2002), making iron availability an expected key controlling factor in marine nitrogen fixation. Based on this, aeolian input of iron via Saharan dust has been suggested to be a mechanism stimulating nitrogen fixation in the south-western North Atlantic (Walsh & Steidinger 2001, Jickells et al. 2005). In the western Central Atlantic, however, enzyme assays identified phosphate, rather than iron, as the main constraining nutrient for *Trichodesmium* N_2 fixation (Webb et al. 2007). There is an ecological argument that too efficient nitrogen fixers would destroy their own ecological niche if they load excess nitrogen into the system. Such ‘overshoots’ in nitrogen fixation do, however, seem to occur in nature (Nausch et al. 2004), driving the system into phosphorus deficiency. There is also evidence that the simple control model involving major nutrients is inappropriate, at least in some locations where regional differences in the availability of minor nutrients are significant in structuring the phytoplankton and microbial communities (Müller et al. 2005). Since climate change is likely to affect both sea-surface temperature (Walsh 2008) and iron input via aeolian dust (Mahowald et al. 2005), we can expect the latitudinal gradient in nitrogen/phosphorus balance in the Atlantic to be sensitive to climate change.

For the shelf seas, inflow from the Atlantic is crucial since it has been estimated that around 90% of nitrogen and phosphorus inputs to the North Sea come from this source (OSPAR 2000). However, much of this nitrogen is in the non-reduced form and so not readily available for primary production. In addition there are large intra- and interannual variations in the inflow.

The role of ocean currents in the transport of carbon between the four systems: shelf pump

According to the inventory of Sabine et al. (2004), the North Atlantic basin stores 23% of the global oceanic anthropogenic CO_2 despite covering only 15% of the global ocean area. The adjacent shelf seas are also efficient at drawing down atmospheric CO_2 and thus play a key role in the global carbon cycle. In the North Sea there is a separation in carbon processing of the shallower southern area from the deeper northern waters (Figure 9). Carbon export occurs in the deeper northern waters, particularly during the summer as particulate organic carbon from algal production sinks to the deeper, cooler waters. Heterotrophic respiration below the thermocline releases CO_2 into the water, where a substantial fraction is transported northwards by the subsurface circulation. According to Thomas et al. (2005), 90% of the CO_2 absorbed in the North Sea is exported to the North Atlantic. The Atlantic water entering the North Sea through the Orkney Shetland gap thus gains approximately 40 mmol C kg^{-1} before leaving the North Sea. During late summer the outward carbon transport via the Norwegian trench is approximately 2.2×10^{12} g C, while in the same period the North Sea absorbs approximately 15% from the atmosphere.

Export of carbon from the North Sea occurs because the thermal stratification of the northern section of the sea allows particulate organic carbon from algal production in the warmer surface waters to be exported down into the cooler subsurface layer. Most of the CO_2 that is subsequently released from heterotrophic respiration of this particulate organic carbon is transported northwards to the

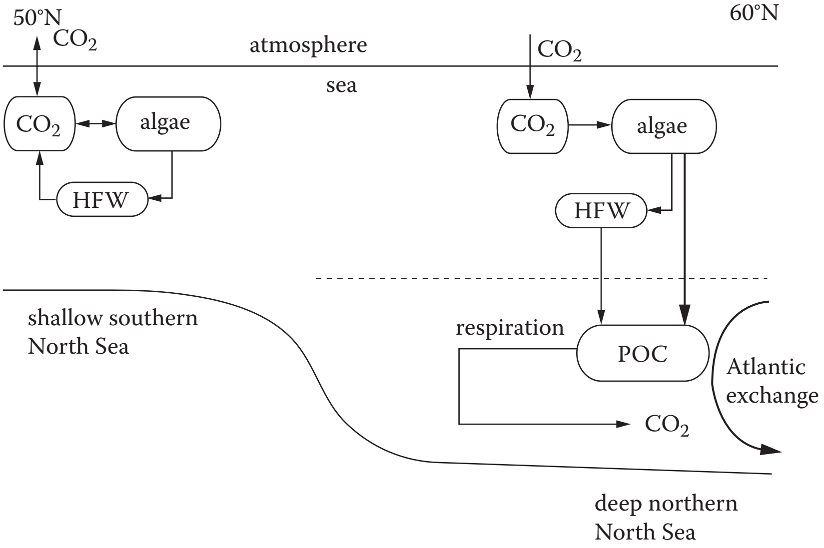


Figure 9 South-north section through the North Sea. In the shallower southern region production and respiration processes occur throughout the mixed water column whereas in the deeper northern North Sea seasonal stratification separates the production and recycling processes of CO_2, POC (particulate organic carbon), and HFW (high-level food web). (Modified from Thomas et al. 2004a. With permission of AAAS.)

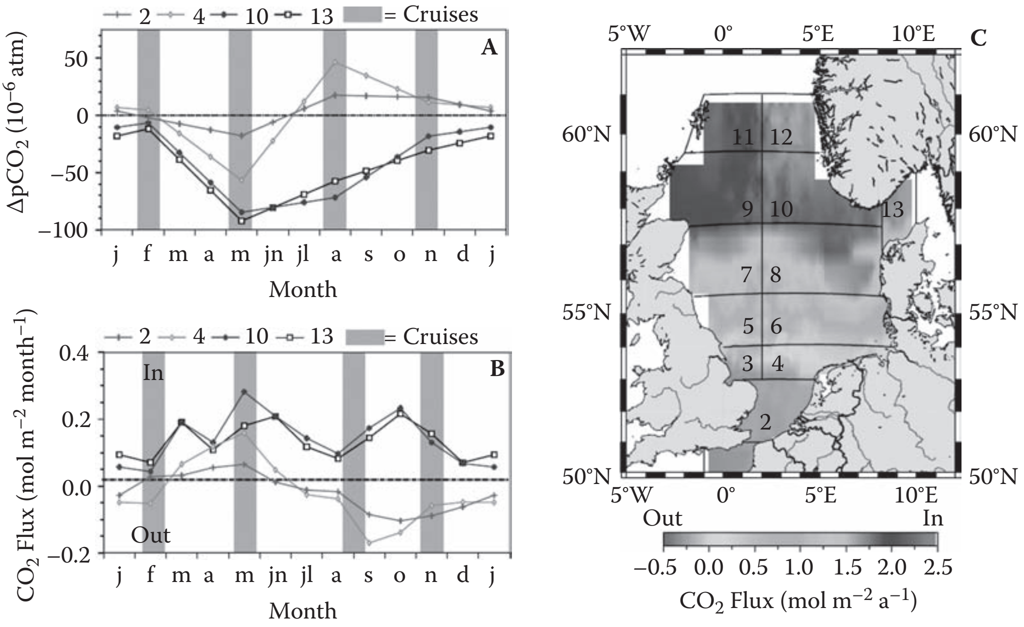


Figure 10 (See colour insert.) Annual cycles of air-sea partial CO_2 pressure differences (A) and calculated fluxes (B) for selected areas in the North Sea, with shading indicating periods of observation. The spatial pattern of air-sea CO_2 fluxes across the North Sea is shown in C. Note positive values for CO_2 flux indicate absorption from air to sea. (From Thomas et al. 2004a. With permission of AAAS.)

North Atlantic Ocean by subsurface ocean circulation (Figure 9). The shallower non-stratified southern section does not contribute to this carbon transport since both algal production and heterotrophic respiration occur within the year-round mixed water column, thus preventing significant exports.

The findings of Thomas et al. (2004a) were based on four cruises spread across a year to reveal seasonal and spatial patterns. The seasonal variations of partial pressure differences (Figure 10A) were measured and interpolated for 13 sectors of the North Sea (Figure 10C) and coupled with measurements of the seasonal variations in CO_2 flux (Figure 10B) to enable the spatial patterns in annual CO_2 flux to be calculated (Figure 10C).

This study showed that the North Sea as a whole acts as a CO_2 sink all year round. The only source is from the southern areas (sectors 1–4) during the late summer (Figure 10c). The greatest drawdown occurs in May during the spring algal blooms, and secondly in October, when storms force CO_2 uptake. Only about 1% of carbon captured by the algae is sequestered in the North Sea sediments; the majority, as described, is exported to the North Atlantic Ocean.

Based on these studies the significance of the North Sea shelf pump for the sequestering of carbon is well established. The effects of global warming on the efficiency of the shelf pump are, however, unclear. A longer stratification season due to warming may further reduce the flux of nutrients to the surface layer. As a result, primary production after the spring bloom and a restructuring of the phytoplankton community may occur. Furthermore, the increased stratification has the potential to increase the dominance of the microbial loop thereby recycling carbon in the surface layer and potentially resulting in a reduced flux of organic material to the deep layer. Thus, carbon outflows due to the shelf pump will probably be reduced, limiting the efficiency of the shelf pump and the contribution of this mechanism to the sequestration of carbon.

The role of ocean currents in the transport of phytoplankton and microzooplankton

The phytoplankton communities of the north-eastern Atlantic are strongly influenced by the inflow of Atlantic water into the North Sea and the Nordic Sea (Skogen et al. 2007). Wind conditions associated with the NAO also affect the development of the upper mixed layer and thus phytoplankton productivity. As demonstrated in freshwater lakes this may potentially affect their nutritional value to higher trophic levels (Diehl 2007). Modifications in vertical mixing and stratification may also alter species composition and the export of primary production to deeper waters.

As discussed on page 12 there is a large interannual variability in the flux of Atlantic water entering the shelf seas. Although this advection transports oceanic phytoplankton cells to different locations, it is the local conditions that determine whether these species can become established in new areas (Hegseth & Sundfjord 2008). In the north-eastern Atlantic there is a weaker latitudinal gradient in temperature compared to the north-western Atlantic. Nevertheless, this weaker gradient can still set barriers to the long-term survival of phytoplankton species but serial seeding can lead to significant temporary range extensions (Edwards et al. 2002). For example, Johnsen et al., (1997) described an advection event that resulted in a widespread bloom of the normally oceanic *Ceratium furca* that persisted over a 6-wk period and reached mid-Norway (63°N). However, blooms may propagate over wide distances without advection. Since many of these organisms produce resting stages or are present at very low population levels in seawater, blooms can initiate if environmental conditions become optimal. For example, a bloom of the coccolithophorid *Emiliania huxleyi* started in Norwegian coastal waters at 60°N and passed the Arctic Circle (70°N) 3 mo later (Hegseth & Sundfjord 2008). Because some bloom-forming species interfere with human activities such as aquaculture, more attention is now paid to monitoring their occurrence, particularly in coastal waters. Increased frequency of recorded HAB outbreaks may be related to factors such as enrichment of coastal nutrients but may just reflect increased monitoring and human activity in the coastal zone. Periodic incursions of warm-water phytoplankton into Norwegian waters have certainly been noted since the early 1900s (Smayda 1958).

The role of ocean currents in the transport of mesozooplankton

Mesozooplankton are of intermediate size, typically with body lengths between 0.2 and 20 mm (Harris et al. 2000). Although the number of mesozooplankton species in a region can be quite high there are usually a few dominant species in terms of biomass (Pitois & Fox 2006). In northern areas of the Atlantic, *Calanus finmarchicus* tends to be dominant, constituting up to 80% of mesozooplankton biomass but in the shelf seas smaller species such as *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia clausi* are common. As with all plankton, the mesozooplankton have little direct control over their horizontal movements, relying on vertical behaviour to constrain dispersal (Backhaus et al. 1994, Aksnes & Blindheim 1996, Slagstad & Tande 1996, Speirs et al. 2004). Because of its ecological importance, *Calanus finmarchicus* has probably been the most intensively studied copepod species in the north-eastern Atlantic. The complex life cycle of *Calanus finmarchicus* strongly affects the extent to which different geographical regions in the north-eastern Atlantic are linked. Backhaus et al. (1994) first proposed that there was a line source of overwintering *C. finmarchicus* below the continental shelf jet (CSJ), which got transported into the North Sea when migrating to the surface in the spring. Deep counter-circulation flowing out of the North Sea would subsequently close the cycle, transporting the next overwintering generation to deep water off the continental shelf. Although there is little evidence for a truly ‘closed’ circuit of transport in the way originally imagined, it has become clear that the North Sea is essentially replenished on an annual basis from the oceanic population centres in the north-eastern Atlantic and the Norwegian Sea (Heath et al. 1999). During the winter, preadult fourth and fifth copepodite stage (CIV, CV) individuals are found at depths of 200–1500 m (Heath et al. 2004) and remain there in a suspended, diapause-like state (Hirche 1996) in which they subsist on stored lipids (Jónasdóttir 1999). In the spring they rise to the surface, moult to the adult stage, and begin reproduction (Heath & Jónasdóttir 1999). The number of generations per year varies between one and three depending on temperature. During the surface reproductive phase, *C. finmarchicus* is transported into the shelf seas. In these shelf regions the individuals of the species play a significant ecosystem role as grazers and as a major food source for larval fish (Heath & Lough 2007, Rowlands et al. 2008). This life cycle has two important implications in relation to regional interconnectivity. Firstly, although *C. finmarchicus* is ecologically important on the shelf, it is essentially an oceanic species. Secondly, its demography is fundamentally affected by circulation (and changes in circulation) in both surface and deep currents.

The ocean-shelf linkage is also potentially the key to understanding the relationship between the negative correlation between the winter NAO index and the abundance of *C. finmarchicus* and the weaker positive relationship with the abundance of its warmer water congener *C. helgolandicus* on the shelf seas (Fromentin & Planque 1996). Originally Fromentin & Planque (1996) attributed the relationship to the fact that more positive winter NAO years typically experience higher temperatures and westerly winds, both of which would affect primary production, and that this favours warmer water species such as *C. helgolandicus*. Subsequently, Stephens et al. (1998) suggested that periods of negative (low) NAO were associated with stronger inflows of Atlantic water to the North Sea, which would lead to increased transport of *C. finmarchicus* from the Norwegian Sea. This hypothesis was further developed to a basin-scale context by Greene & Pershing (2000). Sundby (2000) suggested that the variable advection of *C. finmarchicus* from the core production area of the Norwegian Sea to the North Sea and the Barents Sea is an important factor influencing the recruitment of cod stocks. However, Kimmel & Hameed (2008) have recently questioned the strength of the statistical link between *C. finmarchicus* abundance in the north-eastern Atlantic and the NAO.

Heath et al. (1999) showed that the Wyville-Thompson Ridge forms an effective physical barrier for overwintering *C. finmarchicus*, with much higher densities occurring in the Norwegian Basin and Faroe-Shetland Channel than to the south of the ridge. During winter, diapausing *C. finmarchicus* in the Faroe-Shetland Channel are concentrated below the pycnocline in Norwegian Sea Deep Water (NSDW). During negative winter NAO years winds tend to come from the north-west, favouring production of NSDW and advection of *C. finmarchicus* into the Faroe-Shetland Channel. However, the well-behaved negative relationship between the winter NAO index and *C. finmarchicus* broke down in 1996 and 1997 (Planque & Reid 1998). This appears to be because NSDW production also integrates climatic conditions on a decadal timescale. In 1996 the NAO was strongly negative but following an extended positive period; the abundance of *C. finmarchicus* in the North Sea remained small because although transport into the North Sea was favoured, the NSDW overflow remained small (Heath et al. 1999). The links between the atmospheric drivers and *C. finmarchicus* are mediated by responses to changes in both deep water (affecting the overwintering stages) and surface water circulations and these respond over different timescales.

Calanus finmarchicus has a large geographic domain extending from the Gulf of Maine to the southern Labrador Sea in the western Atlantic and from the North Sea to the Barents Sea in the eastern Atlantic. CPR data revealed that there are three main oceanic population centres in the Norwegian Sea, Irminger Sea and southern Labrador Sea. These population centres are associated with oceanic gyres, which may help to reduce advective losses to regions that are unfavourable for population growth. Aksnes & Blindheim (1996) examined this problem by estimating the advective renewal rate of the Nordic Sea gyre and the subpolar gyre and comparing them to estimates of the intrinsic rate of population increase under various assumptions of fecundity and the number of generations per year. Since the advective renewal rate is equivalent to a per capita loss from the region for a well-mixed population, this comparison provides a rough estimate of whether a region can independently sustain a population. In all cases the biological rate of increase was at least an order of magnitude greater than the advective renewal, and that less than 5% of the annual production in the Nordic seas was lost from the system.

The dominance of biological rates over physical ones is also apparent in modelling studies. Speirs et al. (2006) constructed a spatially explicit coupled physical/biological model of *C. finmarchicus* over its entire geographic range. Development rate and fecundity were driven by a yearly cycle of temperature obtained from the Ocean Circulation and Advanced Modelling Project (OCCAM) ocean circulation model (De Cuevas et al. 1998) and of phytoplankton carbon derived from bottle samples and SeaWiFS (Sea Viewing Wide-Field of View Sensor) satellite data (Clarke et al. 2006). Population control was achieved by density-dependent mortality, which they showed needed to be temperature dependent to match CPR data. The spatial transport of *Calanus* was calculated from the OCCAM flow fields together with an assumed horizontal dispersion. In one experiment Speirs et al. (2006) switched off transport entirely and then ran the model to a quasi-stationary state. The results indicated that transport had a relatively minor impact on the distribution of *Calanus* in the sense that the two major population hot spots in the Norwegian Sea and the subpolar gyre persisted. By contrast, transport was of major importance in extending the population range. The most dramatic impact is in the northern Norwegian Sea, where sea ice prevents sustainable populations in the absence of seasonal influxes of animals.

In a second experiment relating to large-scale transport, Speirs et al. (2006) simulated the propagation of *Calanus* inocula in the Norwegian Sea gyre and the subpolar gyre. Within 2 yr the individual gyre systems were populated. By the third year the Norwegian sea population had become entrained in the Greenland coastal current and was transported through the Irminger Sea and into the subpolar gyre. In both cases the model had nearly reached its fully populated steady state after 5 yr. This surprisingly short invasion timescale suggests a very high level of connectivity, despite the fact that the large-scale demographic impact of transport is limited. These two observations can only be consistent if the environmental factors driving the demographics show coherence over spatial scales at least as large as the distances travelled by individual *Calanus* during their generation time.

High-dispersal capacity coupled with the lack of physical barriers suggest that many marine species with pelagic stages should show weak population genetic structuring (Palumbi 1994). However, the very large scale of the geographic distributions of certain mesozooplanktonic species, together with the possibilities of gene-flow restriction mediated by gyre systems, introduces the potential for regional genetic isolation. To date the evidence for significant genetic differentiation in *C. finmarchicus* across the Atlantic is at best equivocal. Bucklin & Kocher (1996) reported the same mitochondrial 16S ribosomal DNA genotypes in both the eastern and western Atlantic but using the same markers found significant variation within the Georges Bank region. Using different markers, Bucklin et al. (2000) revealed differences between Atlantic and Arctic *C. finmarchicus* populations in Icelandic waters. More recently more sensitive microsatellite markers have been developed (Provan et al. 2007). Provan et al. (2009) used these together with a part of the cytochrome B (CYTB) gene to estimate gene flow across 14 sites in the Norwegian Sea gyre, the Irminger Sea gyre and the North Atlantic off Nova Scotia. They concluded, contrary to previous studies, that there was no evidence for genetic differentiation across the main population centres for *C. finmarchicus*.

From a population dynamics and ecosystem perspective such genetic studies are extremely important because if strong regional differences are found it may not be possible to understand local dynamics without an appreciation of local phenotypic adaptations. However, the present lack of evidence for differentiation within *C. finmarchicus* at the basin scale is in agreement with the high connectivity and short timescales predicted by Speirs et al. (2006). It is also worth noting that genetic differentiation (in the absence of selection) arises through the countervailing effects of population mixing and genetic drift. A full synthesis must await a new generation of coupled physical/biological models that include a genetic model. Although less intensely studied, oceanic transport into shelf seas is also likely to be a key factor in the ecology of other important mesozooplankton such as *Calanus helgolandicus* (Bonnet et al. 2005, Helaouët & Beaugrand 2007).

The role of ocean currents in the transport of macro- and megazooplankton

Macro- and megazooplankton are planktonic organisms larger than 2 cm (Harris et al. 2000). This diverse group includes tunicates, chaetognaths, euphausiids and gelatinous zooplankton and ichthyoplankton but because of its importance for fisheries, the transport of fish larvae is dealt with in a separate section.

It has long been known that marine organisms can be used to characterise water masses and many marine biological studies during the early twentieth century adopted this approach. At this time there was a marked warming of coastal waters associated with a positive phase of the NAO and AMO. Cushing (1982) has described how during this period (1920s–1930s) unusual numbers of surface-living and pelagic subtropical animals were transported to the western British Isles. In the waters off Plymouth (south-western England) it had been noted that the chaeotognath *Sagitta setosa* was characteristic of English Channel water whilst its congener *S. elegans* typified warmer Atlantic water. Changes in the relative abundance of these two species at the E1 observatory have been consistent with changes in sea temperature and with wider ecosystem effects (Hawkins et al. 2003).

Throughout the north-eastern Atlantic there are numerous records of periodic outbursts of gelatinous zooplankton. Whilst there have been several claims that the rate of outbursts may be increasing, due to climate change, overfishing or increases in the availability of hard surfaces required by the planulae larvae (Mills 2001), these claims are hard to verify. Macrozooplankton have generally been poorly monitored in the past, giving at best a fractured baseline to compare with modern observations (Purcell et al. 2007). In addition, these organisms are characterised by pulsed population dynamics (Boero et al. 2008). Most observations come from the shelf seas where species may either be endemic (e.g., *Aurelia aurita*) or oceanic or warmer water species advected into the shelf seas. As well as potential poorly understood impacts on overall food web structuring (Mills 2001), blooms of gelatinous zooplankton can have direct impacts on human activites such as fishing, fish farming and tourism. For example, Båmstedt et al. (1998) reported a mass outbreak of the siphonophore *Apolemia uvaria* along the western Norwegian coast that caused deaths of farmed salmon. This species has a near-global distribution being normally found in offshore waters down to depths of 800 m. *Apolemia* was therefore probably transported from the open Atlantic along the Norwegian coast (Figure 11). Mass invasions of oceanic species associated with increased influx of North Atlantic water on to the European shelf seas and into Norwegian coastal waters are not uncommon. In summer of 2007 a similar event was reported in the popular press involving the oceanic species *Pelagia noctiluca* (Heard 2005) that resulted in complete destruction of a salmon in a sea farm off northern Ireland.

The role of ocean currents in the distribution of fish across system boundaries

Transport of fish eggs and larvae

Dispersal of marine organisms during their planktonic stages is a crucial factor affecting the genetic structuring, recolonisation capacity and the ability of populations to respond to environmental change. The distances and pathways over which planktonic stages are transported are direct functions of the strength of residual currents and the duration of the planktonic stages (Shanks et al. 2003). Because the planktonic stages of many fish are relatively long lived, potential dispersal

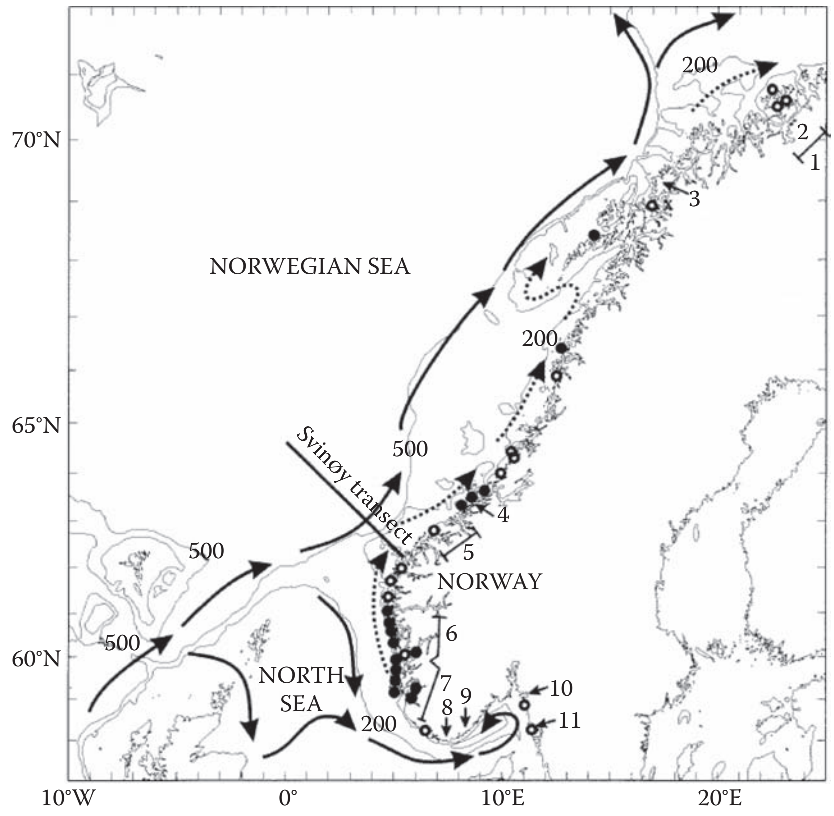


Figure 11 Reported occurrence of *Apolemia uvaria* blooms along the Norwegian coast in 1997 (Båmstedt et al., 1998). Solid circles indicate mass occurrences causing salmon farm problems, open circles indicate low abundance of *Apolemia.* Solid and dotted arrows indicate the main oceanographic flows. (Reproduced with permission of Taylor & Francis.)

distances for individuals will range from tens to hundreds of kilometres (van der Molen et al. 2007). However larval behaviour and oceanographic features can act to restrict dispersal so that a significant portion of offspring are retained close to their natal origins—potentially generating self-recruiting populations. Whilst self-recruitment has been most widely studied in tropical reef fish (Almany et al. 2007) it is also a feature for some temperate species. For example, Iles and Sinclair (1982) proposed that larval retention by oceanographic features, predominantly fronts, was a key mechanism for maintaining genetically discrete substocks of Atlantic herring (*Clupea harengus*). Because of their small size and extended planktonic durations there are few direct observations of fish larval dispersal except where population size and dispersal range are sufficiently small to allow observation or mass marking and recapture (Almany et al. 2007). Most estimates of dispersal distances have been inferred from knowledge of water currents potentially linking known spawning areas and nursery grounds. More recently coupling of oceanographic computer models with particle tracking has allowed more formal testing of these transport paths, including seasonal and interannual variability. Although such models may adequately simulate the dispersal of the essentially passive egg stages, incorporating responsive larval behaviour remains a challenge (Vikebø et al. 2007a). Even for well-studied species such as European plaice *Pleuronectes platessa* (Fox et al. 2006) or walleye pollack *Theragra chalcogramma* (Olla et al. 1996) there is limited understanding of how individual larvae react to environmental cues and trade off the risks of obtaining adequate food against predation (Vikebø et al. 2007a). Experimental studies of temperate fishes have also tended to focus on a limited range of commercially important species (Leis 2007). Because of this we probably underestimate the variety of behaviours, and thus transport pathways, utilised by the early life stages within fish communities as a whole (van der Molen et al. 2007). Despite these problems, particle-tracking models have provided important insights into the transport of early life stages of several fish species in European waters. Most examples suggest drift to be contained within EUR-OCEANS' systems. For example within the North Sea, the transport of plaice eggs and larvae across the southern North Sea is relatively well understood (van der Veer et al. 1998) whilst it is known that residual currents transport haddock eggs and larvae from spawning grounds off the north-west of Scotland, around the northern tip of the United Kingdom and into the northern North Sea (Heath & Gallego 1998). Off Norway the northwards drift of cod eggs and larvae from spawning grounds around the Lofotoen Islands, including aspects of larval behaviour has also been relatively well studied (Vikebø et al. 2007a). Here there is a clear influence of regional linkage since Vikebø et al. (2007b) modelled the impact on Arcto-Norwegian cod of a slowdown in the MOC. According to their model results, a 35% reduction in the MOC would result in a southwards and westwards shift in the distribution of cod year classes from the Barents Sea on to the narrow shelves of Norway and Spitsbergen, reductions in individual growth of the pelagic juveniles and in increasing numbers of larvae and pelagic juveniles being advected towards the western parts of Spitsbergen, and possibly further into the Arctic Oceans, where they are would be unable to survive.

As well as the indirect effects of regional linkages, some species cross between EUR-OCEANS' regions. One of the best-known examples is the European eel (*Anguilla anguilla*). Following spawning in the south-western Sargasso, the larvae (leptocephalii) drift across the open Atlantic (Wang & Tzeng 2000). When the leptocephalii reach coastal waters, they metamorphose into glass eels, which move into estuaries and rivers. Eel populations within European rivers have declined catastrophically since the 1980s and processes occurring in the open ocean, such as shifts in the track of the North Atlantic drift, may be behind this decline (Feunteun 2002, Bonhommeau et al. 2008). The importation of Japanese eels (*Anguilla japonica*) for cultivation trials has also introduced a parastitic nematode (*Anguillicola crassus*). This nematode is now widespread in Europe but its impacts on native eel stocks are not known (Kennedy & Fitch 1990). The European eel thus provides a strong example of where both life history linkages between the Atlantic and the shelf seas and the dispersal of alien species within the shelf seas are of key importance. In terms of transregional linkages, mackerel and blue whiting provide further examples of commercially important species. Starting in February, north-eastern Atlantic mackerel spawn progressively from the Bay of Biscay up the shelf edge and spawning ends around July off the west of Scotland (Bartsch & Coombs 2004). Model-based particle tracking suggested that although most of the larvae drift northwards in the Atlantic current, a smaller proportion are transported southwards and the location of the division that separates the drift routes varies interannually depending on the hydrographic conditions (Skogen et al. 1999).

Interannual variability in oceanographic flows can lead to pulsed recruitment in certain regions. A well-studied example is the western Greenland cod stock, which was historically sustained by periodic influx of cod larvae transported from Icelandic spawning grounds. The strength and timing of the transport are related to the NAO. Because the NAO index has recently been in a positive phase, both transport conditions and local conditions at Greenland have been less favourable for the cod and the western Greenland stock has declined (Dickson & Brander 1993, Stein & Borovkov 2004). Other long time-series exist for catches of Arcto-Norwegian cod and Norwegian spring-spawning herring and it has been shown that the state of these stocks can be linked with cycles of warming and cooling associated with the AMO (Toresen & Østvedt 2000, Sundby & Nakken 2008). Unfortunately, most records of fish distribution and abundance only relate to the adults so it is difficult to examine the responses of the early life stages to oceanographic and environmental variability. We know that there have been significant biogeographic and phenological changes in the plankton of the north-eastern Atlantic since the 1960s but whether similar shifts have occurred for fish larvae is less clear. Across the wider region, analysis of fish larvae in CPR samples was stopped in 1978 due to financial constraints (Coombs 1980) but samples are now being reanalysed and a re-evaluation of biogeographic patterns for north-eastern Atlantic ichthyoplankton should soon become available.

Movements of juvenile and adult fish

Many fish species undergo extensive migrations with the potential to move between EUR-OCEANS' systems. However, the life cycles of most appear to be contained largely within one of the three systems discussed in this review: European shelf seas, Atlantic or Arctic and Nordic Seas. An exception is the Atlantic salmon (*Salmo salar*). This species breeds in over 2500 rivers around the North Atlantic, from Portugal to Russia, and also in Iceland, Canada and the United States. A large number of these river stocks are currently in a depleted state and are considered to be outside safe biological limits (ICES 2008). The main reasons for these declines are thought to be declines in the quality of freshwater habitats and overexploitation, although the latter has been greatly reduced in recent years. However, processes occuring during the marine phase of the salmons' life cycle may also be critical. Salmon spawn in freshwater where their offspring spend from 1 to 7 yr before they emigrate to sea as smolts. They then remain at sea for a further 1 to 3 yr (and occasionally more) before returning to their river of origin to spawn. The precise migration routes of salmon smolts after they enter the sea are not known, but the fish appear to move rapidly away from the coast, and there is some evidence that they may follow major ocean currents. Thus smolts leaving rivers in the United Kingdom and Ireland, for example, move northwards into the Norwegian Sea within a few months of leaving freshwater (Holm et al. 2000, 2003). Subsequent movements are poorly understood but depend, in part, on how long the fish will remain at sea. Salmon of all ages have been caught in fisheries in the Northern Norwegian Sea that have operated during winter and spring months, and the majority of these fish are thought to be on their return migration. A fishery has also operated along the west coast of Greenland in the late summer and autumn; this fishery only takes salmon that would have spent at least 2 yr at sea, and a larger proportion of these fish originate from more southerly rivers. A similar pattern is seen for salmon from North American rivers. However, little is known about the movements and distribution of the fish between these points. Recent studies have shown that the condition of adult salmon returning to their home rivers has fallen as ocean conditions in the North Atlantic have become warmer, and underweight fish have been shown to have disproportionately low reserves of lipids (Todd et al. 2008). Such observations point to multiple trophic-level effects of environment-driven change in the north-eastern Atlantic (Beaugrand & Reid 2003).

Another wide-ranging species is the North Atlantic bluefin tuna (*Thunnus thynnus*), which can travel up to 8000 km in 50 days. The eastern stock has its main spawning areas in the Mediterranean and after spawning they migrate through the Straits of Gibraltar and follow the NAC northward, sometimes into Norwegian waters (Metcalfe et al. 2002). Significant annual variations in migration routes exist but these are not fully understood. The feeding migrations into Norwegian waters, particularly during the 1950s, were found to provide these individuals with access to abundant prey (herring, mackerel, saithe, squid and crustaceans). The condition factors of the bluefin tuna feeding along the Norwegian coast were significantly higher than the condition factors of specimens feeding in the mid-Atlantic. Catches of bluefin tuna in Norwegian waters declined markedly during the 1960s and this species is now more or less absent from these areas. The bluefin tuna stock is, according to the International Commission for the Conservation of Atlantic Tunas (ICCAT), at a critically low level and this is probably the main reason for the absence of this species in the Norwegian Sea.

Several species are largely confined to one of the EUR-OCEANS' systems but components of the population range into adjacent systems. For example, Atlantic mackerel (*Scomber scombrus*) are distributed from Morocco to northern Norway, including the North Sea, the Norwegian Sea and the entrance of the Barents Sea (Iversen 2004). Three main spawning areas are recognised: southern,

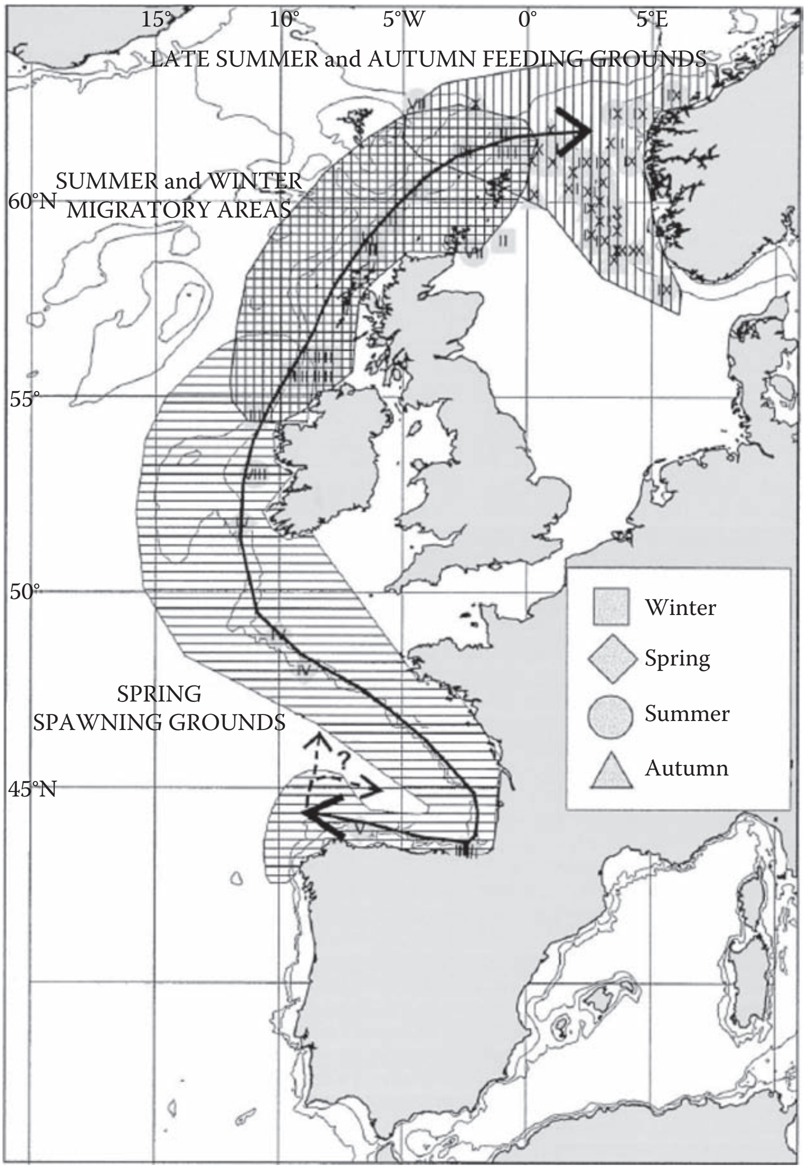


Figure 12 Pathways of mackerel tagged as mature or spawning fish off the Spanish Basque coast. (From Uriarte & Lucio 2001. With permission of Elsevier.)

western and North Sea. However, tagging data raise some doubts over whether the southern component is a truly separated stock (Uriarte & Lucio 2001). After spawning, mackerel from the southern and western areas migrate into the Norwegian Sea and the North Sea to summer feeding grounds (Figure 12). During the autumn most of the mackerel are found in the North Sea where they stay as late as February–March of the following year before migrating back to their spawning areas. Walsh and Martin (1986) found that while the timing and pattern of the post-spawning migration has been relatively stable, the migration routes back to the spawning areas have changed significantly from late summer in the 1970s to January in the 1990s. Walsh et al. (1995) found that the migration pathway of mackerel towards the spawning areas was linked to a tongue of warm water along the

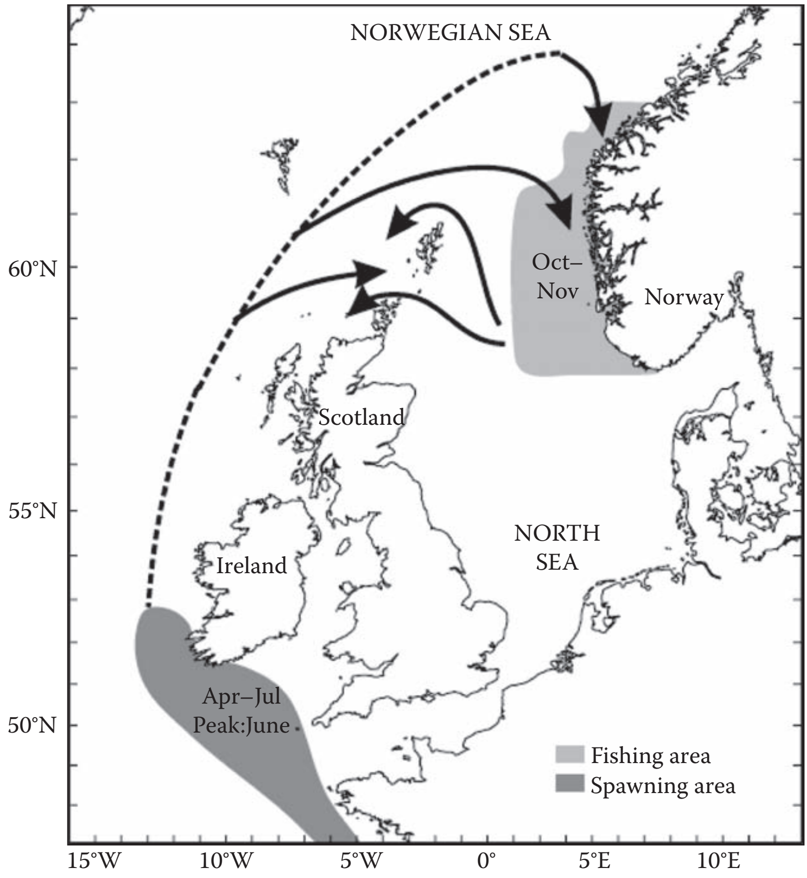


Figure 13 The spawning area, migration route and Norwegian fishing area for western horse mackerel. (From Iversen et al. 2002. With permission of Blackwell.)

shelf edge. Subsequently, Reid et al. (1997) suggested that the migration back to the spawning areas was regulated by temperature; when the sea temperature falls below 9°C, it triggers the migration. In contrast to the prespawning migration, mackerel actively feed post-spawning and because prey availability may be the more important driver, the relationship with water temperature is not so clear during this phase of the life cycle.

Horse mackerel (*Trachurus trachurus*) are also widely distributed, with three spawning components in the north-eastern Atlantic: in the southern, western and North Sea (Iversen 2004). Parts of the western stock, which spawn west of Ireland and in the Bay of Biscay during May–July subsequently migrate into the North Sea and Norwegian Sea (Figure 13). There is a strong correlation between modelled flux of Atlantic water into the North Sea in winter and catches of horse mackerel 6 mo later (Iversen et al. 2002). It was hypothesised that increased temperatures and food production during years with high inflow explained the increased catches.

Blue whiting (*Micromesistius poutassou*) is an important industrial species in the north-eastern Atlantic. Its distribution extends along the continental shelf from the Canary Islands to Spitzbergen, with smaller populations in the north-western Atlantic and the Mediterranean Sea (Was et al. 2008). Adults reach maturation at 2–7 yr old, and undertake long annual migrations from feeding grounds to spawning grounds and back again (Bailey 1982). It has recently been suggested that observed variability in the migration route of blue whiting from the spawning grounds to feeding areas in the Norwegian Sea can be explained by the influence of the subpolar gyre on the westwards extension of the spawning area (Hátun et al. 2007). According to these authors, the spawning areas are shifted eastwards due to colder conditions farther west during periods of strong subpolar circulation. This would lead to a post-spawning migration through the Faroe-Shetland Channel. In contrast, a weak subpolar gyre would lead to warmer conditions spreading farther west and consequently improved conditions for blue whiting spawning in these areas. During such periods the post-spawning migration route will be shifted westwards of the Faroe Islands. The authors suggested that this last condition would lead to improved conditions for recruitment and could explain the relatively high recruitments observed from the late 1990s until 2005. The position of the Arctic front in the Norwegian Sea varies according to the strength of the East Icelandic Current and the Atlantic Current. Since blue whiting do not appear to enter Arctic waters such oceanographic changes will greatly influence their distribution.

The role of ocean currents in the distribution of higher predators across regional boundaries

Large marine organisms such as basking sharks, turtles and whales are all active swimmers capable of travelling large distances. Consequently the major influences of oceanographic flows on their movements are indirect (Figure 3). Population distributions are bounded by physical and biological constraints such as topography, temperature, predators and prey. Of these, the distributions of target prey are probably the most significant.

Archival pop-up tags have recently been used to reconstruct the movements of basking sharks (*Cetorhinus maximus*) around the European continental shelf (Figure 14). These data showed extensive movements of up to 460 km between distinct centres in the shelf seas and along the shelf edge (Sims et al. 2003, 2008). Basking sharks spent most of the time in areas characterised as tidal or shelf break fronts. It was noticeable that individuals foraging along fronts off the south-western peninsula of England moved to three main areas: the Celtic Sea front, the Goban Spur and into the Atlantic at the shelf edge in Biscay (Figure 15). Individuals also moved northwards from these areas

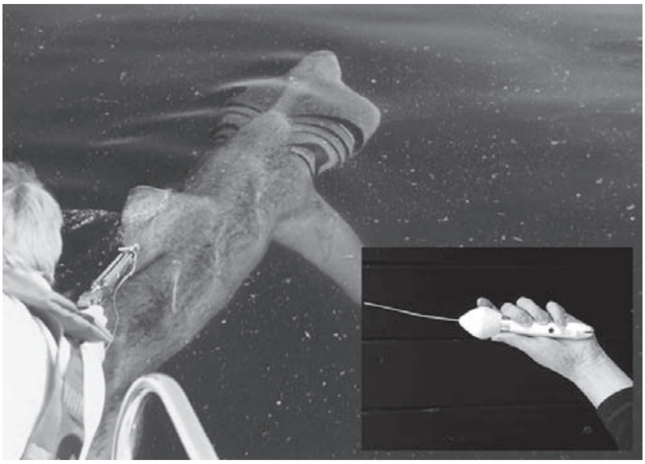
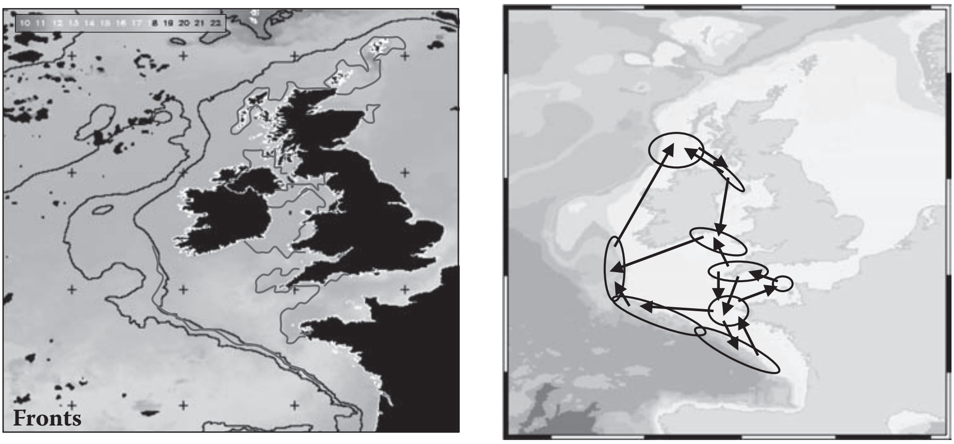


Figure 14 Tagging a basking shark (credit David Sims, Marine Biological Association, United Kingdom) and inset, a pop-up archival tag (Wildlife Computers, Redmond, WA 98052, USA) suitable for attachment to such large marine organisms. The tag records environmental data such as depth, temperature and ambient daylight for at least a year. A release mechanism then operates, the tag floats to the sea surface and the data are transmitted to shore via satellite (Service Argos).



(A) (B)

Figure 15 (See colour insert.) (A) Tidal and shelf break fronts (red lines) on the European shelf and (B) the generalised movement patterns of "tracked" basking sharks between these productive regions. Remote-sensing image is a monthly composite of sea-surface temperature during August 2002 from AVHRR on National Oceanic and Atmospheric Administration (NOAA) satellites. (From Sims et al. 2005. Reproduced with Crown permission.)

along the shelf edge into rich feeding areas in the Hebridean Sea (Sims et al. 2003). Frontal areas are probably targets for basking sharks since they are often associated with enhanced primary and secondary production (Le Fèvre 1986). Interestingly, no sharks tagged off south-western England in spring moved through the Irish Sea during summer, whereas sharks tagged in the fjord-like Clyde Sea in summer travelled relatively rapidly southwards through the Irish Sea to areas off south-western England. Overall, it appears that during summer, basking sharks move between centres of high zooplankton abundance in fronts, tending towards a northwards movement of variable distance (from Plymouth to the Celtic Sea or Hebridean Sea). In winter, some individuals remained or moved into shallow coastal waters, generally in the southern region of the shelf but there was no evidence to support the hypothesis that basking sharks hibernate overwinter in deep waters.

While several species of turtle (loggerhead, *Caretta caretta*; Kemp's ridley, *Lepidochelys kempii*; green, *Chelonia mydas* and hawksbill, *Eretmochelys imbricata*) have been recorded in the north-eastern Atlantic this is probably the result of accidental straying from more southerly waters. Leatherback turtles (*Dermochelys coriacea*) are however regularly encountered in the region. Coastal nesting takes place in the Caribbean, Central and South America and western Africa but feeding occurs over wide areas of the North Atlantic (Hays et al. 2004). Soft-bodied macroplanktonic invertebrates, particularly jellyfish, make up the main component of the diet. Tracking studies of leatherbacks suggests a combination of locomotive strategies that are at times independent of oceanographic processes (Hays et al. 2004) but at others times strongly correlated with them (Luschi et al. 2003). Thus it is probable that the occurrence of leatherback turtles in the open ocean system west of Europe and their subsequent invasions into shelf waters to the west of the British Isles and Norway represents the foraging behaviour of a non-conformist species (Figure 3) focusing on patches of conforming prey (Sims et al. 2008).

The mysticete (baleen) whales are highly mobile and the majority of species are not restricted to any particular region. Species such as minke (*Balaenoptera acutorostrata*) and humpback (*Megaptera novaeangliae*) focus their summer foraging in shelf waters but others like the fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) occupy both offshore and shelf waters. All species typically feed at higher latitudes in summer and migrate towards the tropics to breed in winter. The location of these breeding areas and the paths taken to reach them are poorly known but these migrations represent significant transregional movements. From what is known it is clear that most species do not follow ocean currents (Townsend 1935) although minke whales may track the NAC (Clark 1995). The reason why breeding takes place at low latitudes is unknown but may be a strategy to avoid predation by killer whales (*Orcinus orca*), which have ranges that focus on the productive shelf and polar waters (Corkeron & Connor 1999).

Odontocete (toothed) whales (with the exception of sperm whales *Physeter macrocephalus*) have life histories that are less spatially and temporally compartmentalised, with breeding and feeding occurring in the same areas. As a taxonomic group they are widespread with the majority of species showing distinct habitat preferences by latitude and water depth. For example, bottlenose (*Hyperoodon ampullatus*) and beaked whales (*Mesoplodon* and *Ziphius* spp.) are primarily distributed off shore (>200 m water depth) whilst harbour porpoises (*Phocoena phocoena*) are found almost entirely in shallower waters. Different dolphin species also show segregated distributions, although some, such as bottlenose dolphins (*Tursiops truncatus*), display alternative population strategies (possibly ecotypes as in the western Atlantic with populations at or beyond the shelf break and other populations restricted to localised areas in coastal waters) (Hersh & Diffield 1990). Female sperm whales, like other odontocetes, show preferences for specific habitats, favouring off-shelf waters south of 55°N. In contrast, subadult and adult male sperm whales range north from temperate into Arctic waters and thus straddle offshore latitudinal boundaries for distinct breeding and feeding life-history activities (Rice 1989).

Pinnipeds such as grey and harbour seals (*Halichoerus grypus, Phoca vitulina*) are primarily restricted to shelf waters close to haul-out sites. However species such as harp (*Pagophilus groenlandicus*), bearded (*Erignathus barbatus*) and ringed seals (*Phoca hispida*) that are associated with ice may forage into deeper waters while hooded seals (*Cystophora cristata*), which are typically considered to be Arctic species, forage in off-shelf waters as far south as Ireland (Folkow & Blix 1994). In addition to the regular seasonal movements of individuals across ecosystem boundaries, others occur more episodically. In particularly harsh winters, harp seals may shift their range southwards from Greenland and northern Norway to southern Norway and the northern North Sea (Nilssen et al. 1998). These seal "invasions" can have wider impacts as these polar seals are thought to be vectors for the introduction of phocine distemper virus (PDV) to populations of harbour and grey seals in the North Sea (Dietz et al. 1989). The first well-documented seal epizootic resulting from this viral infection killed an estimated 18,000 common seals in 1988 and resulted in significant impacts on indigenous seal numbers, ranging from 40 to 80% population mortality. A second PDV outbreak occurred in 2002. Similar viral interspecies jumps may occur in odontocete cetaceans (Kennedy 2000) and it has been suggested that offshore pilot whales *Globicephala* spp. may act as a reservoir of morbillivirus infection for cetaceans, including those in coastal waters (Duigan et al. 1995).

Even less predictable, but with some potential for implications over longer time scales, are the extralimital movements of individual animals out of their normal ranges. The occurrence of emaciated, usually juvenile, polar seal species on beaches in southern Europe is an almost annual event and is usually considered a result of straying of young or ill individuals. However the chance discovery that a ringed seal that had been tagged and released off Brittany, France, had made its way back to the population's normal range off Iceland (Ridoux et al. 1998) suggests that there may be an ecological role as a mechanism to allow colonisation of new areas (Wilson 2008). One highly predictable extralimital occurrence is the appearance in late winter and early spring of male sperm whales in the North Sea. As described above, this species typically feeds and breeds in the deep waters off the continental shelf. The annual occurrence of small numbers of male sperm whales in an area without feeding or breeding opportunities is therefore mysterious. The majority of whales that are identified in this area usually eventually perish through starvation or beaching. There have been a variety of explanations proposed for this phenomenon and perhaps the most convincing is the notion that the geography of the North Sea conspires to form a large sperm whale trap (Jauniaux et al. 1998). Whales feeding in seas west of Norway migrate south to breed and some may miss the shelf edge and instead turn into the northern North Sea. Continuing south leads the whales to the shallow, narrow and for this deep water species, potentially impassable English Channel.

Being active swimmers, living marine mammals usually exhibit precise habitat preferences and only indirect ecological coupling to the movements of water masses. However, ocean currents influence the ecosystem impacts of marine mammals after their death. *Post-mortem*, most marine mammals float, either immediately or after some putrefaction. The carcasses are then subject to passive transport by surface currents. Relatively little research on the fate of marine mammal carcasses has been performed and the majority of studies have focused on the impacts of large carcasses landing on the abyssal seafloor. However, seasonal pulses of beach-cast dolphins originating from offshore fisheries (Kuiken et al. 1994) suggest that transport of biomass across regional boundaries could be at times appreciable. Whilst the actual quantity of this biomass will be dwarfed by other processes, the impacts of the delivery of biomass in highly localised areas of the seabed can cause hot spots of sediment oxygen demand and bioaccumulated anthropogenic contaminants as the blubber of marine mammals often contains accumulated lipid-soluble pollutants such as PCBs (polychlorinated biphenyls; Stockton & DeLaca 1982). Historical changes in marine mammal abundance, disease epizootics and the legacies of discards from whaling may add further temporal aspects to the magnitude of this effect (Whitehead & Reeves 2005).

Human-induced links between the regional systems

Introduction

Human activities have resulted in significant changes in the state and functioning of the ecosystems of the north-eastern Atlantic. The physical and biological links previously described provide pathways for the 'products' of these activities, such that initial local- or subregional-scale phenomena may have much wider influence. In addition, the links described in previous sections may be short-circuited by human intervention (e.g., trade). In some cases these products or 'state changes' (in the context of the driver-pressure-state-impact-response [DPSIR] framework) may have negligible deleterious effects, but observing and modelling their behaviour can provide useful insights about the transport mechanisms involved. For example, radionuclides released from nuclear fuel reprocessing operations in north-western Europe have been used extensively as tracers of water circulation throughout the north-western European shelf seas, the Nordic Seas, the Arctic Basin and the Labrador Sea from the 1970s to the present day. On the other hand, anthropogenic activities may have significant direct or indirect impacts on the nature and functioning of the ecosystem, causing ecosystem degradation, or some other undesirable disturbance. In some cases these may be the result of a deliberate action, such as dumping unwanted materials (e.g., munitions) or using rivers to dispose of chemical wastes. However, in many cases the observed changes follow the 'law of unintended consequences'. For example there are now many non-indigenous species that have become widespread following accidental or deliberate introduction (Hulme et al. 2008, IMO 2004).

Alien species introductions

There are many potential pathways for the introduction of non-indigenous species in the marine environment (Hulme et al. 2008) but the principal vector has been shipping (Gollasch 2002). Once a species has been introduced locally it can often be spread further by human vectors or oceanographic pathways. Alien species have been inadvertently transported on ship's hulls since the earliest seafarers. For example, the shipworm *Teredo navalis* was introduced to Norway about 300 years ago in the hulls of wooden vessels, and the barnacle *Balanus improvisus* became established in the early

1800s, probably from North America (Hopkins 2002). In the North Sea, alien species were present in around 98% of samples taken from commercial ship hulls (Gollasch 2002). The introduction of antifouling coatings may have had some impact on this pathway but use of tributyl tin (TBT) has, in turn, led to problems with induction of imposex in certain organisms (especially gastropods) along major shipping routes and in ports (Terlizzi et al. 2001). The other main shipping vector for alien introductions has been the inshore exchange of ballast water, increasingly by large bulk carriers (Ruiz et al. 2000). Between 3 and 5 billion tonnes of ballast water are transferred annually (http://globallast.imo.org). The recognition that this provides a vector for the introduction of non-indigenous species has led to the provision of good practice guidelines by the International Maritime Organisation (IMO) and the adoption of the *International Convention for the Control and Management of Ships' Ballast Water* in 2004 (http://www.imo.org/conventions/mainframe.asp?topic_id=867).

Species introductions have affected all European regional seas, with the most devastating consequences to date being observed in the Black Sea (e.g., comb jelly, *Mnemioposis leidyi*). Such invasions may represent a component in broad-scale regime shifts combined with the effects of overfishing leading to trophic cascades (Daskalov et al. 2007). So far the north-eastern Atlantic has not experienced a similar scale of change although several hundred non-indigenous species have been identified in the region (Gollasch 2002). These include members of the Chlorophyta, Dinoflagellata, Phaeophyta, Rhodophyta, Cnidaria (Hydrozoa), Nematoda, Chordata (Tunicata, Osteichthyes), Crustacea (Copepoda, Cirripedia, Mysidacea, Isopoda, Amphipoda), and Mollusca (Gastropoda, Bivalvia). The scale of introductions has been documented by member states of the OSPAR Commission (www.ospar.org) and the results summarised by Leppäkoski et al. (2002). These actions have culminated in the establishment of the European Research Network on Aquatic Invasive Species (ERNAIS) whose role has been recognised in the European Strategy on Invasive Alien Species (Genovesi & Shine 2003). However, the picture is not static and new non-indigenous species are constantly being recorded; for example, *Mnemioposis leidyi* was observed for the first time in the Baltic Sea in 2006 and in the southern North Sea in 2007 (Boersma et al. 2007).

An example of a phytoplankton introduction with potential nuisance effects is the diatom *Coscinodiscus wailesii*, native to the Indian and Pacific Oceans. This species was observed in the waters off the south-west of the United Kingdom in 1977 and has since spread along the French Atlantic and southern U.K. coasts. It is now being recorded in Helgoland and south-western Norway. *Coscinodiscus wailesii* forms dense, mucilaginous blooms (up to 1400 µg carbon l^{-1}) but is inedible to most zooplankton, causes anoxia near the seabed and clogs fishing gears (Laing & Gollasch 2002). A number of dinoflagellate species have also been introduced in ballast water that are capable of causing HABs. These include *Alexandrium catenatumi* and *A. tamarensis*, which can cause paralytic shellfish poisoning (PSP), and *Karenia mikimotoi* (formerly *Gyrodinium aureleolum)*, which has caused major fish kills in caged sea trout (Goulletquer et al. 2002, Hopkins 2002). Ballast water is also considered the vector responsible for the introduction of the Chinese mitten crab *Eriocheir sinensis* to Germany in 1912. It has spread widely since and can cause significant damage to river and estuary banks, as well as competing with native fauna (Nehring 2002).

Another vector for introductions is aquaculture (Minchin 1996, Hégaret et al. 2008). For example, the Japanese (or Pacific) oyster *Crassostrea gigas* was introduced to France in the 1970s to sustain the oyster industry. This is considered to be a commercially 'successful' introduction but the species may have provided a vector for parasites that have since infected native species (Goulletquer et al. 2002). In contrast, the slipper limpet *Crepidula fornicata*, accidentally introduced along with the oyster imports, can have a negative impact on oyster beds. It has a high reproduction rate and tends to deposit mud on the underlying oysters. Another example is the parasitic nematode *Anguillicola crassus* introduced in a consignment of Japanese eels in the 1980s. The parasite infects the swim bladder of native eels (Køie 1991). Some non-indigenous species have been deliberately introduced for sports fishing (e.g., rainbow trout *Oncorhyncus mykiss*), others as discarded pets or surplus to the restaurant trade (e.g., American lobster *Homarus americanus*, carrying a bacteria [*Aerococcus viridans*] that causes 100% mortality in the European lobster *H. gammarus*). An unusual vector was the carriage of drinking water barrels from southern Australia, resulting in the introduction of the gastropod *Potamopyrgus antipoarum* to the United Kingdom in the 1850s, since spreading widely in coastal waters as far as Norway (Hopkins 2002). Rafting of organisms on a variety of natural materials (e.g., pumice, timber, macroalgae) is recognised as another significant transport mechanism, with evidence demonstrating that human activities have increased this phenomenon with the introduction of plastic debris (Thiel & Gutow 2005) and the occurrence of tar balls (Minchin 1996). Such rafts will follow the surface ocean currents described in previous sections, providing a vector for transregional transport.

Contaminants

Indirect sources of contamination

Plastic debris is now almost ubiquitous in the marine environment and is an extensive literature detailing the impacts of this debris on marine organisms (Derraik 2002). Disposal from shipping has come under increasing control (although this is difficult to enforce) so that most of the recent introductions have a terrestrial origin. Plastics degrade by breaking into smaller fragments and even 'biodegradable' plastics leave a legacy of microparticles. In addition, thermoplastic resin pellets (the 'feedstock' of the plastics industry) are ubiquitous in the world ocean and can act as vectors for organic pollutants such as PCBs, DDT (dichloro-diphenyl-trichlorethane) and PAHs (polyaromatic hydrocarbons) (Rios et al. 2007). Plastic microparticles can become incorporated into the cells of organisms, with potential toxic effects, and can increase the intake of some organic contaminants, such as phenanthrene (Teuten et al. 2007). Examination of archived samples from the CPR has revealed the presence of plastic microfragments on both the Aberdeen–Lerwick and Iceland–Scotland routes (Thompson et al. 2004). The fragments were more numerous on the former route, but for both there was a significant increase in abundance in the 1980s and 1990s compared with the 1960s and 1970s. This indicates that plastic microfragments are increasing in quantity and are being redistributed widely in the north-eastern Atlantic by the ocean currents.

Since the late 1960s there has been concern about the long-term impact of several classes of chemicals in widespread use that are considered to be persistent organic pollutants (POPs). These chemicals have a variety of effects on marine organisms, including endocrine disruption and immunosuppression. They can also affect people by becoming concentrated in marine food webs, with potentially dangerous levels appearing in marine bioresources consumed by humans. Although levels of consumption of marine products in Europe are generally too low for this to be a major concern, peoples in certain European countries, particularly in northern Europe, tend to have much higher per capita consumption rates. PCBs, DDT, PBDEs (polybrominated diphenyl ethers), dioxins and other POPs are known to accumulate in lipid-rich fish, with much higher levels in the Baltic and North Atlantic than in the Southern Hemisphere and elevated concentrations have been recorded in fish oils and farmed salmon fed on these oils (Jacobs et al. 2002). Bioaccumulation of POPs has also been linked to problems in top-level predators such as thyroid dysfunction in seals (Sørmo et al. 2005), immunosuppression leading to *Brucella* infection in hooded seals and impaired reproduction in polar bears (Sonne et al. 2006). It has also been suggested that the stress caused by the presence of POPs in the body may reduce the ability of mammals and seabirds to respond to additional environmental stress, for example from increased temperatures (Jenssen 2006). The PBDEs are part of the group of brominated flame retardants and increasing recognition of their possible ecosystem effects is leading to increased constraints on their manufacture and use (Betts 2008). Another group of chemicals found extensively in the north-eastern Atlantic are the perfluorinated acids (PFAs). These compounds have a wide variety of uses, including surfactants in water- and stain-resistant materials. Their production is being curtailed but there is less regulation on related chemicals that can degrade to PFAs (Jensen & Leffers 2008). They are stable in seawater and have been detected throughout the North Atlantic, including the Denmark Strait overflow and the Labrador Sea, leading to a proposal to utilise their presence as a tracer of ocean circulation (Yamashita et al. 2008).

In the North Sea, offshore oil and gas operations have resulted in some measurable environmental impacts. Routine operations release large volumes of produced water (partly formation water and partly injected for greater oil recovery), which may contain elevated concentrations of heavy metals, chemical additives (e.g., biocides), dissolved oil components (e.g., PAHs, alkyl phenols, toluene, naphthalene) and naturally occurring radionuclides (e.g., ^{226}Ra) (Meier et al. 2004). The quantities of produced water tend to increase as the oil field matures. Concern has been expressed that produced water may have an impact on fish populations, prompting studies on potential hormonal effects of alkyl phenols on fish reproduction (Meier et al. 2004, Martin-Skilton et al. 2006). Routine operations also produce drill cuttings comprising a mix of rock fragments, oil- and water-based drilling mud and a variety of other materials used operationally. Although there are clear local impacts, these tend not to extend more than a few kilometres from the platform (Lepland et al. 2000). However, contamination from this industry can be widespread. Perhaps the best-known example is the transport and accumulation of barium, as particulate barite, in the sediments of the Skagerrak, with a depth distribution in sediment cores correlating with the development of the North Sea oil fields (Lepland et al. 2000). One ecological benefit of the industry has been the provision of artificial reefs in otherwise rather barren environments, with complex depth-dependent ecosystems being observed on the platform substructure, including iconic species such as *Lophelia pertusa* on structures in the northern North Sea (Gass & Roberts 2006). The absence of a resident population suggests recruitment via the Atlantic water inflow east of Shetland carrying larvae from known populations west of Scotland. Man-made subsea structures, particularly in the shelf seas, may therefore act as stepping stones facilitating the range expansion of benthic species.

The industrialised nature and high population density of much of western Europe means that concentrations of many pollutants in north-western European coastal and shelf waters are significantly higher than in other ocean basins. These direct and indirect sources (including significant atmospheric transport) result in widespread contamination by organic and inorganic compounds, remote from the immediate sources, via the oceanographic links described in earlier sections of this review, with the Nordic Seas and Arctic receiving a disproportionate burden (Barrie et al. 1992).

Deliberate point-source releases

In most cases the deliberate dumping of wastes may have significant localised impacts but these do not generally extend to a broader regional scale. Dumping of sewage sludge and industrial wastes were common practices in coastal waters but this has now ceased under the OSPAR Convention. At present, most dumped material consists of dredged spoil, with much smaller quantities of fish wastes, and the chemical content and potential impact appear to be rather limited. However, large quantities of conventional and chemical munitions were dumped in the Baltic Sea and North Sea at the end of WWI and WWII and at other sites such as Beaufort Dyke, at the exit of the Irish Sea. Altogether it is estimated that 300,000 tonnes of WWII chemical munitions such as mustard gas have been dumped in European waters (Kaffka 1996). The potential long-term impact of this source and its spatial extent remains unclear as the original containment (e.g., shells, cases, ships' holds) continues to deteriorate and the contents become exposed to seawater.

Covert dumping of radioactive wastes by the former Soviet Union (FSU) and the Russian Federation took place over several decades in the Barents and Kara Seas. Liquid wastes were disposed of in the Barents Sea between 1959 and 1991 and solid wastes in the Kara sea from 1964 to 1991. The latter included objects containing spent nuclear fuel. The total amounts dumped are estimated at 38 PBq (Bq is disintegration s^{-1}) (International Atomic Energy Authority [IAEA] 1999a), but environmental contamination appears to be limited spatially and does not appear to have been exported to other regions in significant quantities (IAEA 1999b). Many of the radioactive components of solid wastes are not particularly soluble in seawater but long-term monitoring remains a priority.

Accidental releases

Accidental releases include conventional and chemical weapons lost, as opposed to deliberately dumped, as well as shipwrecked vessels containing fuel oil and potentially hazardous cargoes. In addition, two nuclear-powered submarines from the Russian Northern Fleet have foundered in northern European waters. The Kursk sank in 2000 in the Barents Sea, in 116 m, with the loss of 118 crew. The reactor was shut down and no significant leakage has been detected (Amundsen et al. 2001). The vessel was subsequently recovered in stages during 2001 and 2002. The Komsomolets sank in 1989 in about 1600 m of water, with many of the crew being lost. The vessel was carrying two nuclear-tipped torpedoes. The hull was damaged and some leakage was detected during a series of expeditions to monitor and repair the damage. Given the remote location and lack of vertical mixing it was not considered to represent a significant source of contamination to shallower waters. Much of the warhead plutonium was expected to be adsorbed by seabed sediments and not to become mobilised.

A further potential source of radioactive contamination is represented by a large number of redundant reactors from submarine and surface vessels located in bases on the Murmansk Peninsula, with very limited facilities for decommissioning after many years of underinvestment. The situation prompted an international response, with several countries arranging bilateral agreements with Russia to provide specialist advice and assist in improving storage and decommissioning facilities. It is not thought that there has been significant contamination of the wider region to date.

Useful tracers of ocean circulation and interregional transport

As discussed, a wide variety of contaminants has been introduced into the waters of the north-eastern Atlantic, from both diffuse and point sources. Many of these do not pose a direct threat to ecosystem functioning but have proved to be useful tools with which to study ocean processes. These transient tracers have been used—singly or in combination—to study pathways, transport rates, residence times, ventilation rates; to provide validation of model simulations; and to understand the fate of other contaminants (e.g., Heinze et al. 1998, Schlosser et al. 1995). The tracers have included stable chemicals from industrial production, such as chlorofluorocarbons (CFCs) and radionuclides released by human activities such as atmospheric nuclear weapons testing, routine discharges from the nuclear fuel cycle and accidental inputs, providing both diffuse and point-source signals. The production of CFCs for a variety of industrial applications (e.g., refrigerants), since the 1930s, has provided well-defined source terms, with inputs increasing steadily until the early 1990s. CFC-11 and CFC-12 concentrations and ratios (time-varying production rates) have been used to derive mean residence times in the Greenland and Norwegian Seas (Rhein 1991). More recently the tracers F-113 and CCl4 have extended the timescales that can be addressed (Haine et al. 1995). CFCs, in combination with ^{3}H/^{3}He, have been used to estimate the residence times for surface and intermediate waters in the Eurasian Basin (Franke et al. 1998), the Greenland Sea (Bönisch et al. 1997) and the Makarov and Canada Basins (Smethie et al. 2000), and CFC-11 has been used to calculate the rate of North Atlantic Deep Water formation (Smethie & Fine 2001).

Radionuclides released from nuclear reprocessing facilities in the United Kingdom (Sellafield) and France (La Hague) have provided a useful set of tracers to study transport from the shelf seas into the Nordic Seas and the Arctic Ocean. The most widely used have been ^{90}Sr, ^{99}Tc, ^{125}Sb, ^{129}I, ^{134}Cs, ^{137}Cs, and isotopes of plutonium (Dahlgaard 1995, Kershaw & Baxter 1995, Gueguenit et al. 1997). An additional radiocaesium signal was provided by the Chernobyl accident in 1986, with highest concentrations being recorded in the Baltic Sea, subsequently being transported into the North Sea and Norwegian Sea (Povinec et al. 2003). Substantial decreases in the direct discharge of most nuclides since the 1980s have reduced the quantity of such tracers entering the environment.

However, the discharges of ^{129}I and ^{99}Tc have increased due to changes in waste management practices and increased fuel throughput. Both are relatively conservative in seawater and have been used to demonstrate transport pathways and mixing processes over much of the North Atlantic. The use of AMS (accelerator mass spectrometry) has allowed ^{129}I analysis on very small samples (<1 l), permitting shared use of conventional water samplers (conductivity, temperature and depth sensor-rosette array) and submarines (US Navy Scientific Ice Expeditions [SCICEX] 1995 and 1996 described in Smith et al. 1999). These authors demonstrated that the boundary between Pacific and Atlantic origin water lies over the Mendeleyev Ridge and showed the flow of Atlantic water along the Lomonosov ridge on the basis of ^{129}I distributions. They included ^{137}Cs to estimate transit times and dilution factors for Atlantic water from the Norwegian coastal current (60°N) to the continental slope of the Makarov Basin and the Kara and Barents Seas (Smith et al. 1999). As the ^{129}I signal has propagated, measurements have been extended to estimate the ventilation times of North Atlantic waters from a single tracer (Edmonds et al. 2001, Tanhua et al. 2005) and in combination with CFC-11 (Smith et al. 2005) to follow the passage of Denmark Strait overflow water. Increased ^{99}Tc release in the mid-1990s was the result of an increased throughput of stored actinide-rich wastes (through the Enhanced Actinide Removal Plant). This reduced the concentrations of plutonium isotopes and ^{241}Am (of radiological concern) but ^{99}Tc was unaffected. Technetium is readily taken up by certain biota such as the algae *Ascophyllum nodosum* and *Fucus* spp. and lobster (*Homarus gammarus*), allowing the progress of the 'plume' along the U.K. and Norwegian coasts to be readily followed (Kolstad & Lind 2002, Nawakowski et al. 2004, Oliver et al. 2006). Observations of ^{99}Tc in seawater and biota have also been used to look at variability in transport rates from the Irish Sea to the Nordic Seas (Figure 16) in relation to regional and basin-wide transport processes (Kershaw et al. 2004, Orre et al. 2007) and to validate the North Atlantic/Arctic Ocean sea ice model (NAOSIM) developed by the Alfred Wegener Institute for Polar and Marine Research (Karcher et al. 2004).

Future trends for human-induced links between the regional systems

The volume of regional and intercontinental shipping is likely to increase with the potential for further shipping-related ecosystem impacts. However the *International Convention for the Control and Management of Ships' Ballast Water* is due to be implemented in 2009, and a number of active ballast water treatment systems have been, or are due to be, evaluated for their efficacy and safety (http://globallast.imo.org). The recent pattern of decreased summer ice in the Arctic is expected to continue, raising the prospect of new shipping routes (discussed more fully on page 54). This will likely be accompanied by increased military activity and exploration and exploitation of oil and gas and other natural resources (ACIA 2004). The impacts of these activities will certainly affect more southerly regions due to increased transportation of oil and other commodities from or through the Arctic with potential trans-shipment at new or existing facilities (e.g., Shetland) and increased potential for accidental spills in the shelf seas (Department for Environment, Transport and the Regions [DETR] 2001). Changes in energy production will be accompanied, under existing plans, by the decommissioning and removal of the oil and gas industry steel structures, presently providing a habitat for *Lophelia pertusa* and associated organisms. Removal of these structures may lead to undesired biodiversity impacts. New structures for renewable energy capture (wind, tidal) will tend to be in coastal waters due to the costs of transferring electricity along undersea cables and these will provide a different set of 'stepping-stones', allowing range shifts for benthic organisms. Although deliberate dumping at sea is now banned, we will continue to input an enormous range of chemicals into the waters of the north-eastern Atlantic, either as aerosols or through run-off and accidental discharge. Unfortunately we have rather limited knowledge of their long-term impacts, either singly or cumulatively. Moves towards an integrated European Marine Strategy should eventually provide stronger protection of the marine environment of the north-eastern Atlantic but ultimately future trends will depend on the socioeconomic development paths that Europe and the rest of the world follow (Pinnegar et al. 2006).

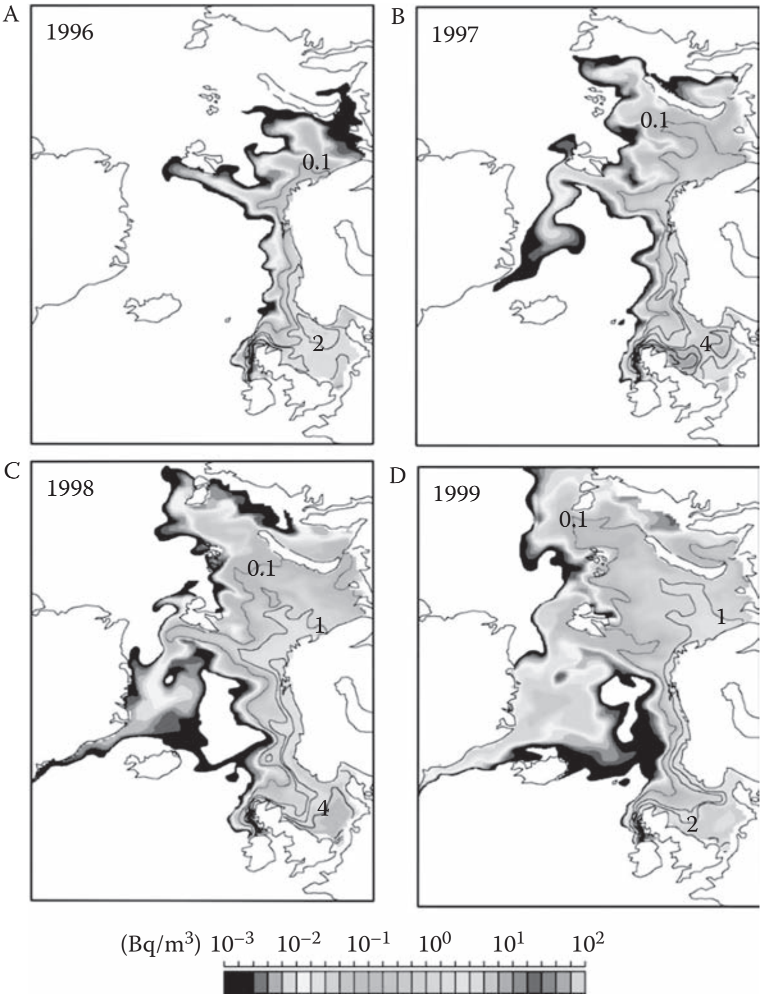


Figure 16 (See colour insert.) Simulated distribution of ^{99}Tc (Bq m^{-3}) in surface water, from the North Atlantic/Arctic Ocean sea ice model (NAOSIM), in September (A) 1996, (B) 1997, (C) 1998 and (D) 1999 (isolines: 0.1, 1.0., 2.0 and every 2.0 Bq m^{-3}). Model simulations were broadly in agreement with observed concentrations. Elevated releases from the Sellafield nuclear fuel reprocessing plant into the Irish Sea began in 1994 due to the startup of the enhanced actinide removal plant (EARP) facility. (From Karcher et al. 2004. With permisson from Elsevier.)

Possible changes in the regional linkages over the next century: the potential impacts of climate change

The background of climate change

The Intergovernmental Panel of Climate Change (IPCC) Fourth Assessment report concluded that most of the observed increase in global average temperatures since the mid-twentieth century is very likely (over 90% certainty) due to the observed increase in atmospheric greenhouse gas concentrations, with most of this increase due to burning of fossil fuels (Solomon et al. 2007). Observations since 1961 show that the average temperature of the global ocean to depths of at least 3000 m has increased and that the ocean has been absorbing more than 80% of the heat added to the climate

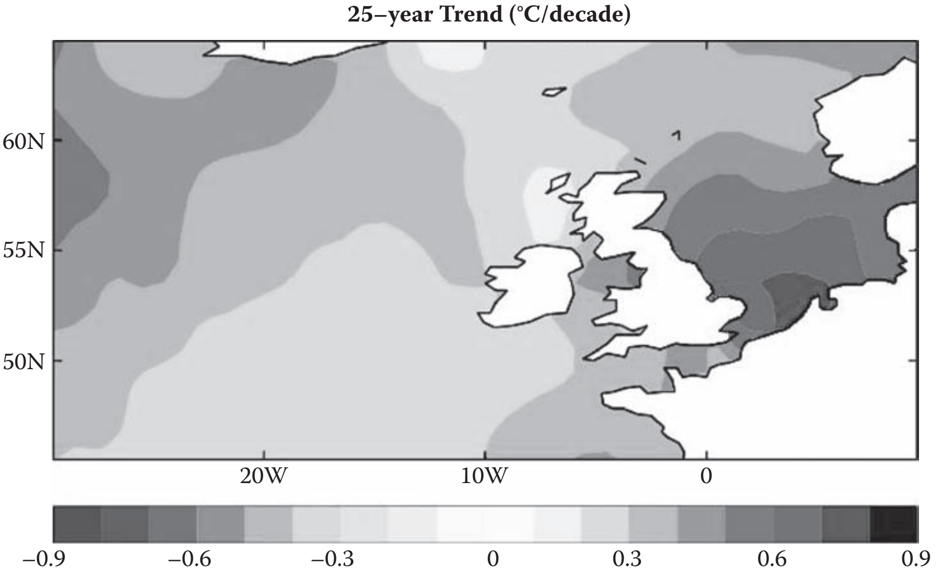


Figure 17 (See colour insert.) The 25-year trend in sea-surface temperature (°C decade-1, 1982–2006) for the north-eastern Atlantic. (From Holliday et al. 2008. Reproduced with Crown permission.)

system (Barnett et al. 2001, Hansen et al. 2005, Bindoff et al. 2007). These global patterns however mask strong regional variability (Pierce et al. 2006) and for the north-eastern Atlantic, observed sea-surface temperatures still remain within the historical envelope (Hobson et al. 2008).

The sea temperature in the north-eastern North Atlantic has shown an increasing trend over the recent three decades and this is probably an indication of climate change caused by emission of greenhouse gases (Figure 17). However, in addition to long-term climate change induced by anthropogenic activity, there is natural variability. Long-term variations caused by solar and tectonic factors and short- and midterm variations related to atmospheric and oceanic conditions exist and have to be separated from the long-term climate change even though it is difficult to distinguish between them. The longest time-series on ocean climate is from north of Kola (Figure 18). It goes back to 1900 and shows a slightly increasing trend over the entire time series. However, on top of this trend several longer- and shorter-term periods are displayed. An approximately 60-yr cycle is evident with

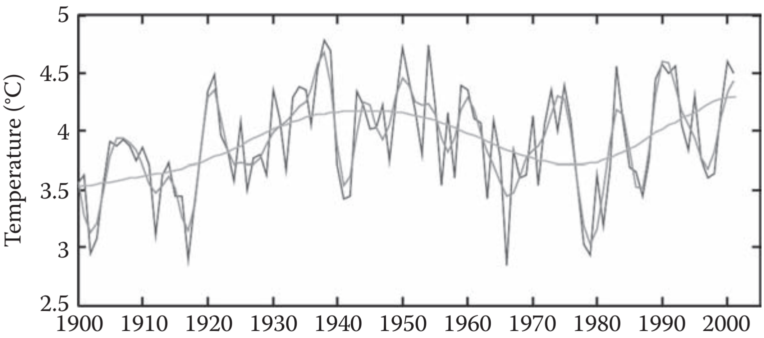


Figure 18 Sea temperature (averaged over 0- to 200-m depth) at the Kola section in the Barents Sea showing the annual mean, 3-yr moving average and long-term smooth. (From Stenevik & Sundby 2007. With permission from Elsevier.)

a maximum in the 1930–1940s and a minimum in the 1960–1970s. Another period displayed in the Kola time series is the 18.6 yr cycle due to the nutation of the earth. In addition, there are decadal-scale periods associated with the NAO, and there is also a clear biannual signal. At present we do not have sufficient knowledge to make predictions of these periodicities in regional climate. The IPCC stated that, "Although progress has occurred, it is still not possible to assess regional responses to shifts in climate trends, and it is unknown if a general warming will increase or decrease the frequency and intensity of decadal-scale changes" (Stenevik & Sundby 2007).

Observations to date suggest that there has been a general increase in wind speeds and the frequency of occurrence of storms in the north-eastern Atlantic; whether this is linked to increased atmospheric greenhouse gas levels is unclear as increased storminess is also associated with a positive mode of the NAO (Hurrell & Dickson 2004, Osborn 2004). Many global climate models do reproduce a general trend towards a positive NAO in the twenty-first century (Terray et al. 2004) although other analyses based on regional downscaling predict weaker trends for wind speeds and storminess (Hulme et al. 2002). Typically, climate models predict a decrease in the total number of extratropical cyclones but an increase in the number of intense wind events (Lambert & Fyfe 2006). Predictions of future climate also indicate that there may be an increase in rainfall at high latitudes associated with a polewards shift of the high-latitude storm tracks. This may have an impact on the distribution of atmospheric inputs to the north-eastern Atlantic region because wet deposition more efficiently removes particulate material from the atmosphere than does dry deposition.

Although the characteristics of key oceanic water masses are changing there is no clear evidence for changes in ocean circulation. Weak warming has been noted in the NAC but long-term cooling is also observed in the North Atlantic subpolar gyre. Since 1995, the upper waters of the North Atlantic subpolar gyre have become warmer and more saline (Bindoff et al. 2007). However, at regional scales, natural climate variability is relatively large, making it difficult to distinguish anthropogenic forcing. In particular, multidecadal changes in the AMO may reflect a 50- to 80-yr pattern of North Atlantic coupled ocean-atmosphere variability (Sutton & Hodson 2005). A major uncertainty in the North Atlantic is the future behaviour of the NAO and North Atlantic MOC (Meinke et al. 2003).

Suggestions that the THC has slowed by 30% since the early 1990s (Bryden et al. 2005) are controversial as recent longer-term observations have shown large natural varibility in flow (Cunningham et al. 2007). Simulations of twentieth century THC strength in a suite of atmosphere ocean general circulation models (AOGCMs), whilst being within the range of observational uncertainty for most models, show periods of higher and lower values and a few show substantial differences (Figure 19). Such variability in model outcomes for this particular oceanographic feature makes intepretation of short-term MOC observations particularly difficult (Houghton et al. 2001). However, all the models suggest some decrease in the strength of the MOC in coming years although none projects a complete switch off (Bindoff et al. 2007). A reduction in MOC strength should lead to temporary cooling in the north-eastern Atlantic (although this reduction would not be enough to offset future warming beyond 50 yr).

Since the third IPCC assessment, there have been significant advances in climate modelling, providing a stronger quantitative basis for assessing the likelihood of future change. However, uncertainty in regional-scale projections remains high. In particular there are uncertainties about changes in wind-induced ocean mixing and sea-level rise. In looking at annual, mean zonally averaged SSTs, the largest individual errors are found at mid- to high latitudes (Figure 20), where the model simulations are frequently negatively biased (Rayner et al. 2003). This bias appears to be associated with poor simulation of the path of the NAC (Solomon et al. 2007).

Although increasingly sophisticated models coupling atmospheric and oceanic processes (AOGCMS) are being used for projection, it can be argued that the representation of marine biological processes within them is still too simplistic. It is clear that changes in biological processing, such as the shelf sea pump described on page 19, have the capacity to significantly modify the future

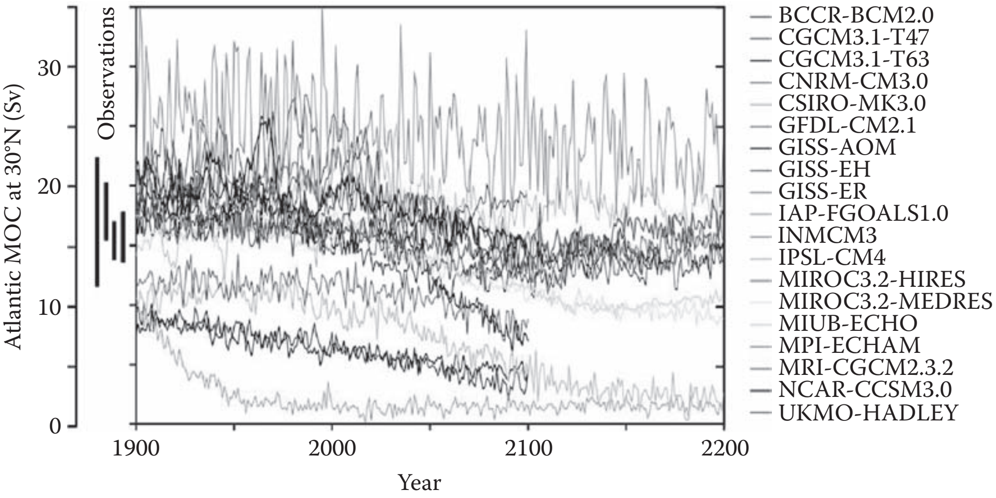


Figure 19 (See colour insert.) Evolution of the Atlantic meridional overturning circulation (MOC) at 30°N in simulations with the suite of comprehensive coupled climate models. (From Meehl et al. 2007, Figure 10.15, p. 773. With permission.)

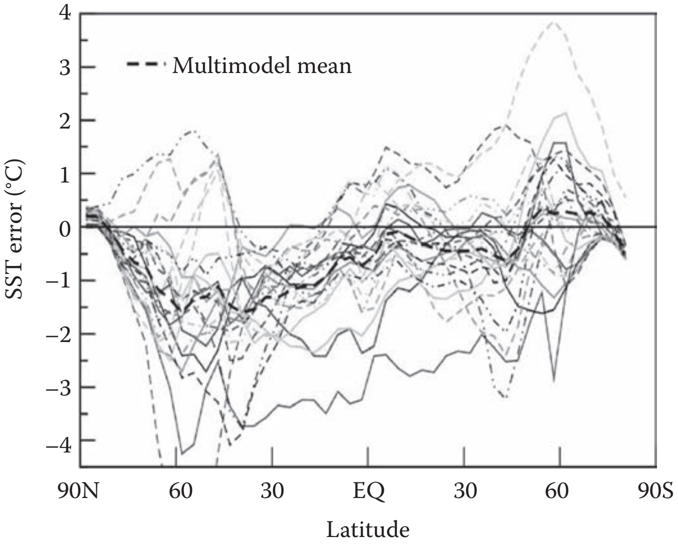


Figure 20 (See colour insert.) Annual mean, zonally averaged SST error, simulated minus observed climatology for a number of atmosphere ocean general circulation models (AOGCMs). The Hadley Centre Sea Ice and Sea Surface Temperature (HadISST; Rayner et al. 2003) observational climatology for 1980 to 1999 is the reference used here, and the model results are for the same period in the twentieth century simulations in the MMD at PCMDI. In the presence of sea ice, the SST is assumed. (From Randall et al. 2007, Figure 8.8, p. 614. With permission.)

global environment (Schmittner et al. 2005b, Bindoff et al. 2007, Schneider et al. 2008). For this reason, EUR-OCEANS has supported the development of improved global, plankton models such as PlankTOM in which a wider range of planktonic organisms are represented as functional groups (Le Quéré et al. 2005).

The likely impacts of climate change in the north-eastern Atlantic

Impacts on regional linkages

Within the north-eastern Atlantic, potential changes in the Arctic have probably received most analysis through the work of the ACIA (2004). This group has produced a number of projections on how the marine environment might be affected by climate change (Tables 1 and 2). These projected changes arise from the combined impacts of local processes and changes in regional linkages such as large-scale atmospheric forcing.

Within the Arctic, a northern high-latitude maximum in surface air warming is consistently found in all AOGCM simulations and at the end of the twenty-first century the projected annual warming is 5°C with a range of 2.8 to 7.8°C. The annual mean temperature response at the end of the twenty-first century under the A1B scenario is characterised by robust and large warming over the central Arctic ocean (5–7°C) particularly in winter/autumn and associated with reduced sea ice. In terms of regional linkages, reduced warming in the North Atlantic (<2°C and even a slight cooling in some models) is consistent with a weakening of the MOC (Bindoff et al. 2007).

In comparison with air temperature modelling, potential climate change in Arctic waters has received less attention, although changes in the THC have been studied but primarily with low-resolution, uncoupled models. Due to the lack of coordination among modelling studies, few definitive projections can be made about changes to such variables as Arctic Ocean temperatures and salinities, stratification and circulation (including the THC). In light of this, future modelling efforts

Table 1 Changes in surface and boundary forcing based on model projections or extrapolation of observed trends

	2020	2050	2080
Air temperature			
Annual mean	+1 to 1.5°C	+2 to 3°C	+4 to 5°C
Winter	+2.5°C	+4°C	+6°C central Arctic
Summer	+0.5°C	+0.5 to 1°C	+ 1°C
Seasonality		Reduced seasonality (warmer winters compared to summers)	
Interannual variability		No change	
Wind			
Means	While changes in winds are expected there is no general agreement on basis of AOGCM results regarding likely magnitude of changes in speed or direction		
Storm frequency	Possible increase in storm intensity regionally (Labrador, Beaufort and Nordic Seas), in general winter storms will decrease slightly in intensity because the pole-to-equator temperature gradient decreases		
Storm tracks	Possible northward shift from present average tracks		
Regional effects	In areas of sea ice retreat there will be an increase in wind-driven effects (currents and waves) because of longer fetch		
Precipitation			
Mean	+2%	+6%	+10%
Seasonality	Decreased seasonality in run-off due to earlier snowmelt, changes in seasonality in precipitation uncertain		
Snow on ice	+1 to 2%	+3 to 5%	+6 to 8%
Sea level	+5 cm	+15 cm	+25 cm
Cloud cover			
General	+3%	+5%	+8%
Spring, autumn	+4 to 5%	+5 to 7%	+8 to 12%
Winter, summer	+1 to 2%	+3 to 5%	+4 to 8%

Note: AOGCM = atmosphere ocean general circulation model.

Table 2 Summary of changes projected in ocean conditions according to the five Arctic Climate Impact Assessment (ACIA)-designated models relative to baseline conditions

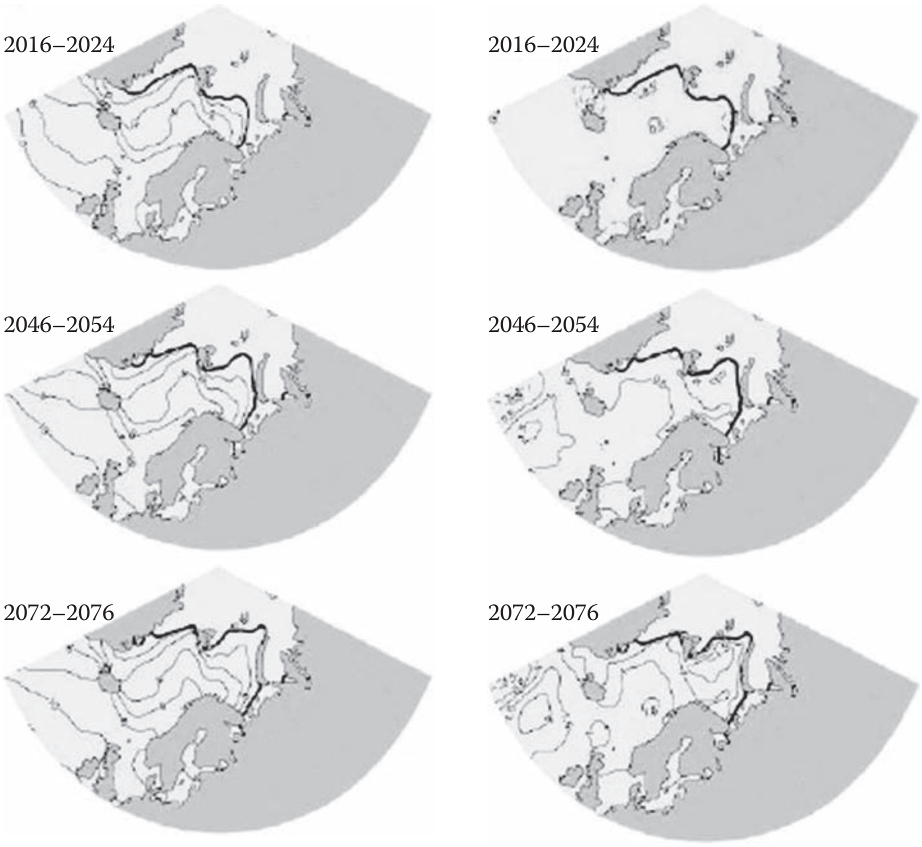
	2020	2050	2080
Sea ice			
Duration	Shorter by 10 days	Shorter by 10–15 days	Shorter by 20–30 days
Winter extent	6–10% reduction	15–20% reduction	Probable open areas in high Arctic
Summer extent	Shelves ice free	30–50% reduction	50–100% reduction
Export to North Atlantic	No change	Reduction beginning	Reduced
Type	Some reduction in multiannual ice	Significant loss of multiannual ice	Little or no multiannual ice
Landfast ice	Possible thinning and retreat in south	Possible thinning and further retreat in south	Possible thinning and reduction in extent in all Arctic marine areas
Sea surface temperature			
Winter/summer (outside MOC regions)	Increase of about same magnitude as in air temperatures in ice-free regions No change in ice-covered regions		
Seasonality	All Arctic and Nordic shelf seas undergo seasonal changes	30–50% of Arctic Ocean to Undergo seasonal changes	50–100% of Arctic Ocean to undergo seasonal changes
Mixed-layer depth	Increase during summer in areas with reduced ice cover and increased winds		
Currents	In regions affected by MOC, modifications to MOC will change strength of the currents		
Ocean fronts	Fronts are often linked to topography but changes in ocean current speeds may cause some to move		
Light exposure	With decreasing ice extent and duration, more areas exposed to direct light		
Nutrient levels	Substantial increases over shelf regions due to retreat of sea ice beyond the shelf break	High levels on shelves and in deep Arctic basins; higher levels due to deeper mixed-layer depth in areas of reduced ice cover	

Note: MOC = meridional overturning circulation.

should attempt to more fully address the range and uncertainty of potential changes in Arctic waters (Figure 21).This will require better resolution in the ocean models and improved coupling between the dynamic atmosphere and dynamic ocean components, particularly in the presence of sea ice (ACIA 2004). Summer sea ice is probably already thinning throughout much of the Arctic with 2007 showing one of the most dramatic declines in the extent of sea ice yet observed (Stroeve et al. 2007). However, once again there is debate about the relative roles played by changes in ice circulation associated with the NAO and Northern Annular Mode and direct warming caused by atmospheric greenhouse levels (Serreze et al. 2007).

The shelf seas pump

Global change, the result of natural and anthropogenic activities will affect directly or indirectly all components of pelagic marine ecosystems. Particularly susceptible to the impacts of global change are the services provided by shelf sea and coastal ecosystems. Despite their small areas, shelf seas play a key role in the global ocean carbon cycle, thereby providing feedbacks to global climate. Tsunogai et al. (1999) extrapolated their results from the shelf pump of the East China Sea to the world shelf areas, assuming that they functioned in the same way. They estimated that the pump would account for a net oceanic uptake of CO_2 of 1 Gt C/yr if the world continental shelf zone would absorb the atmospheric CO_2 at the rate observed in the East China Sea. Without resolving the shelves explicitly, Yool & Fasham (2001) calculated a net pumping rate of 0.59 Gt C yr^{-1} for the



(A) (B)

Figure 21 Evolution of the sea-surface temperature and sea-ice edge (heavy black line) in the BCM CMIP2 integration (modified from Furevik et al. 2002). (A) March SST and sea-ice distributions; (B) shows change since 2000.

shelf seas. Their arguments were supported by the investigations undertaken by Kempe & Pegler (1991) in the North Sea. This amount is smaller than the one calculated by Tsunogai et al. (1999), possibly because the effect of shelf carbon outgassing was included in the latter approach. Thomas et al. (2004b) in their study of the North Sea shelf pump estimated that about 8 million tonnes of carbon are exported each year from the North Sea to the North Atlantic Ocean—representing about 93% of the CO_2 that the North Sea takes up from the atmosphere. Extrapolating across the world's coastal and marginal seas suggests that these areas (just 7% of the world's oceans) may account for around 20% of the global oceanic annual uptake of anthropogenic CO_2, much higher than previously thought.

Based on these studies the significance of the North Sea shelf pump for the sequestering of carbon is well established but the effects of global warming on the functioning and efficiency of the shelf pump are unclear. Longer periods of stratification should reduce the flux of nutrients to the surface layer in those areas not subject to strong tidal mixing. As a result, restructuring of the post-bloom phytoplankton community is likely to occur. Furthermore, more intense stratification has the potential to increase the dominance of the microbial loop increasing the amounts of carbon recycled in the upper mixed layer and potentially resulting in a reduced flux of organic material to the seabed. If this happens, carbon outflows due to the shelf pump could be reduced, reducing the efficiency of the shelf pump and the contribution of this mechanism to the global sequestration of carbon to the deep ocean.

Biogeographical patterns and phenology

Over the course of the last few decades compelling evidence has emerged from the north-eastern Atlantic that biogeographical boundaries have shifted northwards. In particular there have been large distributional changes in the plankton (Beaugrand et al. 2002, Edwards et al. 2002). Such changes are probably also occurring in other oceans but the north-eastern Atlantic is unique in having good coverage with CPR survey routes that have been running for over 70 years (Warner & Hays 1994, Hays et al. 2005).

Using CPR data, both phenological changes (i.e., the timing of life-cycle events on an annual basis) and geographical distribution changes have been recorded (Beaugrand et al. 2002, Edwards & Richardson 2004). Poikilothermic organisms are especially sensitive to temperature changes which impact most aspects of their physiology (Lindley & Daykin 2005). Species will respond to temperature changes over time by moving towards their optimum position within their thermal envelope. This occurs both temporally as in seasonal succession (manifested as a phenological response) or geographically as a geographical movement of the range of the population. These responses can be particularly rapid in planktonic organisms due to their short life cycles. In the study by Beaugrand et al. (2002) large northerly movements of calanoid copepod species typical of the southern shelf edge were detected over the last 50 years. This has been accompanied by a northerly retreat of colder water species. This geographical movement is much more pronounced than any documented in the terrestrial environment being accelerated by advection in the shelf-edge current. For example, while surface isotherms have shifted approximately 100–200 km north, the southern species association has extended its range by more than 10° latitude (>1000 km). In recent years, the warmer water, shelf-edge species have been recorded in the northern North Sea, entering via the Faroe-Shetland Channel (Figure 22).

In other regions of the north-eastern Atlantic, northerly movements of plankton species have been more modest but still significant. Recently in the waters to the south of Iceland, subarctic species have decreased fairly rapidly, to be replaced by cold-temperate mixed-water species and in the Bay of Biscay an increase in subtropical and warm-temperate species has paralleled a reduction in continental and warm-temperate pseudo-oceanic species (Beaugrand et al. 2009). Lindley and Daykin (2005) also showed that the abundance of two subtropical zooplankton copepod species *Centropages chierchiae* and *Temora stylifera* has increased in the Celtic Sea over the last few decades.

These large-scale biogeographical shifts observed in the plankton have also seen paralleled latitudinal movements in fish species distribution in the Bay of Biscay (Quero 1998), North Sea (Perry et al. 2005) and wider north-eastern Atlantic (Brander et al. 2003, Harris et al. 2007). Northerly geographical range extensions have also been documented along the European Continental shelf edge (Beare et al. 2004a, b, Genner et al. 2004). It is noteworthy that fish with northern distributional boundaries in the North Sea have shifted northwards at rates up to three times faster than terrestrial species (Perry et al. 2005). This may reflect the more fragmented nature of the terrestrial environment where range shifts may be limited by the availability of suitable habitat. While these observations have described surface geographical changes in pelagic organisms it is worth remembering the 3-dimensional nature of the marine environment. Recent research has observed not just changes in fish biogeography but also changes in the depth distribution of fish species in response to recent warming (Dulvy et al. 2008). This change can be seen as analogous to the upwards movement of terrestrial organisms in alpine environments.

Further evidence that these distributional changes are genuine responses to environment comes from the western Atlantic. Here cooling and the freshening of the north-western Atlantic over the

Figure 22 (See colour insert.) Long-term changes in the mean number of calanoid copepod species per association from 1960 to 1999 from Continuous Plankton Recorder (CPR) records. (From Beaugrand et al. 2002. With permission of AAAS.)

last decade have had an opposite effect, with some groundfish species (cod) and their prey (capelin) moving further south. However both Rose (2005) and Dulvy et al. (2008) cautioned that we know too little about the interrelationships between the environment, plankton, fish distributions and exploitation to draw definite cause-and-effect conclusions.

Primary production in the north-eastern Atlantic

In well-mixed waters, the timing of the onset of the spring phytoplankton bloom is largely controlled by available light. In these waters climate change should not have a strong impact on the onset of the spring bloom (Sommer & Lengfellner 2008) excepting that lag effects (Wiltshire & Manly 2004) or altered turbidity due to increased precipitation and terrestrial run-off may cause contrary effects (McQuatters-Gollop et al. 2007b). In deeper waters, bloom initiation occurs when phytoplankton cells are constrained above the compensation depth by a shallowing thermocline (Sverdrup 1953, Mann & Lazier 2005). In these areas increased sea temperatures may lead to earlier stratification and an advanced bloom but increased wind mixing, also predicted under climate change, may counter this effect. Once initiated, phytoplankton growth (light-saturated production) is temperature sensitive and mesocosm experiments have shown that increased temperatures during this phase lead to decreased peak biomass, decreased mean cell size and decrease in the proportion of diatoms (Sommer & Lengfellner 2008). All these changes may lead to increased carbon cycling within the pelagic microzooplanktonic community, poorer feeding conditions for copepod zooplankton and thus to a less-efficient energy transfer from primary to fish production under a warmer climate. The increase in overall growing season in the North Sea already observed (Reid et al. 1998, McQuatters-Gollop et al. 2007b) has been associated with an increase in abundance of smaller flagellates that favour warmer and more stratified conditions seen under the current ocean climate conditions.

The thermal responses of bloom-forming phytoplankton coupled with their short generation times means that it can be predicted, with some confidence, that the frequency of HABs will increase. In some areas of the North Sea, warming has already been associated with an increase in certain HAB species (Edwards et al. 2006). However temperature is not the only factor controlling these blooms. Uncertainty about how phytoplankton communities, and the food webs dependent on them, will react to combined changes in temperature and nutrients underlies the controversy surrounding the suggestion that deliberate fertilisation of large areas of the ocean to stimulate primary production might sequester atmospheric carbon dioxide to the deeper ocean (Buesseler et al. 2008, Glibert et al. 2008).

Shifts in algal abundance and species composition will also affect the quality of food available to grazers (Sommer & Lengfellner 2008). Another crucial aspect influencing predator-prey relationships is the degree of temporal overlap. There is evidence that phytoplankton may respond to increased temperatures by shifting the timing of their bloom more radically than their zooplankton predators (Stenseth & Mysterud 2002, Edwards & Richardson 2004). Such differing responses from previously coupled components of marine food webs could lead to trophic uncoupling. This might in turn lead to reductions in the efficiency with which energy is transferred to higher trophic levels and increased sedimentation to the benthos (Turner 2002). Such changes could explain recent increases in some benthic species in shelf seas (Kirby et al. 2007). However, these increases in benthic productivity may not be entirely environmentally driven since commercial fisheries, particularly in the shelf seas, have also altered benthic predation patterns (Heath 2005).

Secondary production in the north-eastern Atlantic

Richardson (2008) gave a recent and comprehensive review of the potential effects of climate change on zooplankton populations globally. Many of the examples were taken from the North Atlantic and included major effects within the region such as latitudinal range extensions and changes in timing of the seasonal cycle. As previously mentioned the north-eastern Atlantic is one of the most comprehensively surveyed regions globally for zooplankton through the CPR programme. However, most analyses of CPR data have concentrated on changes in distribution and phenology rather than productivity per se (Beaugrand et al. 2002, Edwards & Richardson 2004). An additional problem is that the CPR undersamples smaller species of zooplankton and so may have overemphasised the recent observed decrease in total copepod biomass in the north-eastern Atlantic (Pitois & Fox 2006). Beyond largely descriptive studies, predicting how zooplankton communties will respond to future environmental changes from first principles (i.e., physiology) is much more challenging (Helaouët & Beaugrand 2007).

Physiological processes, such as respiration, growth, development and reproduction in zooplankton are highly sensitive to temperature so even small changes in temperature can affect population dynamics. Durbin and Durbin (1992) suggested that warming, through effects on winter temperatures, will have a particularly strong effect on species developing under cold temperatures. For example, a rise of 2°C did not have a major effect on the maturation rate of the copepod *Acartia hudsonica* during spring and fall, whereas there was a larger cumulative effect during winter due to the slower development rate at the lower temperatures. Hence, these authors suggested that those zooplankton which complete a major part of their life cycle during the winter will be the first to be affected by climate warming. The short life-cycle of many zooplankton species can lead to a tight coupling between environmental effects and plankton dynamics. Few zooplankton species are commercially exploited so observed changes in productivity and abundance at lower trophic levels may be more easily attributed to climate change (although in some cases 'top-down' control, which can itself be affected by fisheries, may be important) (Reid et al. 2000). There are a number of key species, for example, copepods of the genus *Calanus*, that occur throughout the North Atlantic systems under review (Heath et al. 1999, Helaouët & Beaugrand 2007). Changes in their distribution and their species composition or trophic interactions resulting from shifts in geographic range undoubtedly will affect overall ecosystem structure and productivity (Beaugrand et al. 2002, 2007, Bonnet et al. 2005, Head & Sameoto 2007, Helaouët & Beaugrand 2007, Valdes et al. 2007). However, since multiple factors vary over different timescales, from seasonal to multidecadel, it has proven difficult to predict the relative impact of any single process on regional dynamics (Helaouët & Beaugrand 2007). It has been shown that climate-induced changes in advection and stratification affect both circulation and transport and vertical processes all of which are important for controlling zooplankton population dynamics. Discriminating between the impacts of local and remote forcing will require coordinated studies of key species across the three North Atlantic systems. Comparative studies between regions should also lead to better understanding of the mechanisms controlling the appearance and spread of new species that have extended their biogeographical ranges. It is likely that changes in the eastern and western Atlantic will occur on different time- and space scales because of differences in the physical drivers in these regions (Pershing et al. 2005, Kane 2007).

Fish in the north-eastern Atlantic

Interest in studying the relationships between environmental factors and the availability of fish to fisheries is not new (Cushing 1982). The earliest attempts at scientific investigation relate to long-term market records such as that of the Bohuslan (Swedish) herring (Ljungman 1882). As time series have built up for more species, especially over the last century, a large literature has evolved on correlations between climate and fish abundance (e.g., Alheit & Hagen 1997, Planque & Fox 1998, Planque & Frédou 1999, Fox et al. 2000, Stige et al. 2006). However, a significant criticism of most of these studies is the lack of physiological or ecological mechanisistic underpinning (Pörtner et al. 2001), increasing the likelihood that a significant portion of reported correlations are artefactual (Myers 1998). Furthermore, most studies have concentrated on commercial species, making it difficult to separate environment causes from the effects of exploitation. Because species at their northerly and southerly range limits are most likely to be exposed to damaging environmental conditions, it may be more sensible to look for shifts in boundaries rather than centres of distribution (Perry et al. 2005, Dulvy et al. 2008). Range shifts may result directly from movements of adult fish away from areas with detrimental conditions but can also be the consequence of differential survival of early life stages towards the edges of a species distribution. With regard to climate change, differing phenomenological shifts between early life stages and their prey may alter the degree of temporal overlap and thus lead to changes in survival (Hays et al. 2005). An ideal study would therefore examine changes for all fish species close to their latitudinal limits; consider non-commercial, as well as commercial species; use time-series covering periods of cooling as well as warming (Dickson et al. 1974) and bear in mind that seasonal conditions affecting certain life stages may be more critical than annually averaged conditions (Cushing & Dickson 1976). Unfortunately there are few time-series for fish that fulfil all these criteria.

Over the last 30 years sea temperatures in the north-eastern Atlantic have been increasing but, as pointed out by Hobson et al. (2008), this is not unprecedented. Analysis of previous warming periods may therefore give indications of how fish populations in the north-eastern Atlantic should respond in the short-to-medium term. During the 1920–1930s there was a marked period of warming in the north-eastern Atlantic. Unfortunately, apart from a few isolated observatories (Hawkins et al. 2003), standardised fishery surveys were not being conducted at this time. Biological responses must therefore be inferred from available data, mostly anecdotal or commercial landings. These records do indeed indicate that boreal species such as cod and haddock shifted northwards (Drinkwater 2006) and in addition there were increased sightings of warm-water species such as bluefin tuna (*Thunnus thynnus*) (cited in chapter 5 of Cushing 1982). In the north-eastern Atlantic century-long time-series exist for both Arcto-Norwegian cod and Norwegian spring-spawning herring. Toresen and Østvedt (2000) showed that the spawning stock biomass of herring has varied with the multidecadal climate signal. In addition Sundby and Nakken (2008) have demonstrated that the spawning locations of Arcto-Norwegian cod propagated northwards and southwards in tune with the AMO throughout the twentieth century. During the warming from the 1920s to the 1930s and 1940s the spawning areas were displaced northwards along the coast, while the cooling from the 1950s to the 1960s and 1970s resulted in a return to the locations favored during the cool 1900s to 1920s. During the recent warming, after the mid-1980s, the spawning areas were displaced northwards again. Also the spawning stock biomass of cod has displayed a similar long-term oscillation as the herring, the stock being large during warm periods and smaller during cold periods (Hylen et al. 2008). Particularly in the English Channel (Stebbing et al. 2002, Hawkins et al. 2003) and North Sea (Perry et al. 2005), recent changes seem to be similar to the historical responses observed to warming and cooling but we have also seen new interactions with the Atlantic through increased abundance in shallower waters of oceanic species such as the snake pipefish (*Entelurus aequoreus*) (Kirby et al. 2006, Kloppmann & Ulleweit 2006). Increasing abundance of snake pipefish in shelf seas may in turn be linked with reduced seabird fledging success as they are nutritionally inferior to sandeel (Harris et al. 2007). Environmental changes in regional connections can therefore have consequences that affect the whole food chain.

The main problem with interpreting such observations is that most of the time-series, except for some of the Norwegian fisheries records, only cover a few decades and relate to a period of almost continual warming (Hobson et al. 2008). If the NAO index reverts to a negative phase this may lead to temporary cooling in the north-eastern Atlantic. but climate models predict overall continued warming against these oscillations, which will lead to sea temperatures that eventually will exceed historical observations. Since most attempts to predict what may happen have taken a 'climate envelope' approach in which future distribution is predicted based on current thermal limits for a species, we may have limited ability to predict future trends once the environment moves outside the historical framework (Sharp 2003). Furthermore, rather than 'smooth' changes over time we may see abrupt realignments ('regime shifts') as communities reorganise in response to changing environmental conditions (Beaugrand 2004). Predicting how marine communities will respond under these conditions is a major challenge but has serious implications for the design of marine reserves, fisheries policies and biodiversity conservation. Among the potential future changes are an increase in production of marine fisheries in the northern North Atlantic (Alcamo et al. 2007) as well as an influx of more southerly species to areas like the North Sea. Reduced sea-ice in the

Arctic and Subarctic Seas may lead to increases in primary and secondary production south of the ice edge to the benefit of important commercial fish stocks in Arctic and Subarctic Seas, for example, cod (*Gadus morhua*) and herring (*Clupea harengus*), species that currently comprise about 70% of the total catch in these areas. An increase in water temperature of 1–2°C in the Atlantic part of the Norwegian and Barents Sea is very likely to result in a change in the distribution of several fish species (ACIA 2004). Capelin (*Mallotus villosus*) is likely to extend its feeding area north and north-eastward. During summer it might begin to feed in the Arctic Basin and migrate to the Kara Sea. Whether capelin will maintain their present spawning grounds along the coast of northern Norway and the Kola Peninsula is unclear. Extensions eastwards may also occur and capelin might begin spawning along the west coast of Novaya Zemlya. Cod is also likely to expand its feeding area eastwards and northwards (Stenevik & Sundby 2007). As cod is demersal it is not likely to migrate north of the Barents Sea and into the Arctic Basin proper. Haddock will probably follow the same pattern as the cod but at present it is likely to remain further south. In the Norwegian Sea, herring is likely to return to feeding and overwintering areas in use prior to 1964 but spawning grounds along the Norwegian coast may be maintained. Mackerel and blue whiting are likely to migrate north-east to the Barents Sea. These species may then compete for food with other pelagic species in the area (Figure 23).

It is notable that the recruitment success of many fish stocks shows an immediate response to interannual environmental changes (Planque & Frédou 1999). Although sea temperatures during the egg and larval periods have been most often linked with year-class success, temperature is likely a proxy for other processes such as prey availability (Sundby 2000) or predation pressure (Fox et al. 2000). Since healthy stocks of potentially long-lived species such as cod contain a spread of age-classes (Longhurst 1998), the spawning stock biomass tends to integrate these high-frequency variations towards the multidecadal environmental patterns (Sundby & Nakken 2008). Climate variations such as decadal-scale trends in the NAO therefore appear to influence fish stocks by increasing the probability of a run of strong or weak year-classes that gradually accumulates in the spawning stock (Stige et al. 2006). This is a somewhat different response to those of short-lived

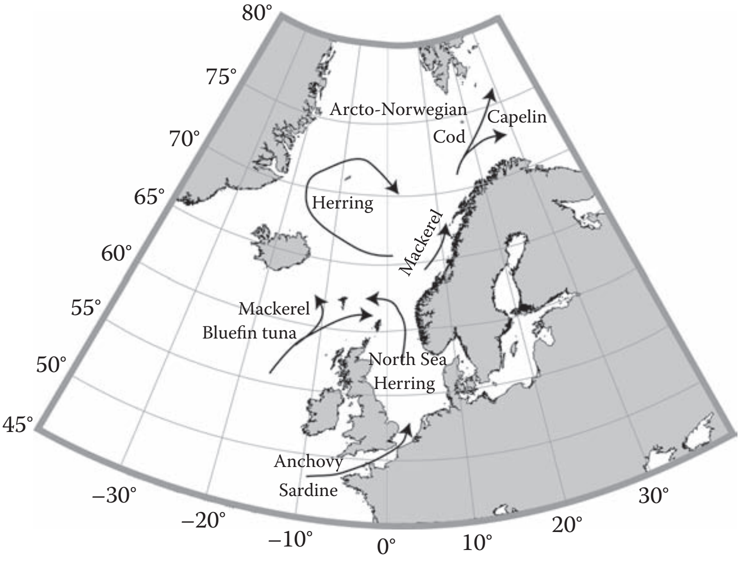


Figure 23 Likely extensions of the feeding areas for some of the main commercial fish populations in the north-eastern Atlantic under climate change. The extent of the movements is for illustrative purposes only and is not based on modelling results. (Reproduced with permission of Cambridge University Press.)

species such as anchovy for which there is a much more immediate and apparent response to interannual variations in stock biomass. It should also be pointed out that the temperature amplitude of the multidecadal oscillation is considerably smaller than the temperature amplitude of the decadal-scale oscillation. For the north-eastern Atlantic, the amplitude of the interannual and decadal-scale sea-temperature variations are typically around 2°C, while the amplitude of the multidecadal signal though the twentieth century is about one-third of that (i.e., 0.7°C) (Figure 18). Nevertheless, this moderate multidecadel climate signal has had a dramatic influence on the marine ecosystem with responses in the distribution of both zooplankton (Beaugrand et al. 2002) and fish stocks (Toresen & Østvedt 2000, Sundby & Nakken 2008). It can be concluded that it is not only the amplitude of the climate signal but also its persistence that affects marine ecosystems. The effects of multidecadal climate oscillations during the twentieth century can provide us with some important clues about how marine ecosystems may respond to anthropogenic climate change. However, temperature increases predicted for the twenty-first century are considerably greater than the AMO change of 0.7°C seen during the twentieth century. This implies a substantial extrapolation beyond our observations and we should expect to see potentially abrupt and non-linear responses.

Higher predators in the north-eastern Atlantic

As discussed on page 30, predictable movements of marine mammals over ecosystem boundaries can be direct (e.g., the annual north-south and inshore-offshore migrations of baleen whales) or incremental, such as the influx of oceanic dolphins into shelf and coastal waters of north-western Europe during the summer (e.g., common dolphin *Delphinus delphis* and striped dolphin *Stenella coeruleoalba*) (Goold 1998). For these southern dolphin species sea temperature appears to be a limiting factor (MacLeod et al. 2005) although this is probably a result of more complex relationships between temperature and prey distribution. As seasonal isotherms continue to move northwards it is conceivable that these summer dolphin migrations will become more exaggerated. However, other long-term climate-related impacts may be more subtle (e.g., changes in social structure of odontocete populations in the north-eastern Atlantic and Pacific have been linked, with a 2-yr lag, to the North Atlantic and Pacific Decadal Oscillations). It is thought these relationships are mediated through links between the atmospheric forcing and the recruitment success of salmon, which are a major prey item for the whales (Lusseau et al. 2004). Within the Arctic region, marine mammals that feed predominantly offshore may benefit from increased primary and secondary production due to reduced ice cover whilst inshore feeders may suffer as primary production is reduced due to increase coastal turbidity linked with increased terrestrial run-off (Bluhm & Gradinger 2008).

Ecosystem effects in relation to the regional linkages in the north-eastern Atlantic

Climate change related effects in the regional linkages of the north-eastern Atlantic will be mostly the results of changes in the atmospheric patterns and ocean currents. As shown on pages 47 and 28 the spread of warmer water species into the North Sea has been strongly associated with the inflow of warm slope shelf water into the North Sea via the Faroe-Shetland Channel (Beaugrand et al. 2002, Beaugrand 2004). The biota of the European shelf seas may therefore show rather rapid responses to climate change, over and above what might be expected from a consideration of the changes in isotherm location.

Similarly, the role of the ocean currents connecting the Atlantic and shelf seas to the Nordic and Arctic Oceans is a key factor in the regional ecology of the Arctic itself (Hegseth & Sundfjord 2008) and it is in the Arctic that the potential impacts of climate change on marine ecosystems have been most thoroughly considered (ACIA 2004, Vikebø et al. 2007b). The changes in physics described in this review will affect all levels of the marine food web (Table 3). Of most concern to humans will be changes at higher trophic levels, which will likely include alterations to the distribution and migration patterns of fish, possible higher growth rates and productivity in some areas, northwards spread of species from more southern areas and a retreat northwards of true Arctic fish species.

Table 3 Potential long-term ecological trends due to climate warming for the Arctic

	Phytoplankton	Zooplankton	Benthos	Fish	Marine mammals and seabirds
Distribution	Increased spatial extent of areas of high production in the central Arctic Ocean	Boundary for colder water/warmer water species moves northwards	Boundary for colder water/warmer water species moves northwards	Boundary for colder water/warmer water species moves northwards Timing and location of spawning grounds and feeding migrations to alter	Polewards shift in species distributions
Production	Increased production in central Arctic Ocean and Barents Sea	Difficult to predict	Difficult to predict, depends on phenological responses of phyto-plankton and zooplankton	Wind-driven advection patterns of larval drift may change, phenological responses may cause mismatches with prey for early life stages	Strong declines in populations of ice-associated mammals, increases in temperate species, seabird responses hard to predict
Biodiversity	Dependent on mixing depth: shallow mixing favours diatoms, intermediate mixing favours *Phaeocystis*, deep mixing may favour nanoflagellates	Adaptable Arctic species such as *Calanus glacialis* may be favoured	Cold water species likely to decline over much of the area, warmer water species (e.g., polychaetes and blue mussel) should increase	Cod, herring and some flatfish likely to move north and become more abundant; capelin, polar cod and Greenland halibut likely to decline	Declines in polar bear and ringed, harp, hooded, spotted, ribbon and possible bearded seals. Increased distribution of harbour and grey seals. Possible declines in bowhead, narwhal, grey and beluga whales. Ivory gulls and several of the small auk species likely to decline; response of other seabirds hard to predict

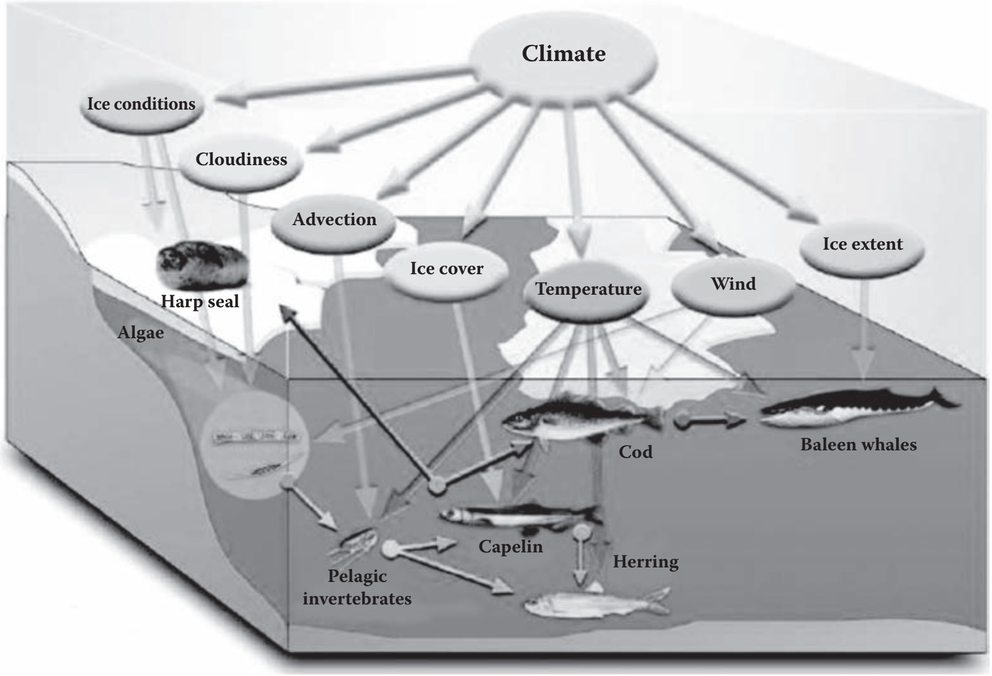


Figure 24 (See colour insert.) Interactions of climate change factors with biological components of the Nordic and Arctic Seas ecosystem. (Reproduced with permission of Cambridge University Press.)

In turn this will affect marine mammals (Figure 24). For some organisms, such as polar bears (*Ursus maritimus*), the extensive loss of sea ice will lead to reduced breeding success and population declines (Derocher et al. 2004) whilst for others, such as the bowhead whale (*Balaena mysticetus*) increased offshore productivity may prove beneficial (Bluhm & Gradinger 2008).

As noted in ACIA (2004) Nordic and Arctic Seas are likely to be heavily affected by increased human activity as summer sea ice reduces. There are strong indications that this is already happening with extensive prospecting for oil and minerals in newly accessible areas. Not only will this increase the risks of pollution incidents and introduction of non-indigenous species but also loss of sea ice during the summer will open new ocean connections to the Pacific (Figure 25). Indeed there is some evidence that this has already led to the spread of Pacific species into the north-western Atlantic, as shown by the occurrence of the Pacific chain-forming diatom *Neodenticula seminae* in the Labrador Sea (Reid et al. 2007).

The spread of non-indigenous species

The warming of north-eastern Atlantic waters is likely to increase both the dominance of existing non-indigenous species and the number of successful new invasions, but it is unclear how this will impact ecosystem functioning (Sax et al. 2007). Climate change is likely to promote earlier recruitment and faster growth rates and initiate reproduction in non-indigenous species already established in the region. Stachowicz et al. (2002) found that the initiation of recruitment of non-indigenous sessile marine invertebrates in the United States was strongly correlated with winter water temperatures. The pelagic larvae of these species arrived earlier in the season compared with native species when winter seawater temperatures were warmer. In addition, experiments demonstrated that non-indigenous ascidians were able to outgrow native species when seawater temperatures were raised higher than normally experienced in the region. In the European shelf seas, increases in seawater temperature have led to species, such as the Pacific oyster (*Crassostrea gigas*), naturally

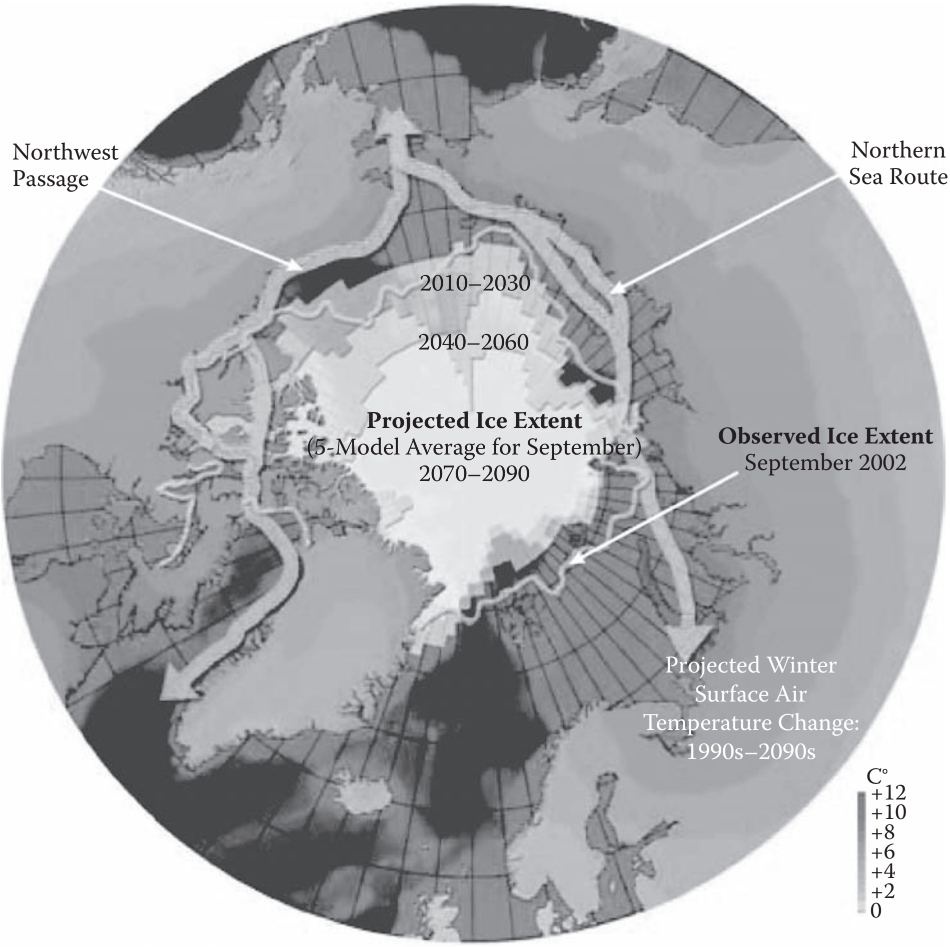


Figure 25 (See colour insert.) Potential navigation routes in the Arctic. (Arctic Council 2006. With permission.)

recruiting to regions beyond its zone of introduction (Nehring 2003, Diederich et al. 2005, Cardoso et al. 2007). *Crassostrea gigas* has been shown to cause significant changes in community structure, sediment porosity, bioturbation activity and biogeochemical cycling in areas where it has become established (Ruesink et al. 2006).

Increased storm intensity within the north-eastern Atlantic may also increase the rate of unintentional release of organisms from aquaculture installations (Naylor et al. 2001). This is a significant problem as it is estimated that up to 80% of adult salmon entering rivers in Norway are escapees (Fiske & Lund 1999). When aquaculture escapees breed with natural populations, hybridisation and subsequent introgression can lead to a reduced fitness in the hybrids, with the F2 generation hybrids suffering from higher mortality rates and increased susceptibility to infectious disease (Skaala et al. 2006). With an increasing dependence of aquaculture on non-indigenous species to meet the growing global demand for seafood, it is likely that the industry may become an even more significant pathway of introduction (Cook et al. 2008).

Climate change is also likely to increase the number of new invasions to the north-eastern Atlantic through northwards range expansions (see pages 45 and 53) and increased survivorship of species introduced from warmer ocean basins. The arrival of new species will accelerate over the next few years with the increasing use of the Arctic Ocean as a shipping route between Asia and Europe (Minchin 2006, Reid et al. 2007). In addition, the implementation of the total ban on TBT in antifoulants in 2008 is likely to increase the likelihood of non-indigenous species surviving as hull fouling on commercial vessels.

The introduction of non-indigenous species is widely recognised as a major threat to biodiversity (United Nations 1992, Worm et al. 2006), potentially leading to habitat modification, changes in ecosystem functioning, extinction of native fauna and flora, disease transfer and genetic effects such as hybridisation with native congeners (Lovei 1997, Ruiz et al. 1997, D'Antonio et al. 2001). Unfortunately, predicting how an increase in the dominance of non-indigenous species and new invasions will influence community composition and the functioning of the north-eastern Atlantic is a major challenge. Concerted European and global action is urgently required to advance environmentally sound shipping and aquaculture practices to minimise the risk from new invasions.

Conclusions

This review has demonstrated that strong linkages exist between the North Atlantic Ocean, North Atlantic shelf seas and the Arctic and Nordic Seas. These are due to atmospheric, oceanic and human movements, which in turn affect the dispersal of nutrients, organisms and contaminants throughout the region. Studying the North Atlantic and the associated shelf seas as an integrated 'basin-scale' system is a key challenge for the early twenty-first century. Similarly, all the major components of the regional ecosystem food webs will need to be considered together. This concept underpins the 'end-to-end' approach which aims to couple models from physics all the way to the higher tropic levels (Travers et al. 2007). Future progress will depend on the extensive use of mathematical models but these need feeding with data from existing and new observation systems along with the relevant experimental studies needed to parameterise vital rates. Even with modern computing capabilities, it is impossible to represent all trophic levels to the same degree. One suggested approach is to concentrate the biological resolution at the level of the species (or trophic level) of interest and to decrease the resolution, both up and down the trophic levels, moving away from the target (deYoung et al. 2004). This is a pragmatic suggestion but implies that we will need to develop separate models for specific questions. Other researchers propose a 'tool-box' approach by which subsystem models can be coupled in different configurations. Despite these difficulties, significant progress is being made in constructing practical 'end-to-end' models (Steele et al. 2007, Travers et al. 2007, Cury et al. 2008). Along with the accompanying observations and process studies, such models provide tools for the improved, integrated understanding of marine ecosystems that will help to meet the increasing demands for ecosystem-based marine management (Cury et al. 2008).

This review has shown that the major linkages within the north-eastern Atlantic are due to the ocean currents. In turn these are affected by regional atmospheric forcing displaying dominant modes such as the AMO and NAO (Hurrell & van Loon 1997, Marshall et al. 2001, Hurrell & Dickson 2004). Atmospheric forcing also plays a critical role in local processes such as water column warming and stratification, particularly in the shelf-seas (Sharples et al. 2006). Although the broad mechanisms by which atmospheric forcing influences water exchange between the open ocean and the shelves are clear, the role of shelf-break mixing remains poorly understood. Better understanding of how these large-scale horizontal and vertical processes operate is needed.

This review has shown how physical forcing ultimately affects all trophic levels in the north-eastern Atlantic (Cushing 1982, Fasham et al. 2001, Mann & Lazier 2005, Frederiksen et al. 2006). Studies covered in this review have clearly demonstrated that basin-scale forcing affects both biogeography and ecosystem structure and function. There is clear evidence that regions within the north-eastern Atlantic are warming particularly rapidly. Studies reviewed have shown how species ranges are changing in response and how new alien species may become established. Such changes will affect ecosystem structure, trophic interactions, and potentially productivity. Clearly, climate change is now high on the scientific, political and societal agendas but our ability to predict how the north-eastern Atlantic ecosystem will respond is still limited. This review has also shown that the North Atlantic is a particularly important component of the global carbon cycle (Thomas et al. 2004a, Pätsch & Kühn 2008). However, it remains uncertain how the shelf seas biological pump will be affected by climate change and how such changes will feed back to the global climate. An integrated approach in the linked systems of the North Atlantic related to ecosystem structure is clearly called for, renewing and extending the approach taken in the early 1990s in the Joint Global Ocean Flux Study (JGOFS) programme (Ducklow & Harris 1993).

There is a clear challenge to develop better predictive ability for at least the dominant components of the North Atlantic pelagic ecosystem, the related biogeochemical processes and the feedbacks with the climate system. Society increasingly demands an ecosystem approach to management of marine resources (Jennings 2005) and this will require new collaborative research programmes. The variability and changes we are observing in the north-eastern Atlantic affect population dynamics, trophic functioning, and dispersal and migration patterns. An integrated approach will advance studies of ecosystems throughout the north-eastern Atlantic and lead to better understanding of the processes involved in population variability of key species and their interactions. In addition, the global scale of the climate, environmental and anthropogenic forcings considered in this review, combined with the strong linkages between the shelf and deep ocean ecosystems, suggest a need to focus on integrated basin-scale processes rather than on individual regional programmes. This will of necessity require better international cooperation as no single nation has all the resources needed for such studies.

Ultimately the aim must be to develop an integrated ecosystem approach to management of human activites in the north-eastern Atlantic. A predictive understanding of the mechanisms by which climate change, biodiversity, and habitat dynamics and exploitation interact to influence the dynamics of the associated ecosystems should be a goal. This approach should lead to improved scientific ecosystem-based approaches to conservation of natural resources, the maintenance of biodiversity, and a better understanding of the key role of this region in the global carbon cycle.

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ZOOPLANKTON DIEL VERTICAL MIGRATION — A REVIEW OF PROXIMATE CONTROL

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Abstract Diel vertical migration (DVM) is a characteristic behavioural pattern performed by zooplankton in which their vertical distribution changes over the 24-h day. Here the proximate control of zooplankton DVM is reviewed. Light has emerged as the major proximate cue controlling DVM behaviour and the understanding of zooplankton visual physiology and the light-mediated behaviour underlying DVM is expanding. Field and laboratory evidence exist to support each of the three major hypotheses for the exogenous role of light in DVM: (1) preferendum or isolume, (2) absolute intensity threshold, and (3) relative rate of change. Light may also play an endogenous role in DVM by entraining circadian rhythms in vertical movement or activity. This appreciation of the role of light has improved modelling efforts into the causes and consequences of DVM. The most important recent advance in the study of DVM is the recognition that this behaviour is a phenotypic response in many species and is most commonly activated by chemical cues (kairomones) from fish predators. High levels of kairomones signal high levels of predation pressure, and DVM-related photobehaviours, such as swimming responses on relative rates of irradiance change, are altered such that migration occurs and zooplankton achieve a refuge from visual predators.

Introduction

Zooplankton characteristically undergo diel vertical migration (DVM) in which they move vertically in the water column at different times of the 24-h day. There are three general patterns (Hutchinson 1967). The most common is a nocturnal pattern consisting of a single daily ascent with minimum depth reached between sunset and sunrise and a descent to maximum depth during the day. Normally the ascent begins near sunset and the descent near sunrise. A second pattern, twilight DVM, begins with a rise to a minimum depth beginning at sunset. A descent occurs later in the night and is termed the *midnight sink* or *nocturnal sinking*. There is a second rise to minimum depth as sunrise approaches and subsequent descent to maximum depth during the day. Finally, reverse DVM involves an ascent to a minimum depth during the day and descent to maximum depth at night. DVM is not constant within a species because there can be ontogenetic changes (e.g., Uye et al. 1990, Verheye & Field 1992, Huang et al. 1993, Osgood & Frost 1994, Hays 1995, Nishihama & Hirakawa 1998, Tester et al. 2004) as well as spatiotemporal differences for the same stage (Bollens & Frost 1989a, Hays et al. 1996, Fragopolulu & Lykakis 1990, Ohman 1990, Dagg et al. 1997, Hays et al. 2001).

This contribution outlines advances in the study of DVM since Forward's (1988) review. Different aspects of DVM have been considered by other authors during the past 20 years. Haney (1988, 1993) examined aspects of the environmental control of DVM in freshwater species and Pearre (2003) discussed the hunger-satiation hypothesis in vertical migration. Folt & Burns (1999) considered the contribution of DVM to zooplankton distributions. Lampert (1989, 1993) and Hays (2003) reviewed the adaptive significance of DVM. Ringelberg (1999) and Ringelberg & van Gool (2003) assessed the photobiology of *Daphnia* sp. involved in DVM. Queiroga & Blanton (2005) considered the involvement of vertical migration in horizontal transport of crustacean larvae and Naylor (2006) reviewed the same topic for estuarine and coastal zooplankton. Larsson & Dodson (1993) and Brönmark & Hansson (2000) examined general aspects of chemical communication in aquatic environments with a focus on planktonic communities. Lass & Spaak (2003) reviewed chemically mediated antipredator defences in the plankton, while Rittschof & Cohen (2004) discussed the use of modified amino sugars as kairomones in zooplankton DVM. De Meester et al. (1999) reviewed the role that genetic selection may play in variable DVM apart from phenotypic plasticity.

This review focuses on proximate (causal) cues involved in DVM. Light is generally agreed to be the most important external factor (Forward 1988) and so photon capture by zooplankton, particularly visual spectral sensitivity, is discussed. Field and laboratory studies addressing the various hypotheses for the use of exogenous light stimuli by migrating zooplankton will then be considered. The most important advance in the study of proximate cues is the recognition that DVM is a phenotypic response that is activated by chemical (kairomones) and perhaps mechanical cues from fish predators in some migrating species. Supporting studies and the chemistry of the active molecules are presented. Although marine and estuarine species are mainly considered, the extensive studies of freshwater *Daphnia* sp. and *Chaoborus* sp. larvae, as well as those with hypersaline brine shrimp (*Artemia*) larvae, are included. Apart from being an exogenous stimulus, light may also serve as an endogenous cue by entraining circadian rhythms. The current literature on endogenous rhythms underlying DVM is expanding and is reviewed, as is DVM in polar regions. Finally, modeling studies that incorporate the proximate basis of migration behaviour are discussed, and future directions for DVM research are presented.

Spectral sensitivity as related to DVM

Given the proximate role of light as an exogenous and endogenous cue for DVM, it is important to consider zooplankton visual spectral (wavelength) sensitivity because this physiological characteristic influences the light available to a given migrator. Most data on spectral sensitivity of zooplankton visual systems come from behavioural studies. Behavioural methods provide the most integrative assessment of spectral sensitivity because they incorporate photoreception as well as sensory processing. However, even similar organisms may behave differently when given a light stimulus (e.g., Cohen & Forward 2002), which makes comparisons of photobehaviour between species difficult. Other common methods of spectral sensitivity determination include microspectrophotometry (MSP) and both intra- and extracellular electrophysiology. These methods have not been used extensively on zooplankton because the small size of these organisms makes conducting these experiments a challenge. When interpreting data using MSP and electrophysiology, it is important to consider that the spectral sensitivity of the organism will be based not only on the absorbance spectrum of the visual pigment, but also on dioptric modifications to the light, as well as the path length and absorption coefficient of the pigment in the photoreceptor (Frank & Widder 1999). In addition to these techniques, molecular genetics approaches to visual pigment identification (e.g., Crandall & Cronin 1997, Porter et al. 2006) hold promise for future studies on zooplankton spectral sensitivity.

The spectral sensitivities of visual systems are commonly interpreted in terms of the match or mismatch between the wavelengths of peak visual/behavioural sensitivity and those wavelengths most abundant in the environment (reviewed in Lythgoe 1979, Land & Nilsson 2002). There have been several excellent reviews of spectral sensitivity in crustaceans, although much of the work discussed concerns benthic species (Marshall et al. 1999, 2003, Johnson et al. 2002). Forward (1988) reviewed behaviourally determined spectral sensitivities of freshwater, estuarine and coastal zooplankton species that undergo DVM and concluded the spectral sensitivities of these species were not generally matched to the different daytime spectral environments of their respective habitats (i.e., open ocean ~470 nm, coastal ocean 500–550 nm, estuaries and freshwater 550–600 nm). Rather, all spectral sensitivity maxima clustered between 460 and 530 nm (Figure 1 in Forward 1988). The downwelling light spectrum during twilight consists of peaks in the blue/green and red spectral regions, with a loss of yellows (540–625 nm, Chappuis effect, Figure 2 in Forward 1988). Accordingly, zooplankton spectral sensitivity appears adapted to maximizing photon capture in the blue/green spectral region at twilight when migration is occurring, rather than at other longer wavelengths that may dominate during daylight, particularly in estuaries and in freshwater.

Few recent studies have examined spectral sensitivity in migrating zooplankton from shallow-water habitats but what studies there are support Forward's (1988) analysis. Freshwater habitats are perhaps the most interesting in this case because the optical properties of water in these environments are heavily influenced by vegetation and land run-off, resulting in a maximal transmission of light at longer wavelengths than in coastal regions and the open ocean. Accordingly, zooplankters would be expected to have maximum spectral sensitivity offset to shorter (blue/green) wavelengths if they were adapted to the ambient twilight spectrum, rather than to the longer wavelengths of light dominant in this habitat during the day. The freshwater mysid *Mysis relicta* undergoes nocturnal DVM and possesses a single visual pigment with a sensitivity maximum at 520 nm (Gal et al. 1999). This wavelength was 43 nm shorter than the wavelength of peak irradiance measured at 20–23 m depth during the day at the study site. Gal et al. (1999) interpreted this offset sensitivity in *M. relicta* as a mechanism to enhance visual contrast against the downwelling background. While this may be the case, an equally plausible alternative explanation for this offset sensitivity would be to maximise photon capture at twilight during DVM.

Given that the spectral transmittance maximum in coastal water is at 500–550 nm, spectral sensitivities can be matched simultaneously to the daylight and twilight light environments. Spectral sensitivities of four coastal copepod species were determined behaviourally by Cohen & Forward (2002); two species undergo nocturnal DVM (*Centropages typicus*, *Calanopia americana*), one species undergoes reverse DVM (*Anomalocera ornata*), and another was a non-migrator (*Labidocera aestiva*). Photobehaviour varied among species, which made direct comparisons difficult, yet all species had peak responses between 480 and 520 nm, as expected for either maximum sensitivity at twilight or in daytime coastal water. A twilight-sensitive eye is present in larvae of the stomatopod *Gonodactylus aloha*. The planktonic larvae of this stomatopod possess a single visual pigment with maximum absorbance at 499 nm that disappears on metamorphosis to the benthic adult, which possesses at least 10 spectral classes (Cronin et al. 1995).

By far the most attention has been paid in recent years to spectral sensitivities of vertically migrating deep-sea crustaceans (reviewed in Marshall et al. 1999, 2003). The spectral composition of downwelling sunlight at mesopelagic depths in clear ocean water has a spectral maximum at approximately 474 nm (Jerlov 1976), with minimal change at twilight because light is already dominated by blue wavelengths (Frank & Widder 1996). Downwelling light is not the only visual stimulus at mesopelagic depths because bioluminescence also serves as a major visual cue, with the majority of luminescent emission at blue/green wavelengths (440–515 nm; reviewed in Widder 2002, Warrant & Locket 2004). Therefore, spectral sensitivity that is tuned for maximum sensitivity either to downwelling light (450–475 nm visual pigments) or to bioluminescent emissions (465–495 nm visual pigments; Douglas et al. 1998) would likely serve the animal well in providing enough sensitivity to downwelling light at twilight to cue DVM.

Some euphausiids and the hyperiid amphipods have maximum visual sensitivities around 470 nm, maximizing capture of downwelling light (Frank & Widder 1999, Cohen & Frank 2007). Buskey et al. (1989) examined spectral sensitivity behaviourally in two species of vertically migrating calanoid copepod. *Pleuromamma gracilis* (Family Metridinidae) inhabits the upper mesopelagic, whereas *P. xiphias* lives deeper in the mid-mesopelagic. Both species were maximally sensitive to light at 480 nm, which corresponds to either downwelling light or luminescence detection. Another mesopelagic metridinid copepod that exhibits DVM, *Gaussia princeps*, has a spectral sensitivity maximum determined electrophysiologically at 494 nm, which is optimal for luminescence detection while providing adequate photosensitivity for DVM (Cohen unpublished data). Similarly, most mesopelagic crustacean migrators are spectrally adapted for the detection of bioluminescence with an average visual pigment absorption maximum λ_{max} at 493 nm (reviewed in Marshall et al. 1999, 2003).

A small group of deep-sea crustaceans (*Janicella spinacauda*, *Oplophorus gracilirostris*, *O. spinosus* and *Systellaspis debilis*) have electrophysiological spectral sensitivity maxima at both shorter (~400-nm) and longer (500-nm) wavelengths (Frank & Case 1988). One suggestion for the functional significance of short-wavelength sensitivity in these species was for vertical migration (Frank & Widder 1994). DVM in these crustaceans could be cued by their dual visual pigments determining a difference in the underwater light spectrum at twilight at longer wavelengths that was not present at shorter wavelengths, resulting from the Chappuis effect by which yellow wavelengths are preferentially attenuated by the atmosphere during twilight (Frank & Widder 1994). Subsequent measurements of the spectral distribution of underwater light at twilight disproved this hypothesis; negligible spectral change occurs at the day depth of these species, therefore a spectral cue for DVM would be absent (Frank & Widder 1996). The function of short-wavelength visual sensitivity in these species is likely related to their own bioluminescence production because all have ventrally directed photophores or perhaps as a spectral depth gauge (Frank & Widder 1996).

Hypotheses for the role of light in DVM

The three main hypotheses for the use of light as an exogenous stimulus during DVM are (1) preferendum or isolume hypothesis, (2) absolute intensity threshold hypothesis and (3) the rate-of-change hypothesis. The historical development of these hypotheses and underlying photobehaviour are considered in detail by Ringelberg (1964), Forward (1988), Haney et al. (1990), and Haney (1993). All three hypotheses were developed to explain the use of light during nocturnal and twilight DVM. Each hypothesis is described in the following sections with recent supporting field and laboratory evidence.

Preferendum or isolume hypothesis

The preferendum or isolume hypothesis states that zooplankton follow a preferred or optimal light level during vertical migration (Ewald 1910, Rose 1925, Russell 1927). A variation of the hypothesis is that if the isolume moves vertically faster than zooplankton swimming, the zooplankton visual system adapts to a lower or higher light level and they move with a new preferred light level (Buchanan & Haney 1980). There are very few older field studies that demonstrate zooplankton are migrating with isolumes (reviewed in Forward 1988). The lack of evidence may result from both measurements of migrating zooplankton and accurate measurements of isolumes.

Most studies that have considered the relationship between migration and isolumes have monitored zooplankton during DVM as sound-scattering layers (SSLs) using acoustic techniques. The problems are that the species composition of the layers is frequently unknown and different species and developmental stages of the same species can migrate at different depths and speeds. For example, during the day smaller individuals occur higher in the water column for euphausiids (Andersen & Sardou 1992, Kaartvedt et al. 1996, Frank & Widder 2002), copepods (Buskey et al. 1989, Hays et al. 1994) and fishes (Giske et al. 1990). During DVM, the leading edge of the ascent at sunset can be composed of smaller individuals (Haney et al. 1990, Wiebe et al. 1992).

As pointed out by Widder & Frank (2001), measuring isolumes under water is challenging because (1) the spectral composition of downwelling light changes with depth, (2) diffuse attenuation coefficients may change with depth, (3) light intensities are low at depth requiring special light-measuring systems and (4) the spectral responsivity of the optical sensor (often a narrow waveband) is not typically matched to either the spectral composition of the light environment or the often broad spectral responsivity of a zooplankter's visual system. Frequently, isolume movements are predicted using intensity measured at the surface and a constant diffuse attenuation coefficient, which can lead to errors in the actual light level at any depth.

To circumvent these problems, Widder & Frank (2001) made light measurements with a novel radiometer whose spectral responsivity was based on physiologically determined visual spectral sensitivities of the krill *Meganyctiphanes norvegica* and the sergestid shrimp *Sergestes arcticus* (Frank & Widder 1999). Because these two migrators have similar spectral sensitivities, the investigators filtered their low-light autoradiometer to the spectral sensitivity of these animals and measured isolumes from a submersible as they would appear to a shrimp's eye. Due to the expansion of the spectral composition of downwelling irradiance on ascending, they found that ascent speed of the shrimp isolume was not constant at all depths but averaged 8.8 cm s^{-1} at depth and 6.7 cm s^{-1} in shallower water. These ascent speeds were very different from those calculated using surface light measurements and the average diffuse attenuation coefficient (Widder & Frank 2001). While one argument against the preferendum hypothesis has been that zooplankton swimming speeds cannot keep up with moving isolumes, the data showed that swimming speeds of *S. arcticus* were adequate to ascend with the observed isolumes (Widder & Frank 2001).

These results indicate that the spectral sensitivity of the organism under study should be considered when measuring light levels under water as related to DVM. Widder & Frank's (2001) approach was to filter the photodetector to simulate the spectral sensitivity of the study organism to obtain relative irradiance measurements in 'shrimplux' units. These units are comparable to photometric lux units, which are based on the spectral sensitivity of the light-adapted human eye. An alternative approach is to use the spectral sensitivity of the organism to calculate wavelength-specific weighting factors that can be applied to the environmental light data to calculate the relative amount of light available for the organism underwater. This approach has been used with the mysid *Mysis relicta* to convert underwater light measurements to 'mylux' units (Gal et al. 1999) and with the copepod *Calanopia americana* (Cohen & Forward, 2005b) to calculate 'copelux' units.

Field studies related to the preferendum hypothesis indicate that the depths of zooplankton during the day are frequently associated with isolumes and depth changes occur with changes in light levels underwater. This relationship has been observed for copepods (Buskey et al. 1989), SSLs of zooplankton and micronekton (Balino & Aksnes 1993), and mesopelagic fishes and krill (Giske et al. 1990, Rasmussen & Giske 1994, Kaartvedt et al. 1996). Furthermore, Frank & Widder (2002) followed the movements of crustaceans and gelatinous zooplankton as related to isolumes during the day when there was an influx and efflux of turbid water at the sampling site. The animals were associated with specific isolumes before the influx, ascended to the depth of the same isolumes during the water influx and returned to the original depth of the isolumes once the turbid water left the area and the light levels increased. They concluded that "these species were adjusting their depth distributions to remain within a range of preferred irradiances" (Frank & Widder 2002). Alternatively, Gal et al. (1999) found that *Mysis relicta* had day depths at a range of light levels; the top of the distribution varied from 3.1×10^{-8} to 1.1×10^{-5} mylux units over four summer sampling events.

The results of field studies of actual DVM associated with isolumes are less consistent (for review of older studies see Forward 1988). Onsrud & Kaartvedt (1998) found that the krill *Meganyctiphanes norvegica* followed an isolume during their ascent at dusk but the ascent ceased 10–30 m from the surface. In contrast, DVM of *Chaoborus punctipennis* (Swift & Forward 1988, Haney et al. 1990), *C. flavicans* (Wagner-Doebler 1990), and the mysid *Neomysis americana* (Abello et al. 2005) is not related to the speed of movement of isolumes at sunset.

There are few studies of the behaviour underlying depth maintenance with an isolume during the day or migration with an isolume during DVM. One such study involves larvae of the crab *Rhithropanopeus harrisii*, in which larvae vertically migrate with the threshold light intensity for phototaxis (Forward 1985). This result led to the hypothesis that the one isolume that could be perceived by all species and would be easiest to use for depth maintenance and migration is the light level corresponding to the lower visual threshold (Forward 1988). Buskey et al. (1989) tested this hypothesis for the copepods *Pleuromamma gracilis* and *P. xiphias*, which occur at particular daytime depths that consistently correspond to particular isolumes. They determined the spectral sensitivity maximum to be 480 nm and then determined the threshold intensity at this wavelength that evoked negative phototaxis in the laboratory. These data did not support the lower visual threshold hypothesis because the isolume at the day depth was much higher than the threshold intensity for phototaxis. Therefore, the mechanism used by zooplankton, particularly those in the open ocean, to remain with an isolume remains uncertain.

Absolute intensity threshold hypothesis

The absolute intensity threshold hypothesis is a variant of the preferendum hypothesis and has only been applied to nocturnal DVM. An ascent at sunset is initiated once the light intensity decreases below a particular threshold and a descent at sunrise occurs when the light intensity increases above a threshold intensity. This hypothesis was originally applied to nocturnal DVM of the chaetognath *Sagitta hispida* (Sweatt & Forward 1985a,b). Since then, field studies of larvae of *Chaoborus punctipennis* found the initiating cue for DVM was an absolute light level (Swift & Forward 1988). Upwards and downwards migration occurred when the ambient underwater intensity was just below the threshold intensity for negative and positive geotaxis (i.e., swimming directed up and down in the water column, respectively, in response to the gravitational field). There was no evidence that larvae migrated with an isolume or that migration was related to the relative rate of change in light intensity. Similarly Wagner-Doebler (1990) found that *C. flavicans* larvae began an ascent once light levels decreased below a certain light level. In contrast, Haney et al. (1990) found that movement out of the substratum during the ascent phase of nocturnal DVM of *C. punctipennis* was not related to a constant light level.

More recently Cohen & Forward (2005b) measured the light responses of the copepod *Calanopia americana* in the laboratory and related them to twilight DVM in the field (Cohen & Forward 2005a). The results suggested that the ascent at sunset is related, at least in part, to a decrease in light to an absolute light intensity and the descent at sunrise also occurs when light intensity increases above a threshold intensity. Similarly Yoshida et al. (2004) found that DVM of the copepod *Calanus sinicus* may be cued by changes in absolute light intensity.

Rate-of-change hypothesis

The rate-of-change hypothesis states that the cues for initiating vertical movements are the relative rate and direction of change in light intensity from the ambient level (adaptation intensity), which can vary over the day. This hypothesis has been applied to nocturnal and twilight DVM. Light can act as orienting, controlling, and initiating cues as related to this hypothesis (Bainbridge 1961, Forward 1985). Aspects of light that can serve as an *orienting* cue are the angle of polarization, light:dark contrast at the critical angle and direction of highest intensity (Forward 1988). Recent studies have not specifically studied the orienting function of light because most assume that the direction of highest light intensity serves as the reference direction for phototaxis.

Control involves the way in which light affects the readiness of zooplankton to migrate by controlling the level of light adaptation. This relationship has been shown for *Daphnia magna* (Ringelberg et al. 1967), the copepod *Acartia tonsa* (Stearns & Forward 1984), larvae of the crab *Rhithropanopeus harrisii* (Forward 1985) and larvae of the brine shrimp *Artemia franciscana* (Forward & Hettler 1992). The trend is that the lowest relative change in light intensity to evoke behavioural responses involved in nocturnal DVM occurs on adaptation to light levels present at the time of vertical movements (twilight). Faster rates of change are necessary to evoke responses on adaptation to light levels above and below those at twilight.

Finally, migration is *initiated* by the change in light intensity, which is considered the primary stimulus by Ringelberg (1995a). Migration direction (ascent or descent) depends on the direction of change (increase or decrease). As demonstrated by Ringelberg (1991b, 1995a) for *Daphnia* spp., DVM is not related to the absolute change in light intensity but rather to the relative rate of change in light intensity, which is calculated as $(1/I)(\mathrm{d}I/\mathrm{d}t)$. Since I is the adaptation intensity and t is time, the units for relative change are t^{-1}.

As pointed out by Haney et al. (1990), there are two variations of the rate-of-change hypothesis as related to the initiating cue. First is the relative stimulus threshold hypothesis, which states that DVM is initiated by a threshold rate of change in light intensity after which vertical movement proceeds at a constant rate. Alternatively, the stimulus velocity hypothesis states that the speed of migration is proportional to the speed of relative change in light intensity, that is, there is no threshold rate and the speed of vertical movement varies with the acceleration of relative rates of change in light intensity.

Two recent studies may support the relative stimulus threshold hypothesis. field studies of DVM of the copepod *Calanopia americana* (Cohen & Forward 2005a) found that the ascent at sunset was related to the rate of decrease in light intensity but the descent at sunrise began before a rate of light increase could be detected by the light-measuring system. Wagner-Doebler (1990) found that the descent of *Chaoborus flavicans* larvae was triggered by the rate of increase in light intensity but the descent velocity was independent of the rate of increase in light intensity.

In contrast, Haney et al. (1990) found that the rapid ascent at sunset of *C. punctipennis* larvae began at a relative rate of change of 1.7×10^{-3} s^{-1} but upwards velocity was highly correlated with the relative rate of decrease in light intensity, which supports the stimulus velocity hypothesis. The emergence and vertical migration of the mysid *Neomysis americana* may also conform to the stimulus velocity hypothesis (Abello et al. 2005). Ascent from the substratum into the water column is cued by the relative rate of decrease in light intensity. The ascent speed increases as emergence times occur later after sunset, while the descent speeds at sunrise increase during twilight and decrease after sunrise. Since the relative rate of decrease becomes faster after sunset (Figure 1) and the relative rate of increase becomes slower after sunrise, ascent and descent velocity increases are related to the rate of light intensity change.

Ringelberg (1999) reviewed DVM of *Daphnia* spp. and concluded that the stimulus velocity hypothesis was supported because the ascent and descent speed at sunset and sunrise in the field are related to the magnitude of the relative rates of change in intensity (e.g., Ringelberg et al. 1991, Ringelberg & Flik 1994). This relationship is also seen in laboratory studies of *Daphnia* spp. because the vertical ascent velocity is linearly related to the relative rate of decrease in light intensity (Ringelberg 1991a, van Gool & Ringelberg 2003) and the descent velocity is linearly related to the rate of relative increase in light intensity (Ringelberg 1991a, van Gool & Ringelberg 1997, 1998a,b). Interestingly the vertical displacement velocity increases faster in the presence of fish kairomones (see p. 90) if the relative rate of change in light intensity accelerates over time (van Gool & Ringelberg 1997, 1998a,b). Ringelberg & van Gool (2003) explained this response by postulating that specific relative rates of change in light intensity induce a specific vertical displacement velocity (photobehavioural system 1) that is not affected by fish kairomones. However, there is a second phototactic mechanism (photobehavioural system 2) that is sensitive to fish kairomones and food.

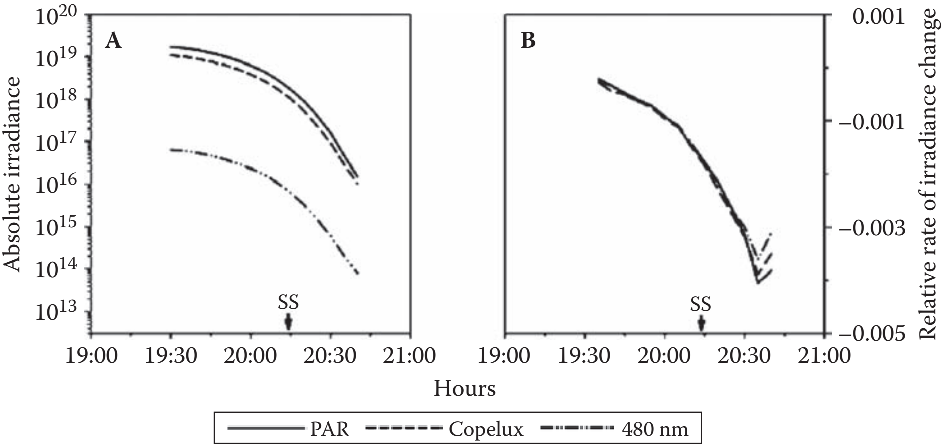

Figure 1 Change in underwater light intensity at sunset: a comparison of units. Spectroradiometric light measurements were made on 27 July 2003 at 0.5-m depth about 1.5 km inside the mouth of the Newport River Estuary (North Carolina, USA). (A) Absolute irradiance data are plotted as photosynthetically active radiation (PAR) (solid line; 400–700 nm, photons m^{-2} s^{-1}), Copelux (dashed line; normalised to spectral sensitivity of the copepod *Calanopia americana* between 360 and 740 nm), and 480-nm quantal flux (dashed-dotted line; photons m^{-2} s^{-1} nm^{-1}). Time of sunset (SS) is indicated. (B) Relative rate of irradiance decrease calculated from absolute irradiance data and plotted as in panel A. (Replotted from Cohen & Forward 2005a.)

An acceleration in the relative change in light intensity affects this system and vertical displacement velocities increase at a faster rate than seen for photobehavioural system 1.

These studies indicate that relative rates of change in light intensity are used as a cue for DVM and it is interesting to compare field measurement of the rates of change with laboratory-determined rates that evoke behavioural responses involved in DVM. Cohen & Forward (2005a) compared the rate of change at sunset of photosynthetically active radiation (PAR), light available for photoreception by the copepod *Calanopia americana* (copelux) and light at the spectral sensitivity maximum for this species (480 nm; Cohen & Forward 2002). The relative rates of change (Figure 1) were remarkably similar and the only variation occurred at the end of twilight when the maximum rate of decrease was observed. These results suggest that measurement of the relative rates of change are robust, at least in shallow water systems, and can be made using a variety of light detection systems. The pattern of change is characterized by an increase in the relative rate of change to a maximum about 20 to 45 min after sunrise and before sunset followed by a rate decrease (Figure 1; Ringelberg 1991b, 1995a, Ringelberg & Flik 1994, Cohen & Forward 2005a).

Although the relative rate of change in light intensity can vary with latitude and season (McFarland et al. 1999), field measurements of the maximum relative rates of increase at sunrise and decrease at sunset in different studies are relatively consistent (Table 1). The average relative rate of change at sunrise is 3.2×10^{-3} s^{-1} and the value for sunset is -3.0×10^{-3} s^{-1} (Table 1). Sensitivity of zooplankton to relative rates of change in light intensity varies with species, adaptation intensity, kairomones (see p. 86), and food. Nevertheless, the average lowest values for all species (Table 2) measured were 2.2×10^{-3} s^{-1} for an increase in intensity and -2.1×10^{-3} s^{-1} for a decrease in intensity. This comparison is surprising because a logical prediction is that zooplankton should be sensitive to rates of change that are well below the maximum rates at sunset and sunrise. However, the comparison shows that the average threshold rates for zooplankton photoresponses are just below the maximum rates of change under water. One possible explanation is that the high threshold prevents zooplankton from vertically migrating in response to rates of change in light

Table 1 Field measurements of maximum relative rate of change in light intensity

	Relative rate of light intensity change	Reference
Sunrise	$2.3 \times 10^{-3}\ s^{-1}$	Ringelberg & Flik 1994
	$4.0 \times 10^{-3}\ s^{-1}$	Ringelberg 1995a
Sunset	$-4.0 \times 10^{-3}\ s^{-1}$	Forward 1985
	$-2.0 \times 10^{-3}\ s^{-1}$	Ringelberg 1991b
	$-2.2 \times 10^{-3}\ s^{-1}$	Ringelberg & Flik 1994
	$-3.0 \times 10^{-3}\ s^{-1}$	Ringelberg 1995a
	$-2.7 \times 10^{-3}\ s^{-1}$	Frank & Widder 1997
	$-4.2 \times 10^{-3}\ s^{-1}$	Cohen & Forward 2005a

Table 2 Relative rate of change in light intensity: thresholds for photoresponses

	Rate of intensity change	Species	Reference
Rates of increase	$2.1 \times 10^{-3}\ s^{-1}$	*Daphnia magna*	Daan & Ringelberg 1969
	$3.0 \times 10^{-3}\ s^{-1}$	*Artemia franciscana*[a]	Forward & Hettler 1992[a]
	$0.7 \times 10^{-3}\ s^{-1}$	*Daphnia galeata x hyalina*[a]	van Gool & Ringelberg 1997[a]
	$3.1 \times 10^{-3}\ s^{-1}$	*Calanopia americana*	Cohen & Forward 2005b
Rates of decrease	$-1.7 \times 10^{-3}\ s^{-1}$	*Daphnia magna*	Ringelberg 1964
	$-1.8 \times 10^{-3}\ s^{-1}$	*Rhithropanopeus harrisii*	Forward 1985
	$-1.0 \times 10^{-3}\ s^{-1}$	*Daphnia hyalina*[a]	Ringelberg 1991a[a]
	$-2.8 \times 10^{-3}\ s^{-1}$	*Artemia franciscana*	Forward & Hettler 1992
	$-0.9 \times 10^{-3}\ s^{-1}$	*Daphnia longispina*	Ringelberg 1993
	$-4.6 \times 10^{-3}\ s^{-1}$	*Calanopia americana*[a]	Cohen & Forward 2005b,c[a]

[a] Species and associated references for which predator kairomones have been shown to alter photobehavioural response thresholds.

intensity that occur on movement of clouds relative to the sun. Underwater measurements of rates of change in intensity as clouds move across the sun are needed to evaluate this explanation.

Both chemical cues released from predators (discussed on p. 86) and feeding affect behavioural responses to relative rates of change in light intensity, yet all studies to date suggest the effects of food and predator chemical cues on photoresponses involved in nocturnal DVM are separate. If zooplankton undergoing nocturnal DVM are ascending to feed (e.g., Pearre 2003) and descending to avoid visual predators (Zaret & Suffern 1976, Stich & Lampert 1981), then predictions are that food, as it affects hunger and satiation, should have its greatest effect on photoresponses at sunset and chemical cues from visual predators should affect photoresponses at sunrise. In accordance with these predictions, responses of brine shrimp larvae to relative rates of decrease in light intensity are activated by starvation (Forward & Hettler 1992). If fed, the larvae do not respond, which predicts they would only ascend at sunset if sufficiently starved. Feeding and starvation had no effect on responses to rates of increase in light such as occur at sunrise, which are activated by exposure to chemical cues from fishes (Forward & Hettler 1992, Forward 1993).

Similarly, *Daphnia galeata* × *hyalina* show an increased phototactic response to a relative decrease in light intensity when exposed to low, as opposed to high, food concentrations (van Gool & Ringelberg 2003). Furthermore, responses to rates of increase in light intensity increase as food concentrations increase (van Gool & Ringelberg 1995, 1998a,b), which predicts that well-fed animals will readily descend at sunrise. In contrast to brine shrimp larvae, chemical cues from fishes affect photoresponses that occur at both sunrise and sunset by *D. galeata* × *hyalina* (van Gool & Ringelberg 1997, 2003).

Phenotypic plasticity in DVM behaviour

The largest advance in the study of DVM in recent years is the understanding that a major cause in the variability of this behaviour involves phenotypic plasticity in migration on exposure to cues from predators. Table 3 lists the studies, including those on processes apart from DVM, that have reported instances in which chemical cues from predators (kairomones; see p. 90) alter biological processes in marine zooplankton. Despite the widespread appreciation of predator-induced plasticity in morphological, physiological, and behavioural phenotypes of organisms in a range of habitats, including the marine benthos (see Tollrian & Harvell 1999), phenotypic plasticity in DVM is one of very few areas in which similar phenomena have been reported for marine zooplankton (Table 3). This situation will likely change as more studies examine predator-induced plasticity in marine zooplankton biological processes. The area of morphological and life-history plasticity is of particular interest as there is a rich literature for freshwater zooplankton (reviewed in Lass & Spaak 2003, Pohnert et al. 2007), and recent work on marine zooplankton suggests similar plasticity occurs in these organisms (Vaughn 2007, Vaughn & Strathmann 2008). Here field and laboratory evidence that DVM is a response to predator cues is reviewed and then the potential identities of chemical cue molecules from predators are discussed. The major focus is on zooplankton in marine systems but some attention is paid to freshwater studies because this work forms the basis of our understanding of predator-induced phenotypic plasticity in DVM.

Field and mesocosm evidence

It is generally agreed that the function of nocturnal DVM is to allow zooplankton the opportunity to feed near the surface under low-irradiance conditions that reduce the risk of visual predation (Lampert 1993). Strong evidence for DVM as a predator-avoidance mechanism has come from field and mesocosm studies in both freshwater and marine systems suggesting that both rapid (hours to days; Dawidowicz et al. 1990, Neill 1990, Bollens & Frost 1991, Frost & Bollens 1992, Loose 1993a) and long-term (seasons to years; Gliwicz 1986, Bollens & Frost 1989a, Ringelberg et al. 1991, Bollens et al. 1992, Hays et al. 1996, Horppila 1997, Muluk & Beklioglu 2005) exposure to

Table 3 Studies of predator kairomone effects on marine zooplankton morphology, physiology, and behaviour

Process	Zooplankton species	Predator species	Reference
Diel vertical migration	*Artemia franciscana* nauplii	*Brevoortia tyrannus*	Forward & Hettler 1992
			Forward & Rittschof 1993
	Artemia franciscana nauplii	*Brevoortia tyrannus*	
		Fundulus heteroclitus	
		Lagodon rhomboides	
		Mnemiopsis leidyi	McKelvey & Forward 1995
	Calanopia americana	*Fundulus heteroclitus*	Cohen & Forward 2005c
		Mnemiopsis leidyi	
	Rhithropanopeus harrisii zoea	*Fundulus heteroclitus*	Forward & Rittschof 2000
Non-DVM photobehaviour	*Rhithropanopeus harrisii* zoea	*Mnemiopsis leidyi*	Cohen and Forward 2003
Swimming speed/direction	*Temora longicornis*	*Chelon labrosus*	van Duren & Videler 1996
Feeding	*Acartia hudsonica*		
	Acartia tonsa	*Menidia menidia*	Cieri & Stearns 1999
	Mysis mixta	*Clupea harengus*	Hamŕen & Hansson 1999
Reproduction and development	*Dendraster excentricus* plutei	*Microstomus pacificus*	Vaughn & Strathmann 2008
Morphology	*Littorina scutulata* veligers	*Cancer* spp. zoea	Vaughn 2007

Note: DVM = diel vertical migration.

predators can alter the magnitude of migrations and induce migrations in previously non-migrating zooplankton populations.

The clearest evidence for DVM as a predator-avoidance mechanism comes from work in freshwater environments. Gliwicz (1986) observed non-migrating populations of the copepod *Cyclops abyssorum* in alpine lakes without fishes, while DVM occurred in *C. abyssorum* populations in fish-stocked lakes, with the magnitude of migration depending on how long ago the lakes were stocked. In Lake Maarsseveen (The Netherlands), *Daphnia galeata* × *hyalina* are non-migratory for most of the year, then undergo DVM for a short, 6- to 7-wk period each May–July, coinciding with the presence of large schools of juvenile perch *Perca fluviatilis* (Ringelberg et al. 1991). A similarly discrete seasonal period of migration is observed for *Daphnia hyalina* in Lake Constance (Germany; Stich & Lampert 1981). Reversible nocturnal DVM like that in Lake Constance was recreated by Loose (1993a) by placing *D. hyalina* in a thermally stratified plankton tower and adding water from a second tank containing variable numbers of cyprinid fish. Non-migrating *D. hyalina* were rapidly induced to migrate with the addition of these chemical cues from fish, and DVM ceased with removal of the cues (Loose 1993a, but see Jamieson 2005). Other crustacean zooplankton, such as the copepod *Diaptomus kenai*, are preyed on by chaoborid larvae, which undergo nocturnal DVM. This copepod adopts a reverse DVM strategy that can be rapidly (<4 h) induced in non-migrating populations by the addition of *Chaoborus* larval odour (Neill 1990).

Analogous studies in marine environments are less common. In Dabob Bay (Washington, USA), the strength of migration behaviour in the copepod *Calanus pacificus* showed a strong positive relationship with the abundance of fishes actively preying on it (Bollens & Frost 1989a). Another copepod species in Dabob Bay, *Pseudocalanus newmani*, typically either lacks DVM or undergoes reverse DVM when its invertebrate predators are abundant and undergoing nocturnal DVM (Ohman et al. 1983, Ohman 1990). Reverse DVM in *P. newmani* is stronger during periods of elevated invertebrate predation pressure (Frost & Bollens 1992). Interestingly, *P. newmani* is also capable of switching to nocturnal DVM in several weeks when vertebrate predators are abundant (Frost & Bollens 1992).

Vertical migration of the copepod *Acartia hudsonica* in a shallow lagoon in the San Juan Islands (Jakles Lagoon, Washington, USA) is likewise related to predator abundance. On a series of cruises during 1989–1990, Bollens et al. (1992) found *A. hudsonica* exhibited stronger nocturnal DVM behaviour during periods of higher abundance of the dominant fish, threespine stickleback *Gasterosteus aculeatus*, with no relationship to either water transparency or thermal stratification. In a series of enclosure experiments in Jakles Lagoon, the copepod *Acartia hudsonica* was exposed to caged and uncaged predatory *Gasterosteus aculeatus* (Bollens & Frost 1989b, 1991, Bollens et al. 1994). In initial experiments lasting 9 days, *Acartia hudsonica* in the lagoon undertook nocturnal DVM, as did copepods in enclosures with uncaged (free) fish, whereas no DVM occurred in control (fish-free) and caged fish enclosures (Bollens & Frost 1989b). Additional enclosure experiments with uncaged fish (Bollens & Frost 1991) suggested selective predation on genetically fixed non-migrators was not occurring in uncaged fish treatments, but rather visual or mechanical stimuli during daytime encounters between free fish and copepods drove the copepods to deeper daytime depths.

Bollens et al. (1994) re-examined the possible role of chemical cues from fish in maintaining *A. hudsonica* DVM, and explicitly tested mechanical/visual cues as stimuli to explain the vertical distribution of copepods observed in Jakles Lagoon. Using enclosures as in their previous studies, Bollens et al. (1994) tested chemical exudates by replacing 1% of enclosure surface water with fish exudates (lagoon water incubated with foraging *Gasterosteus aculeatus*), then sampling the vertical distribution of *Acartia hudsonica* 1 h later (~1200). This procedure was repeated on three consecutive days, and control enclosures received transfers with lagoon water handled the same way but lacking fish. They found no difference between daytime depths of copepods in the control and treatment enclosures and concluded that chemical exudates did not affect the vertical distribution of

A. hudsonica (Bollens et al. 1994). However, they did find a significant increase in mean depth in a subsequent daytime experiment in which rubber fish mimics were moved throughout the upper 2 m of the enclosures to simulate striking fish and *A. hudsonica* vertical distribution was immediately sampled; night-time fish mimic experiments in the same enclosures showed no significant difference in *A. hudsonica* mean depth immediately following the stimulation. Bollens et al. (1994) concluded from these experiments that vertical migration in *A. hudsonica* was triggered by mechanical or visual cues, but not chemical cues, from *Gasterosteus aculeatus.*

Ringelberg (1995b) argued that this conclusion was not justified, suggesting the experiments using mechanical/visual cues were not designed to capture DVM, but rather an immediate and perhaps transitory escape response to the mechanical/visual stimulus of oscillating fish mimics. It was also argued by Ringelberg (1995b) that a rhythmic stimulus such as the light:dark cycle is required to generate a rhythmic behaviour such as DVM, citing Loose's (1993a) finding that chemical exudates from fish alone are not sufficient to evoke DVM behaviour. Rather, a rhythmic light cue is required, with chemical exudates functioning in triggering DVM by affecting thresholds for these photoresponses (e.g., Ringelberg 1991b). Therefore, by immediately sampling the vertical distribution of *Acartia hudsonica* at noon, Bollens et al. (1994) had no rhythmic light cue. Bollens et al. (1995) replied to this comment by underscoring the variability in DVM, and that cues other than rhythmic changes in light may still be involved in triggering the behaviour. Furthermore, they remark that, "*Acartia* … may prove to be the exception rather than the rule among marine copepods" in terms of the role chemical exudates play in triggering DVM.

While this may be the case, it is still not certain that Bollens et al. (1994) can claim their fish exudate treatment did not have an effect on *Acartia hudsonica* DVM. It was assumed by Bollens et al. (1994) that *A. hudsonica* in the control (fish-exudate-free) treatment did not undergo DVM, and that because the daytime depth distribution of copepods in treatments with and without fish exudates were similar (Table 1 in Bollens et al. 1994), DVM was not occurring. This assumption is problematic because *A. hudsonica* in control treatments were likely still undergoing DVM after 2 days in the enclosures based on data from their earlier study (Table II in Bollens & Frost 1989b). If this was the case, then no difference would be expected between fish exudate and control treatments if DVM was induced by the rhythmic light signal. Hence, the mean day depths would be the same, as they were in Bollens et al. (1994).

Laboratory evidence

Considerable progress on predator-induced phenotypic plasticity in DVM behaviour has been made in laboratory studies to support the field evidence given in the preceding section. In some studies, the odour condition of the water was modified and zooplankton were exposed to a light:dark cycle in laboratory columns or aquaria. Vertical position and DVM were then observed over extended periods. This approach is useful for documenting general phenotypic plasticity in DVM behaviour and for examining chemical cue identity (e.g., Loose et al. 1993). In another approach, behaviour of zooplankton in odour-treated water is observed immediately on stimulation by light cues that induce the ascending or descending swimming behaviour of DVM. This method allows for a more sophisticated understanding of how predator odour affects DVM behaviour at the proximate level (e.g., van Gool & Ringelberg 1997, Forward & Rittschof 2000). In both cases, zooplankton are not responding directly to chemicals released from predators, but rather their response to a light stimulus is modified by these chemical cues. Since these chemicals are produced by predators but benefit the zooplankter receiving the chemical information, they are termed *kairomones* following the infochemical terminology of Dicke & Sabelis (1988).

Predator kairomones affect vertical distributions of zooplankters maintained in the laboratory in a manner consistent with DVM as a predator-avoidance mechanism. *Daphnia magna* assume a deeper mean day-depth within 2 days of being introduced into thermally stratified columns when fish kairomones are present relative to when these kairomones are absent (Loose et al. 1993). Similarly, *D. mendotae* position themselves in warmer surface waters of thermally stratified laboratory columns without predator kairomones, but display DVM with daytime residence in deeper, cooler water when exposed to kairomones from the invasive predatory cladoceran, *Bythotrephes longimanus* (Pangle & Peacor 2006). The observed shift in *Daphnia mendotae* vertical distribution lowered its somatic growth rate (Pangle & Peacor 2006). Further field and modelling work with *D. mendotae* suggested such non-lethal effects of predators may affect population growth as much as or more than the lethal effects from predators (Pangle et al. 2007).

For third and fourth instar *Chaoborus flavicans* larvae collected from a pond with fishes and then maintained in laboratory columns without a thermal gradient, the presence of fish kairomones resulted in lower densities in the upper column during the day, with no difference at night (Tjossem 1990). Mean depths at midday and midnight were also deeper for fourth instar larvae of *C. flavicans* when placed in thermally stratified aquaria with odour from a predatory fish. This response was reversible on subsequent placement in predator odour-free water (Dawidowicz et al. 1990). *Chaoborus flavicans* appeared highly photosensitive during fish odour exposures (i.e., positively phototactic; Dawidowicz et al. 1990), which fits with the proposed mechanism for phenotypically plastic zooplankton DVM behaviour (see this section). As with *Daphnia mendotae* (Pangle & Peacor 2006) the change in *Chaoborus flavicans* vertical distribution induced by fish kairomones resulted in a one-third reduction in growth rates. Interestingly, kairomones themselves and not temperature alone were responsible for some of this non-lethal effect on growth rates (Dawidowicz & Loose 1992).

While laboratory studies using multiday observations of animals in columns can demonstrate DVM behaviour and provide a useful bioassay for kairomone activity (e.g., Loose et al. 1993, see next section), they provide relatively little information on the proximate effects of kairomones on the behavioural responses involved in DVM. This problem can be overcome by analysing the effects of kairomones directly on the photobehaviours involved in cueing DVM-related swimming responses. From such studies, it is apparent that predator kairomones affect zooplankton DVM-related photoresponses, particularly the responses to relative rates of change in light intensity.

Among *Daphnia hyalina* (Ringelberg 1991a) and *D. galeata* × *hyalina* (van Gool and Ringelberg 1995, 1997, 1998a,b, 2002, 2003) alterations in the percentage response and displacement velocity to different relative rates of change in light intensity occur on exposure to different concentrations of fish kairomones. When *Daphnia* are presented with a suprathreshold constant relative rate of change in light (e.g., $1.3 \times 10^{-3}\ s^{-1}$), larger percentages of individuals respond with a behavioural swimming response when fish kairomones are present than do without kairomones, yet there is no kairomone effect on daphnid displacement velocities (van Gool & Ringelberg 1997). However, fish kairomones increase displacement velocities, and in turn migration amplitudes, when the rate of change stimulus is presented as an accelerated increase or decrease rather than a constant rate (van Gool & Ringelberg 1997, 2003). An accelerated rate of change better simulates the naturally occurring change in light level at twilight (Figure 1).

Studies of marine zooplankton have yet to examine phenotypic plasticity of the swimming response on accelerating rates of change. However, studies with several taxa have examined fish kairomone effects on the percentage of organisms responding during constant rates of change. Larvae of the brine shrimp *Artemia franciscana* exposed to fish kairomones display a descent response to a relative step increase in light intensity, but kairomones had no effect on responses to intensity decreases (Forward & Hettler 1992, Forward 1993). McKelvey & Forward (1995) and Forward & Rittschof (1993, 1999) used this kairomone-induced photobehavioural activation as a bioassay to explore the identity and specificity of the kairomone molecules (see next section).

Similarly, in the coastal copepod *Calanopia americana*, the threshold relative rate of decrease in light intensity that induced an ascent response shifted from $4.6 \times 10^{-3}\ s^{-1}$ without kairomones to $5.8 \times 10^{-3}\ s^{-1}$ with fish kairomones (Cohen & Forward 2005c). These results suggest that when predator abundance is low, this copepod species ascends earlier in the evening when relative rates of light intensity change are lower but when predator abundance is high the ascent occurs later in the evening when rates of change are faster. The functional significance is that if fish predators are present, the copepods ascend later in twilight when light levels for visual predators are lower.

Photobehaviours other than responses to relative rates of intensity change also demonstrate phenotypic plasticity. Zoea larvae of the estuarine crab *Rhithropanopeus harrisii* ascend at sunset using the relative rate of intensity change as a stimulus but descend with an isolume at sunrise by negative phototaxis when light is above their lower threshold for phototaxis (Forward et al. 1984, Forward 1985). Phenotypic plasticity in the ascent phase of *R. harrisii* DVM is unknown but exposure to fish kairomones decreases the *R. harrisii* lower threshold for phototaxis (Forward & Rittschof 2000). This effect would result in an earlier descent of zoea at sunrise when visual predators are present, lowering their predation risk.

Kairomone identity

A definitive chemical identity of the kairomones that activate DVM in zooplankton is lacking, although several putative compounds have been suggested. While some similarities exist in the chemical nature of the kairomones active in freshwater and marine systems (e.g., source specificity, polarity, molecular size, stability), it seems likely that chemically distinct cues function in these systems. The chemical identities of putative kairomones have been recently reviewed by Lass & Spaak (2003) and Rittschof & Cohen (2004). Pohnert et al. (2007) reviewed some of the difficulties in identifying kairomones involved in planktonic interspecific interactions.

DVM-inducing kairomones may be generalised molecules indicating elevated risk of predation rather than chemically discrete indicators of individual predator species. Exudates from either planktivorous or piscivorous fish species induce DVM in *Daphnia magna* (Loose et al. 1993, von Elert & Loose 1996, von Elert & Pohnert 2000). Similarly, odours from several planktivorous fish species and a non-visual predator (the ctenophore, *Mnemiopsis leidyi*) alter DVM-related photobehaviour in *Artemia franciscana*, whereas odour and physical stimulation from other non-visual invertebrate predators only weakly affect photobehaviour (McKelvey & Forward 1995). In the marine copepod *Calanopia americana*, fish odour decreases the photobehavioural sensitivity to rates of light intensity change, whereas ctenophore odour removes this photobehaviour entirely (Cohen & Forward 2005c). Thus, similar kairomones may serve to identify both visual and non-visual planktivores (e.g., ctenophores).

Trimethylamine (TMA) has been suggested as the DVM-inducing fish kairomone for *Daphnia hyalina* (Boriss et al. 1999). Subsequent studies have argued that TMA does not affect *Daphnia* DVM behaviour when tested at ecologically relevant concentrations (Pohnert & von Elert 2000). Fish kairomones in freshwater are low molecular weight, non-volatile, polar compounds that resist peptidase degradation and are thermally and pH stable (Loose et al. 1993). Their biological activity depends on hydroxyl groups, but not on amino, carboxy, sulphate or phosphate groups. Furthermore, there is some evidence that kairomones are not a component of fish mucus or its constituent mucopolysaccharides (von Elert & Loose 1996, von Elert & Pohnert 2000). However, bacteria associated with freshwater fishes and their mucus may play a role in kairomone production (Ringelberg & van Gool 1998, Beklioglu et al. 2006). In addition to their effect on DVM, fish kairomones also alter freshwater zooplankton life-history traits, although the kairomones that affect DVM and life-history traits appear to be different molecules (von Elert & Stibor 2006).

Fish kairomones in marine systems also are low molecular weight, polar compounds with good temperature and pH stability (McKelvey & Forward 1995), yet these molecules appear to be degradation products of mucopolysaccharides in fish mucus (Forward & Rittschof 1999, 2000, Cohen & Forward 2005c). As such, they serve as structural polymers for fish and migratory zooplankton use these regularly released and rapidly degraded compounds as information molecules (Rittschof & Cohen 2004). Bioassay-guided fractionation studies with *Artemia franciscana* nauplii and *Rhithropanopeus harrisii* zoea suggest that active kairomones derived from killifish *Fundulus heteroclitus* mucus were less than 10 kDa and contained sulphated or acetylated amino groups (Forward & Rittschof 1999, 2000). Glycosaminoglycan polysaccharides in freshly collected *F. heteroclitus* mucus could be digested by heparinases and chondroitinases to generate active kairomones. Furthermore, constitutive enzymes from fish mucus (>30 kDa to <100 kDa) could digest heparin and chondroitin sulphate polysaccharides to generate active kairomones (Forward & Rittschof 1999). Both uronic acids and sulphated glycosaminoglycans are present in *F. heteroclitus* mucus at adequate concentrations for biological activity (Cohen & Forward 2005c).

Collectively, these results suggest fish kairomones that activate marine zooplankton DVM are, at least in part, amino sugar degradation products of mucopolysaccharides. Mucus from ctenophores is similar in aspects of its biochemical composition to fish mucus, which explains its ability to alter DVM-related photobehaviour in both brine shrimp and copepods (McKelvey & Forward 1995, Cohen & Forward 2005c). Amino sugars clearly mimic fish kairomones, and they may be a major bioactive component of fish kairomones for marine zooplankton, but the exact chemical nature of the kairomones remains unknown. It is possible that the kairomone molecules include protein moieties bound to amino sugars, or amino sugars and other molecules are required in blends to fully activate or deactivate DVM responses (Rittschof & Cohen 2004).

An analogous chemical communication system to fish kairomone effects on marine zooplankton DVM may exist in fish kairomone effects on cnidarian nematocyst discharge. Cnidocytes on cnidarian tentacles are used in prey capture when a mechanical disturbance caused by prey, including fishes, discharges a nematocyst that punctures the prey body surface. For several cnidarian species, the frequency of the mechanical disturbance needed to discharge nematocysts is tuned to that of a vibrating fish when cnidocytes are exposed to exogenous chemical stimuli (Watson & Hessinger 1989). Two receptor classes have been identified: one that is sensitive to acetylated amino sugars and the other sensitive to a subset of amino acids (Thorington & Hessinger 1988, Watson & Hessinger 1989). Various low molecular weight acetylamine-containing sugars, as well as low molecular weight (<3000 Da) fractions of fish mucus, have been shown to lower the frequency needed to trigger nematocyst discharge (Thorington & Hessinger 1988, Purcell & Anderson 1996). Further comparative work between DVM-related kairomones and cnidocyte-tuning kairomones is certainly warranted.

Endogenous rhythms in DVM

Endogenous rhythms potentially contribute to vertical migration. Although they can take the form of rhythmic responses to light or gravity, the most direct participation is as a rhythm in vertical movement or activity. A true endogenous rhythm should persist in the laboratory under constant conditions, such as constant light (L:L) or constant dark (D:D), as opposed to an exogenous rhythm in which zooplankton vertically migrate in response to cues in the light:dark cycle. Much of the consideration for the involvement of endogenous rhythms is based on Rudjakov's (1970) model for nocturnal vertical migration. He proposed that zooplankton have an endogenous rhythm in which the active phase of the rhythm results in an ascent near the time of sunset and the inactive phase produces a descent due to passive sinking later in the night. Since a zeitgeber for the rhythm would be the light:dark cycle, a circadian rhythm would be observed in constant conditions with a free-running period of about 24 h. In contrast, circatidal rhythms in vertical migration with periods close to 12.4 h usually underlie selective tidal stream transport (Forward & Tankersley 2001) but not DVM. Forward (1988) reviewed the literature on rhythms and concluded that there was limited evidence from older studies that zooplankton have circadian rhythms in activity or vertical swimming that contribute to DVM.

However, recent studies have clearly demonstrated zooplankton have circadian rhythms in vertical migration, which perhaps results from improved methods for monitoring vertical migration under constant laboratory conditions. The general procedure is to place zooplankton under constant conditions in a column and monitor their vertical position or movements with a time lapse video system (e.g., Duchene & Queiroga 2001, Forward et al. 2007) or event detectors (e.g., Gerhardt et al. 2006). Alternatively, activity can be monitored as vertical swimming (Zeng & Naylor 1996a,b, Macquart-Moulin 1999) or swimming in a circular tank with infrared photoelectric cells and automatic recorders (e.g., Champalbert et al. 1991). The light for viewing zooplankton with a video system is either infrared or far-red light around 800 nm. Far-red light is preferred because (1) no heat is generated in the column, (2) wavelengths in this range are readily transmitted though water, (3) most video cameras are very sensitive to light in this wavelength range and (4) zooplankton are generally insensitive to red and far-red light (e.g., Cronin & Forward 1988). Thus, zooplankters are in apparent darkness when viewed with far-red or infrared light.

Recent studies have demonstrated rhythms in both meroplankton and holoplankton. Among meroplankton, postlarvae (megalopae) of the blue crab *Callinectes sapidus* have been extensively studied. The blue crab has a complex life cycle in which estuarine-dependent females migrate to estuary inlets to spawn. Their larvae are advected seawards to high-salinity continental shelf waters (Tankersley et al. 1998, Carr et al. 2004) where development proceeds through a series of seven zoeal (larval) stages, followed by metamorphosis to the postlarval or megalopal stage (Costlow & Bookhout 1959). Postlarvae are transported back to estuaries (Epifanio & Garvine 2001) where they settle and undergo metamorphosis to the first juvenile (J1) instar stage (Heck & Thomas 1981, Orth & van Montfrans 1987, Etherington & Eggleston, 2000).

Throughout early development there is an ontogenetic change in the biological rhythm in vertical migration. Stage I zoea lack an endogenous rhythm in vertical migration on larval release (Lopez-Duarte & Tankersley 2007, Forward unpublished data). However, a circadian rhythm in vertical migration is evident in the megalopa stage. Tankersley & Forward (1994) studied vertical migration of groups of megalopae by monitoring the number of megalopae in the upper two-thirds of a water column at 0.5-h intervals in constant darkness. Abundance increased at the time of day in the field and decreased at the time of night. The average free-running period length was 24.6 h. The rhythm predicted that megalopae should undergo reverse DVM. This prediction agreed with field studies in offshore and coastal areas, which found abundant blue crab megalopae in the neuston during the day (Smyth 1980, McConaugha et al. 1983, McConaugha 1988, Epifanio et al. 1989). At night a small proportion of the megalopae move down in the water column (McConaugha 1988).

The circadian rhythm in vertical migration persists in megalopae that enter an estuary and does not switch to a circatidal rhythm on exposure to a tidal cycle in salinity change or exposure to chemical cues from the settlement habitat (Forward et al., 1997). However, the phasing of the rhythm changes with moult stage and metamorphosis to the first crab stage in estuaries. Intermoult megalopae under constant conditions in the laboratory swim during the time of day in the field but premoult megalopae switch and swim at the time of night in the field (Forward et al. 2005). Early and late juveniles continue to have a circadian rhythm in which they swim at the time of night (Forward et al. 2004, 2005). The switch in the phase of vertical migration from an ascent during the time of day to an ascent at the time of night does not require re-entrainment because the switch occurred when individual megalopae were held under constant conditions from the intermoult stage through metamorphosis to the first crab stage (Forward et al. 2007). The circadian rhythm predicts that juvenile blue crabs should undergo nocturnal DVM in the field. This prediction agrees with the field study of Reyns & Eggleston (2004), which found juveniles swimming in the water column during the night. This pattern underlies secondary dispersal of juveniles from settlement habitats.

Field studies of the phyllosoma larvae of spiny lobsters suggested they undergo DVM (Yeung & McGowan 1991). On release, stage I larvae of the lobster *Panulirus argus* undergo a twilight vertical migration in constant conditions (Ziegler 2007). Larvae remain near the bottom of a column during the time of day, aggregate in the upper one-third of a column near the time of subjective sunset,

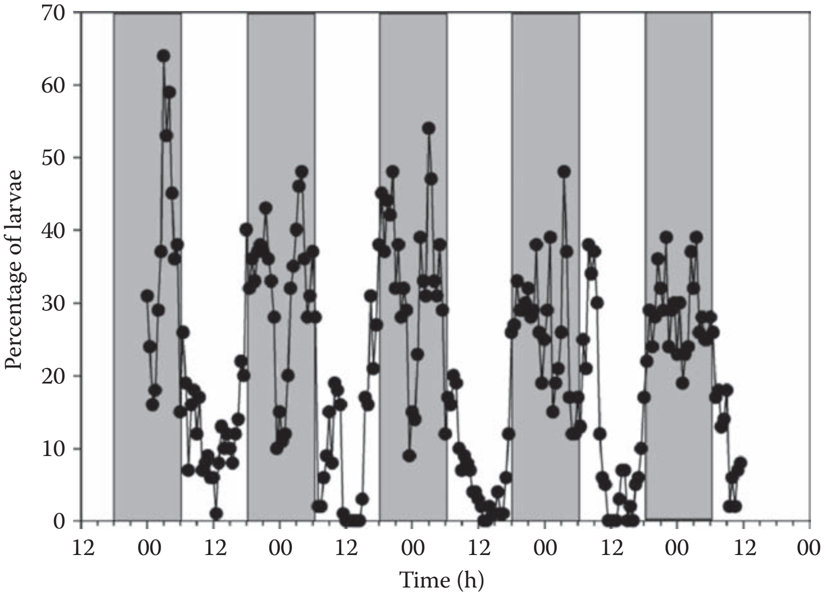

Figure 2 Endogenous vertical migration rhythms of stage I phyllosoma larvae of *Panulirus argus* under constant conditions. Percentage of larvae in the upper third of the column shown as a time series at 0.5-h intervals. Night phase of the entrainment light:dark (L:D) cycle is represented by grey shading. (Replotted from Ziegler 2007.)

descend near the time of midnight and aggregate near the surface again prior to the time of sunrise (Figure 2). The average free-running period was 23.5 h. In contrast, phyllosoma larvae of the lobster *P. guttatus* undergo a nocturnal DVM pattern in constant conditions with an average free-running period of 23.17 h (Ziegler 2007). They ascend to the surface of a column near the time of sunset and remain aggregated near the surface throughout the night. They descend near the time of sunrise and are inactive on the bottom during the day.

Among fishes, *Solea solea* larvae undergo nocturnal DVM in the field (Koutsikopoulos et al. 1991) and have an endogenous activity rhythm that contributes to vertical migration. Under constant conditions in the laboratory, larvae older than 2 wk (Champalbert & Koutsikopoulos 1995) and juveniles (Champalbert & Castelbon 1989 as *S. vulgaris*) displayed a circadian rhythm in activity in which they were active at the time of night and inactive during the time of day. Champalbert et al. (1991) failed to find a circadian rhythm in phototaxis of larval and juvenile *S. solea*.

Similarly, larvae of the Atlantic menhaden *Brevoortia tyrannus* also undergo nocturnal DVM in offshore areas (Govoni & Pietrafesa 1994). Young larvae (<8 mm total length) had a circadian rhythm in which they aggregated in the upper one-third of a column during the time of night and descended during the time of day when maintained under constant darkness. Older larvae had a similar circadian rhythm in activity in which they were active during the time of night and inactive during the time of day. All rhythms had free-running period lengths around 24 h and none of the rhythms was related to tidal times (Forward et al. 1996).

Among holoplankton, the coastal copepod *Calanopia americana* undergoes twilight DVM (Cohen & Forward 2005a). When placed under constant dark conditions in a column, the twilight pattern persisted (Cohen & Forward 2005b). Copepods aggregated in the upper part of the column around the time of sunset in the field, descended around midnight and aggregated in the upper column in the later half of the night. The circadian rhythm had an average free-running period of 23.8 h and was not related to food concentration in the water column or tidal phase in the field.

Daphnia magna and *D. longispina* also undergo a twilight DVM pattern in constant dark in a shallow tank (Young & Watt 1993) in which the midnight sink was under endogenous control. In other studies, Young & Watt (1996) found that endogenous rhythms contributed to the control of DVM in some clones of *D. longispina,* but Loose (1993b) failed to find an endogenous rhythm in vertical migration of *Daphnia galeata* × *hyalina* in constant dark in a plankton tower. More recently, a circadian rhythm in the distribution of ommatidial pigments was described for the eye of *Daphnia longispina* and *D. magna* and related to DVM (Cellier-Michel et al. 1998, Cellier-Michel & Berthon 2003, Cellier-Michel et al. 2003).

The krill *Meganyctiphanes norvegica* undergoes nocturnal DVM (Buchholz et al. 1995, Onsrud & Kaartvedt 1998). While exogenous responses to light provide a cue for DVM in this species (Frank & Widder 1997, 2002), a circadian rhythm in swimming also contributes to this behaviour. When placed under constant dark conditions krill swim actively during the time of night and decrease swimming during the time of day (Velsch & Champalbert 1994). The free-running period length was close to 24 h.

Among species that migrate from the benthos into the water column, the ostracods *Asterope mariae* and *Philonedes interpuncta* undergo nocturnal DVM in which they emerge from the substratum at dusk and swim to the surface (Macquart-Moulin 1999). They remain at the surface for less than 1 h and then return to the benthos. A circadian rhythm contributes to this migration pattern because both species continue to migrate in constant darkness. The average free-running period length for *Asterope mariae* was 24.05 h and 23.17 h for *Philonedes interpuncta*. The entrainment cue appears to be the decrease in light intensity at sunset (Macquart-Moulin 1999).

Similarly, three species of bentho-planktonic cumaceans (*Bodotria scorpioides, B. arenosa* and *Iphinae rhodaniensis*) also undergo nocturnal DVM in which they are associated with the benthos during the day and swim in the water column at night. A circadian rhythm in vertical swimming contributes to DVM as all three species continue to migrate in constant darkness (Macquart-Moulin & Castelbon 1990). The swimming phase began at the end of the day phase and continued until the middle of the night. The average free-running period was 23.2 h for *Bodotria scorpioides* and *Iphinae rhodaniensis* and 22.83 h for *Bodotria arenosa*.

Thus, circadian rhythms in vertical swimming are present in zooplankton and the timing of the activity and vertical movements corresponds to DVM patterns observed in the field. Although past studies clearly indicate that responses to light underlie nocturnal DVM (Forward 1988), the biological basis of reverse DVM is less well understood (e.g., Tester et al. 2004). Because the endogenous pattern of vertical movements by blue crab megalopae (e.g., Tankersley & Forward 1994) mimics the reverse DVM pattern observed in the field (McConaugha 1988), rhythms may also play a major role in reverse DVM.

The biological basis of twilight DVM is usually attributed to an ascent at sunset in response to light, a descent around midnight due to inactivity after feeding to satiation (reviewed by Pearre 2003) or predator avoidance (Tarling et al. 2002), a rise near sunrise for a second feeding bout and descent in response to light at sunrise. An endogenous twilight DVM pattern was observed for larvae of the lobster *Panulirus argus* (Ziegler 2007), the copepod *Calanopia americana* (Cohen & Forward 2005b) and *Daphnia magna* and *D. longispina* (Young & Watt 1993). Because food was present during trials with the copepod and *Daphnia* species, it was not clear whether the midnight sink and subsequent rise at the time of night were due to a cycle in swimming activity or feeding. Alternatively, because no food was present in trials with *P. argus* (Figure 2), a rhythm in feeding could not contribute to the migration pattern. These results suggest that while feeding may be important, there can be an endogenous component to the twilight DVM pattern. Tarling et al. (1999) proposed a similar hypothesis that the midnight sink of *Meganyctiphanes norvegica* was controlled by an endogenous rhythm after assessing DVM around the time of a lunar eclipse.

DVM in polar regions

It is interesting to consider DVM under conditions of constant light in polar regions. If the light:dark cycle provides the proximate cues for DVM, then migration during continuous light is problematic. First, without the light:dark cycle, endogenous rhythms in vertical movements or activity cannot be entrained. However, they could be entrained before conditions of the midnight sun and free run during continuous light. This situation would produce a vertical migration pattern, but it would move out of phase with the original light:dark cycle. Alternatively, circadian rhythms are frequently not expressed under conditions of continuous high-level light (e.g., Dunlap et al. 2004) Second, if light intensity changes little over the 24-h day, isolumes would vary little in depth and threshold intensities for initiating DVM would not occur. Third, the relative rate of change in intensity over the day would be insufficient to cue upwards and downwards movements.

Field studies of marine zooplankton DVM at times of the midnight sun have produced variable results (review in Conover & Huntley 1991, Blachowiak-Samolyk et al. 2006). Some studies suggested that particular species undergo DVM (Dale & Kaartvedt 2000, Fortier et al. 2001, Arashkevich et al. 2002) whereas others reached the opposite conclusion that DVM was either absent or very weak (Hansen et al. 1990, Huntley & Escritor 1991, Fischer & Visbeck 1993, Falkenhaug et al. 1997, Johnson et al. 2007). Recently the extensive studies of Cottier et al. (2006) using Acoustic Döppler Current Profiles (ADCP) measurements and Blachowiak-Samolyk et al. (2006) using data from stratified vertical net hauls concluded DVM was not present. However, zooplankton did not maintain a constant depth under the midnight sun over the 24-h day. Blachowiak-Samolyk et al. (2006) concluded that variability in vertical depth resulted from random patchiness and habitat changes but Cottier et al. (2006) concluded that forage-type migrations by individuals resulted in unsynchronised vertical migration. Cottier et al. (2006) found that synchronised DVM began once nighttime returned in autumn. DVM in freshwater vertical migrators at high latitudes appears similarly affected, with increased day length associated with relaxed DVM behaviour (Hansson et al. 2007).

Modelling approaches to the study of DVM

As our appreciation of the complexity of the proximate causes of DVM grows, modelling approaches are proving increasingly useful to explore both the control of the behaviour itself and its ecological and biogeochemical significance. Relatively few studies (Andersen & Nival 1991, Richards et al. 1996) seek to predict DVM in terms of the proximate role of light and other factors. More often, the proximate factors triggering DVM behaviour (e.g., light level, food availability, etc.) are combined with the ultimate cause of DVM, such as avoidance of visually orienting predators and feeding, to predict zooplankton vertical distribution by minimizing mortality risk while maximizing energy gain (e.g., Giske et al. 1997, Han & Straškraba 1998, De Robertis 2002). Both approaches are valuable and are discussed here. Modelling approaches have also been used to demonstrate the utility of nocturnal and twilight DVM with a tidal component to facilitate horizontal transport (e.g., Hill 1995, Manuel & O'Dor 1997).

Our understanding of the proximate controls on DVM is sophisticated enough to begin parameterizing models that test the major hypotheses for the role of light in nocturnal DVM. Andersen & Nival (1991) predicted the vertical distribution of krill *Meganyctiphanes norvegica* using behavioural responses to light and food as forcing variables. Parameters involved maintaining population depths around an isolume and modelling ascents and descents on relative rates of irradiance change. Sensitivity analyses suggested relative rates of irradiance change were more critical than isolumes in determining *M. norvegica* vertical distribution.

The model results of Andersen & Nival (1991) were used to predict behavioural thresholds for swimming responses on relative rates of irradiance change, which fit reasonably well with some acoustic estimates of migrating SSLs composed mainly of *M. norvegica* (Tarling et al. 2000). Interestingly, these thresholds (about -2×10^{-4} s^{-1}) are lower than have been reported for other zooplankters (Table 2). This suggestion is possible because the eye of the mesopelagic *M. norvegica* is likely more sensitive to light (e.g., Myslinski et al. 2005) than that of the shallow-water species reported in Table 2.

The three major hypotheses for the proximate role of light in DVM (isolume, absolute irradiance, rate of irradiance change) were modelled by Richards et al. (1996). In all three cases, vertical distributions similar to nocturnal DVM were obtained. Incorporating zooplankton swimming responses to relative rates of irradiance change as predicted by the stimulus velocity hypothesis resulted in a rapid biomass peak in the surface after sunset and a rapid decrease at sunrise. However, exogenous factors other than light or endogenous rhythms that were not included in the model were needed to explain common aspects of DVM behaviour, such as ascent after the midnight sink. Like Andersen & Nival (1991), the strength of this modelling approach is its ability, once parameterised with laboratory and field data, to find which aspect of the light field is responsible for cueing migration behaviour.

The role of light in DVM has more frequently been modelled by optimizing risk of mortality from visual predators and energy gain from feeding for individual zooplankters (i.e., Gilliam's rule, as described in De Robertis 2002). In this case, light levels alter the risk of mortality through light-dependent visual predation rather than directly cueing zooplankton swimming behaviour. Using optimization models forced by light level, predator abundance and vertical distribution, food, and temperature, Han & Straškraba (1998) and Tarling et al. (2000) found that vertical distributions of zooplankton can follow variable DVM patterns. Light, predation pressure and food appeared to be the major regulating factors in both models. Density-dependent foraging may also play a role in spreading out *M. norvegica* populations at night, but not in setting their mean daytime population depth (Burrows & Tarling 2004).

De Robertis (2002) similarly modelled zooplankton vertical distribution through an optimization of mortality risk and energy gain but also incorporated size-dependent vulnerability to predation. His model predicted smaller, less-conspicuous migrating individuals should ascend earlier at sunset and descend later at sunrise. This prediction was supported by acoustic observations on krill *Euphausia superba* (De Robertis et al. 2000) and has been observed for other marine zooplankton as well (e.g., Frank & Widder 1997). This modelling approach relies on individual zooplankters being able to sense energy gain and predation risk, for which phenotypically plastic photobehaviour influenced by food and predators could serve as a proxy (De Robertis 2002). With increasing data on phenotypic plasticity of photobehaviour in a variety of zooplankton species, it should be possible to accurately model plasticity in zooplankton DVM in the context of a variable environment.

A different modelling approach was taken by Eiane & Parisi (2001), who used artificial neural networks to model zooplankton DVM as an individual stimulus-response process to environmental inputs. In this way, light was combined as both a regulator of mortality risk and a proximate behavioural stimulus for zooplankton swimming. Food level and predator presence were also provided as sensory inputs to alter zooplankton behaviour. Migration strategies had improved performance (i.e., model fitness) with added sensory inputs (Eiane & Parisi 2001). This approach, like that of De Robertis (2002), could allow for future incorporation of phenotypic plasticity in zooplankton behavioural responses, which may provide better predictions of the variability in DVM.

Distributions of vertically migrating zooplanktivorous predators may be structured by light-mediated predation in much the same way as the vertical distributions of their migrating zooplankton prey. For example, Clark & Levy (1988) predicted that light plays a major role in the timing of migrations in zooplanktivorous juvenile sockeye salmon *Oncorhynchus nerka* to avoid visually orienting piscivores. Juvenile *O. nerka* should migrate with an isolume to feed on zooplankton during 'antipredation windows' at sunrise and sunset and reside in deeper waters during the day to avoid their own visual predators (Clark & Levy 1988, Levy 1991). A similar crepuscular feeding pattern is predicted for juveniles of the mesopelagic fish *Maurolicus muelleri* in winter, whereas adult vertical distribution depends less on light and more on the vertical distribution of their zooplankton prey (Rosland & Giske 1994).

Future directions in DVM research

Early studies on the proximate control of DVM, reviewed by Russell (1927), correctly identified the importance of light in triggering this behaviour. More recently, our understanding of predator-induced phenotypic plasticity in zooplankton photobehaviour has helped to better link the proximate control of DVM to its ultimate causes (Ringelberg & van Gool 2003). The future holds the promise to integrate the role of light more fully with other proximate environmental factors, to understand more deeply the sensory biology underlying phenotypic plasticity of DVM in individual zooplankters and to characterise better the importance of DVM in global biogeochemical cycles.

Abiotic and biotic factors

As noted in the sections of this chapter, light plays a dominant role in DVM, yet there does not appear to be a single unifying mechanism through which light acts to cue vertical swimming behaviour. Rather, the photobiological control of DVM behaviour may differ among species, as well as within a species between the ascent and descent phases of migration, or by redundant light-related proximate cues during the same phase of migration (Forward 1985, Cohen & Forward 2005b). Future studies should consider all potential hypotheses for the role of light in cueing DVM behaviour because the applicability of one mechanism does not necessarily exclude others. Broad comparisons of photobehavioural mechanisms will be interesting as more species are studied in a larger range of habitats, particularly the open ocean (e.g., Ringelberg 1995a).

Light at ultraviolet (UV) wavelengths (UV-B/UV-A, 280–400 nm) is a major ecological factor in marine environments (reviewed by Häder & Worrest 1991, Browman 2003, Tedetti & Sempéré 2006). UV radiation has been suggested as a potential proximate and ultimate cue for DVM (reviewed by Leech & Johnsen 2003). Some studies have found that diel vertical distributions of freshwater zooplankton vary depending on UV level (Leech & Williamson 2001, Cooke et al. 2008) but no such UV effect on vertical distribution was observed in marine copepods (Bollens & Frost 1990). There may be distinct differences among taxa in terms of the role UV plays in influencing zooplankton vertical distributions (Leech et al. 2005a,b). Further work integrating UV visual sensitivity, UV damage/repair mechanisms, and UV-mediated DVM with predator-induced plasticity in this behaviour will be needed to understand fully the variability of DVM in freshwater and marine habitats. In particular, UV avoidance may play a role in systems where DVM persists in the absence of predators (e.g., Blinn et al. 1988).

Factors other than light, both biotic and abiotic, clearly have some influence on DVM behaviour. Predator kairomones and their effect on zooplankton photobehaviour have been and will continue to be a major area of study. The ecology and evolution of phenotypic plasticity is often studied in terms of reaction norms for a given trait in a variable environment (reviewed in Stearns 1989). The reaction norms governing kairomone-induced phenotypic plasticity of DVM vary with genotype (Neill 1992, De Meester 1993, 1994, De Meester et al. 1995), and further work is needed to understand the genetic basis of phenotypic plasticity in zooplankton DVM. Future work on the chemical ecology and evolution of predator kairomones and photobehaviour is warranted. All studies to date have used behavioural approaches to investigate whole-animal photoresponses to kairomones. With more information on the chemical nature of the kairomones, it should be possible to characterise kairomone receptors and to elucidate the neural pathways regulating this interaction between chemical and visual sensory modalities.

In addition to kairomones, biotic factors such as parasites also influence regular DVM behaviour, typically causing a shallower distribution of organisms through enhanced photobehaviour, along with a change in body colour (e.g., Torgersen et al. 2002). Further research into the mechanisms underlying parasite-induced changes in photobehaviour would be interesting, particularly when compared with photobehavioural changes induced by predator kairomones. Zooplankton swimming responses to environmental characteristics of the water column such as temperature, salinity, pressure, and dissolved oxygen have been studied extensively and may influence zooplankton behaviour during DVM directly or by modifying photobehaviour (reviewed in Forward 1988, Bergström & Strömberg 1997, Lougee et al. 2002). A better understanding of how these abiotic factors affect DVM at the proximate level in conjunction with each other and with light is needed.

Individual-based DVM measurements

The small-scale physiology and behaviour of individual zooplankters in variable environments, including DVM behaviour, have been recognised previously as being a research priority fundamental to understanding biological processes in the global ocean (Marine Zooplankton Consortium 1 1989, Marine Zooplankton Consortium 2 2001). Laboratory studies are well suited for observations of individual and small groups of zooplankters, and phenotypic plasticity in DVM behaviour should continue to be investigated at this level. Field studies of zooplankton DVM commonly involve enumerating organisms at different depths over time. Pearre (1979, 2003) commented that such population-level observations are not appropriate for understanding aspects of migration in individual animals.

However, recent attempts to make field observations at the level of individual migrators are promising. Kaartvedt et al. (2007, 2008) used hull-mounted and submerged acoustics to observe DVM behaviour of individual mesopelagic fishes and jellyfishes. They observed saltatory vertical migrations in individuals of two mesopelagic fish species, *Maurolicus muelleri* and *Benthosema glaciale* (Kaartvedt et al. 2008). They were also able to resolve both migrating and non-migrating layers of the scyphozoan jellyfish *Periphylla periphylla*, with asynchronous migration activity of individuals between the layers (Kaartvedt et al. 2007). Time-depth recorders have successfully been used to observe vertical movements of other gelatinous zooplankton (e.g., Seymour et al. 2004, Hays et al. 2008) and could be used with other zooplankters as well. Future studies will ideally be capable of capturing both animal position and environmental variables to analyse better the proximate control of DVM in the field. Such devices are currently being used in biotelemetry studies of diving predators that feed on migrating zooplankton (Hays 2003). In addition, the use of submersibles to track migrating layers of zooplankton (e.g., Frank & Widder 1997, 2002) and potentially individual migrants while accurately measuring the underwater light field would provide a powerful tool to test hypotheses on the role of light in DVM.

Autonomous robots offer another approach to characterizing migration behaviour at the individual level and could be used to test competing hypotheses for the proximate control of DVM. T.G. Wolcott (unpublished data) developed a robotic ‘plankton mimic’ capable of sensing, integrating and responding behaviourally to light, temperature and salinity parameters within the water column. With suitable environmental sensors, such instrumentation could allow for hypotheses regarding proximate controls on DVM behaviour to be tested *in situ*, which is necessary when fine-scale physical and chemical data are not adequate for constructing numerical models. Other autonomous drifters can mimic DVM behaviour of zooplankton populations by migrating between subsurface water layers, facilitating population-level advection estimates or serving as Lagrangian tracers to mark zooplankton populations for repeated sampling (De Robertis & Ohman 1999).

DVM and biogeochemical cycles

A better understanding of the proximate mechanisms governing zooplankton DVM behaviour, and how biotic and abiotic factors contribute to variability in DVM, will improve predictive models of DVM and other biological processes. Such models are needed for zooplankton at both the species and population levels, particularly in the context of biogeochemical cycling (Marine Zooplankton Consortium 2 2001). Migratory zooplankton play an important role in global biogeochemical cycles by modifying and transporting inorganic and organic material throughout the water column (Longhurst et al. 1990, Zhang & Dam 1997, Steinberg et al. 2002, Buesseler et al. 2007). Predictions of zooplankton abundance and variability in migration behaviour, particularly for numerically abundant species, could improve flux estimates (Marine Zooplankton Consortium 2 2001). Interestingly, layers of migrating zooplankton moving vertically in the water column may be a direct source of episodic turbulent mixing of inorganic nutrients and gases between surface and deep-water masses (Kunze et al. 2006). The magnitude of this process would depend on the overall size of the scattering layer and the size of the migrants that constitute it, as well as the temporal duration over which migrations occur. Understanding the controls on DVM variability in strongly migrating species will help in determining the global significance of this process.

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CEPHALOPODS IN THE NORTH-EASTERN ATLANTIC: SPECIES, BIOGEOGRAPHY, ECOLOGY, EXPLOITATION AND CONSERVATION

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Abstract Cephalopods play a significant role in coastal and oceanic ecosystems, both as consumers of invertebrates and small fish and as the prey of some fish, seabirds and marine mammals and other large predators. Approximately 30 species of cephalopod have been recorded in the north-eastern Atlantic and adjacent waters, including 18 teuthid (squid), seven sepiolid (bobtail), three sepiid (cuttlefish) and 10 octopod (octopus) species. A number of these are exploited commercially and support important target and by-catch fisheries in Western Europe. During the past decade, annual landings of cephalopods from the north-eastern Atlantic (International Council for the Exploration of the Sea [ICES] area) have ranged from 40,000 to 55,000 t, including substantial catches of long-fin (loliginid) squid (7000–11,000 t per annum), short-fin (ommastrephid) squid (3000–10,000 t), cuttlefish (including sepiolids; 16,000–24,000 t) and octopods (12,000–18,000 t). The most important exploited species in the north-eastern Atlantic are *Eledone cirrhosa*, *Illex coindetii*, *Loligo forbesi*, *Loligo vulgaris*, *Octopus vulgaris*, *Todarodes sagittatus*, *Todaropsis eblanae* and *Sepia officinalis*. Other species including *Alloteuthis subulata*, *Gonatus fabricii* and certain sepiolids, appear to be abundant and may be marketable. Cephalopods tend to rapidly concentrate heavy metals and other toxic substances in their tissues and this plays an important role in the bioaccumulation of these pollutants in marine predators as well as having implications for human consumption. High levels of cadmium and mercury are often recorded in cephalopod tissues. Another important environmental issue concerns the potential impact of widespread human activity on cephalopod spawning areas, particularly bottom-fishing operations but also shipping, and oil exploration and production. In contrast to many finfish species that spawn annually over a number of years, most cephalopods live only 1–2 yr and die after spawning. Therefore, failure to reproduce and recruit adequately in any given year may seriously impact the long-term viability of cephalopod stocks. Climate change is expected to have a significant effect on many species in the north-eastern Atlantic. This review provides a detailed account of the zoogeography, biology and ecology of cephalopods in the north-eastern Atlantic, on a species-by-species basis. Important economic, ecological and conservation issues affecting cephalopods in this area are also discussed.

Introduction

The Class Cephalopoda comprises three major extant divisions, of which two, the Decapoda (squid and cuttlefish) and Octopoda (octopus), are represented in the north-eastern Atlantic. They range in length from 1.5 cm in pygmy (bobtail) squid (Sepiolidae) to 20 m in giant squid (Architheuthidae). Cephalopods exhibit the highest degree of development in invertebrate nervous systems, as expressed through complex behaviour patterns, learning ability and the display of complex colour changes. In contrast to other molluscs, most cephalopods lack an external shell, are highly mobile as adults and occupy similar ecological niches to predatory fish. They are opportunistic predators, taking a wide variety of prey (cannibalism has frequently been recorded). Cephalopods are also preyed on and sustain a large number of marine predators such as fish, birds and marine mammals, especially whales (e.g., Clarke 1996, Croxall & Prince 1996, Smale 1996, Santos et al., 2001a). Their importance as prey is almost certainly greater than suggested by stock biomass alone since they are characterised by very high individual growth rates and a high production/biomass (P/B) ratio (Boyle, 2002). Many species are powerful swimmers and undertake long feeding and spawning migrations, thus influencing ecosystem functioning and community structure on a seasonal and regional basis. Cephalopods are important elements in marine food webs and interact significantly with commercially exploited finfish species. Historical evidence suggests that, in certain areas, fishing pressure has changed ecological conditions and shifts in community structures have occurred, with cephalopod stocks gradually replacing predatory fish stocks (Caddy & Rodhouse 1998). However, while squids are short-lived and often thought of as r-selected pioneer species, their life history also includes typical k-selected features. There are few if any proven examples of ecological replacement of fish by squid where fish have been overexploited. Balguerías et al. (2000) found that, although Saharan Bank fisheries were historically based on sparids and currently take mainly cephalopods, there was no evidence that ecological replacement had occurred.

Cephalopods play a significant role in marine ecosystems and are becoming an increasingly important fisheries resource in the north-eastern Atlantic (Sacau et al. 2005), previously an area identified by Caddy & Rodhouse (1998) as having relatively low exploitation of cephalopods. The main commercial squid species in U.K. waters is the long-fin squid *Loligo forbesi* (Boyle & Pierce 1994) but cuttlefish *Sepia officinalis* is currently the most commercially important cephalopod (Anonymous 2005). Since 1995, annual U.K. landings of loliginid squid have ranged from 1600 to 3200 t, making the United Kingdom the second most important fishery nation for loliginid squid within the International Council for the Exploration of the Sea (ICES) Area after France (Stowasser et al. 2004). Other species of commercial interest in U.K. waters are the squids *Alloteuthis subulata, Illex coindetii*, *Loligo vulgaris, Todarodes sagittatus,* and *Todaropsis eblanae*, and octopus, *Eledone cirrhosa*. Both *Todarodes sagittatus* and *Todaropsis eblanae* were part of a substantial fishery off Shetland and Norway in the 1980s (Joy 1989, Hastie et al. 1994) but are currently of relatively minor commercial importance (Stowasser et al. 2004). Large numbers of the oceanic squid *Gonatus fabricii* may also sporadically occur in fishing hauls. This species is of considerable ecological interest as the main prey of large predators such as sperm whales (Santos et al. 1999, 2002, Bjørke, 2001) and is attracting interest as a potential commercial resource in Norway and Greenland.

Cephalopods tend to contain high levels of metals in their tissues. This is a natural phenomenon, but higher concentrations are expected to occur in polluted waters. The concentration of heavy metals and other toxic substances by cephalopods plays an important role in the bioaccumulation of these pollutants in marine predators (Koyama et al. 2000). Accumulation rates in cephalopod species appear to be rapid (Craig 1996) and various studies of cephalopods reported high levels of cadmium (Caurant & Amiard-Triquet 1995, Bustamante et al. 1998, Koyama et al. 2000, Stowasser et al. 2005) and, to a lesser extent, mercury (Frodello et al. 2000). Inputs of pollutants to the marine environment include discharges associated with oil production operations, industrial emissions and river discharges (Sheahan et al. 2001, Ridgway et al. 2003). Trace elements such as heavy metals and radionuclides contained in these discharges can accumulate in coastal and deeper waters, leading to an increase of metal and radioactive burdens in biota and thus increasing contaminant loads for human consumption (Kunisaki, 2000, Bustamante et al. 2000, 2003, Betti et al. 2004, Stowasser et al. 2005).

Sampling of cephalopods tends to be opportunistic, whether from commercial fisheries or research catches, reflecting the relatively low importance attached to these species by European fishery managers and governments, despite the growing economic value of cephalopod fishing. Consequently, reports of spatial and temporal variation in distribution, abundance and life history parameters need to be viewed with some caution. Differences may be local and short-lived, reflecting the known plasticity and environmental sensitivity of life history parameters, but may also be an artefact of inadequate sampling.

Another important environmental issue concerns the potential impact of widespread human activity, particularly extensive bottom-fishing operations, shipping, oil exploration and production, for example on cephalopod spawning areas. In contrast to many finfish species that spawn annually over a number of years, most cephalopods live only 1–2 yr and die after spawning. Therefore, failure to reproduce and recruit adequately in any given year may seriously impact the long-term viability of cephalopod stocks and populations (Caddy 1995).

Given the ecological and economic importance of cephalopods, their tendency to bioaccumulate heavy metals and other contaminants and the potential vulnerability of the many species to large-scale seabed operations are clearly very important environmental issues. Many finfish stocks are at all-time low levels and interest in cephalopods as a fishery resource has never been greater (e.g., the current interest in directed squid fishing in U.K. coastal waters where squid have previously been landed mainly as a by-catch; Young et al. 2006). The purpose of the following review therefore is to provide information on the distribution, biology, ecology, exploitation and conservation of common cephalopod species found in the north-eastern Atlantic, with particular emphasis on species found in U.K. waters.

The cephalopod fauna of the north-eastern Atlantic

Of a global total of 786 recognised species of living cephalopods, approximately 30 have been recorded in the north-eastern Atlantic. Seven teuthid (squid), one sepiolid (bobtail), one sepiid (cuttlefish) and two octopod (octopus) families are represented. The current taxonomic classifications of these are summarised in Table 1, although it should be noted that molecular taxonomic studies continue to lead to changes in the accepted taxonomic status of many cephalopods. In general terms, north-eastern Atlantic cephalopods can be arranged in the following groupings: long-fin squids (four spp.), short-fin squids (four spp.), other squids (ten spp.), bobtails (seven spp.), cuttlefishes (three spp.) incirrate (non-fin) octopods (five spp.) and cirrate (finned) octopods (five spp.).

Long-fin squids (family Loliginidae)

Long-fin or loliginid squids belong to the suborder Myopsina and are characterised by a membrane of tissue over their eyes. They are typically small- to medium-sized squid and a number of species are suitable for human consumption and are of commercial importance. Loliginid squid are associated with coastal environments. The eye membrane is thought to have a protective function for living in shallow, turbid waters. All other squid families belong to the suborder Oegopsina and are characterised by having ‘naked’ eye pores. Two genera and four species of loliginid squid are found in the north-eastern Atlantic.

Alloteuthis media

Biogeographic distribution The European common squid *Alloteuthis media* (Linnaeus, 1758) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental

Table 1 Classification of cephalopods found in the north-eastern Atlantic: Phyllum Mollusca (Linnaeus, 1758), Class Cephalopoda (Cuvier, 1797), Subclass Coleoidea (Bather, 1888)

Superorder	Order	Suborder	Family	Subfamily	Genus	Species
Decapodiformes (Young et al., 1998)	Teuthida (Naef, 1916)	Myopsina (Orbigny, 1841)	Loliginidae (Lesueur, 1821)		*Alloteuthis* (Wulker, 1920)	*media* (Linnaeus, 1758) *subulata* (Lamarck, 1798)
					Loligo (Lamarck, 1798)	*forbesi* (Steenstrup, 1857) *vulgaris* (Lamarck, 1798)
		Oegopsina (Orbigny, 1845)	Architeuthidae (Pfeffer, 1900)		*Architeuthis* (Steenstrup, 1857)	*dux* (Steenstrup, 1857)
			Cranchiidae (Prosch, 1847)	Taoniinae (Pfeffer, 1912)	*Galiteuthis* (Joubin, 1898)	*armata* (Joubin, 1898)
					Teuthowenia (Chun, 1910)	*megalops* (Prosch, 1847)
			Gonatidae (Hoyle, 1886)		*Gonatus* (Gray, 1849)	*fabricii* (Lichtenstein, 1818)
			Histioteuthidae (Verrill, 1881)		*Histioteuthis* (Orbigny, 1841)	*bonnellii* (Ferussac, 1834) *reversa* (Verrill, 1880)
			Ommastrephidae (Steenstrup, 1857)	Illicinae (Posselt, 1891)	*Illex* (Steenstrup, !880)	*coindetii* (Verany, 1839)
				Ommastrephinae (Posselt, 1891)	*Ommastrephes* (Orbigny, 1834)	*bartramii* (Lesueur, 1821)

		Todarodinae (Adam, 1960)	*Todarodes* (Steenstrup, 1880)	*sagittatus* (Lamarck, 1798)
			Todaropsis (Girard, 1890)	*eblanae* (Ball, 1841)
	Onychoteuthidae (Gray, 1849)		*Onychoteuthis* (Lichtenstein, 1818)	*banksii* (Leach, 1817)
Sepiolida (Fioroni, 1981)	Sepiolidae (Leach, 1817)	Rossinae (Appellof, 1898)	*Rossia* (Owen, 1834)	*glaucopis* (Lovern, 1845) *macrosoma* (Chiaie, 1830)
			Neorossia (Boletzky, 1971)	*caroli* (Joubin, 1902)
		Sepiolinae (Appellof, 1898)	*Rondeletiola* (Naef, 1921)	*minor* (Naef, 1912)
			Sepietta (Naef, 1912)	*neglecta* (Naef, 1912) *oweniana* (Orbigny, 1839)
			Sepiola (Leach, 1817)	*atlantica* (Orbigny, 1839) *aurantiaca* (Jatta, 1896)
Sepiida (Zittel, 1895)	Sepiidae (Keferstein, 1866)		*Sepia* (Linnaeus, 1758)	*elegans* (Blainville, 1827) *officinalis* (Linnaeus, 1758) *orbignyana* (Ferussac, 1826)

(continued on next page)

Table 1 (continued) Classification of cephalopods found in the north-eastern Atlantic: Phyllum Mollusca (Linnaeus, 1758), Class Cephalopoda (Cuvier, 1797), Subclass Coleoidea (Bather, 1888)

Superorder	Order	Suborder	Family	Subfamily	Genus	Species
Octopodiformes (Young et al., 1998)	Octopoda (Leach, 1818)	Incirrina (Grimpe, 1916)	Octopodidae (Orbigny, 1840)	Bathypolypodinae (Robson, 1928)	*Bathypolypus* (Grimpe, 1921)	*arcticus* (Prosch, 1847)
					Benthoctopus (Grimpe, 1921)	*piscatorum* (Verrill, 1879)
				Eledoninae (Grimpe, 1921)	*Eledone* (Leach, 1818)	*cirrhosa* (Lamarck, 1798)
				Allopsidae (Verrill, 1881)	*Haliphron* (Steenstrup, 1861)	*atlanticus* (Steenstrup, 1861)
				Graneledonae (Voss, 1988)	*Graneledone* (Joubin, 1918)	*verrucosa* (Verrill, 1881)
				Octopodinae (Orbigny, 1840)	*Octopus* (Cuvier, 1797)	*vulgaris* (Cuvier, 1797)
		Cirrina (Grimpe, 1916)	Cirroteuthidae (Keferstein, 1866)		*Cirroteuthis* (Eschricht, 1836)	*massyae* (Grimpe, 1920) *muelleri* (Eschricht, 1836)
					Cirrothauma (Chun, 1911)	*murrayi* (Chun, 1911)
					Grimpoteuthis (Grimpe, 1920)	*wulkeri* (Grimpe, 1920)
			Opisthoteuthidae (Verrill, 1896)		*Opisthoteuthis* (Verrill, 1896)	*grimaldi* (Joubin, 1903)
			Stauroteuthidae (Grimpe, 1916)		*Stauroteuthis* (Verrill, 1879)	*syrtensis* (Verrill, 1879)

shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (21°N) to the North Sea (60°N) (Guerra 1992). It is most common south of 50°N, in the Bay of Biscay, English Channel and throughout the Mediterranean. *Alloteuthis media* and its congener *A. subulata* are thought to be sympatric throughout much of their geographic range (Roper et al. 1984). In U.K. waters, these species are particularly abundant in the English Channel (Rodhouse et al. 1988) and Irish Sea (Nyegaard, 2001).

Biology and ecology It has been suggested that *Alloteuthis media* and the very similar *A. subulata* may be intraspecific forms rather than true, separate species (Laptikhovsky et al. 2002). However, these types are highly sympatric, with overlapping ranges and they do not appear to be simply due to minor differences between separate populations. *Alloteuthis subulata* is usually distinguished from *A. media* by its exceptionally long tail and fins that are more than 50% of the mantle length (ML) in males (Nesis 1987). Recent morphometric and genetic information supports a sister-species relationship between *A. media* and *A. subulata* as well as significant genetic differentiation between Atlantic and Mediterranean *A. media* (Anderson et al. 2008). At present, however, there is little information about their population structures, for example, whether *A. subulata* forms a single, continuous, mixed population across its range or is divided into a number of smaller, discrete population units with limited gene flow between them.

Alloteuthis subulata

Biogeographic distribution The European common squid *Alloteuthis subulata* (Lamarck, 1798) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (20°N) to the North Sea (60°N). It also occurs throughout the Mediterranean (Roper et al. 1984). *Alloteuthis subulata* lives in shelf waters, particularly in the North Sea (Grimpe 1925, Steimer 1993), the Kattegat and the western Baltic Sea (Herrmann et al. 2001, Hornborg, 2005). In U.K. waters, *A. subulata* is often found in abundance in the English Channel (Rodhouse et al. 1988) and Irish Sea (Nyegaard, 2001). It occurs from the coastline to a possible maximum depth of 500 m (Guerra 1982), but primarily between 20 and 120 m (Roper et al. 1984). In Portuguese waters, it is often found in abundance at depths of 20–200 m (Moreno 1990, 1995). Within the western Mediterranean, it is usually recorded in depths of 30–280 m (González & Sánchez, 2002). In some parts of its range, *A. subulata* is thought to be migratory. For example, in the North Sea, juveniles are thought to leave the area at an age of about 3 mo in November and return the following spring at a length of about 5 cm ML. In this area, males and females move inshore in early summer but are absent during winter (Yau 1994). However, in other areas (e.g., English Channel), this species can be found year-round (Rodhouse et al. 1988).

Biology and ecology In Portuguese waters, progressive maturation in *Alloteuthis subulata* occurs from winter to late spring, with the males maturing slightly earlier than the females (Moreno 1990, 1995). Maturation commences at 3–4 cm mantle length (ML) in both sexes. Lengths at maturity (i.e., the length at which 50% of animals are mature, ML_{50}) of 7.7–8 cm and 7–7.5 cm have been reported for males and females respectively (Moreno, 1995). The maximum size at maturity of female *A. subulata* is about 12 cm ML (Yau 1994).

A potential fecundity of 1,200–19,000 eggs per female (average 6000 eggs, size range 8–12 cm ML) has been reported. Nyegaard (2001) observed a batch count of about 150 mature eggs laid per session, thus indicating that female *A. subulata* may spawn intermittently and produce up to 40 separate batches of eggs. The number of batches produced may depend on condition and mortality during the spawning season (Nyegaard 2001).

Table 2 Main predators of *Alloteuthis subulata*

Predators	Source
Whales	
Bottlenose whale (*Hyperoodon ampullatus*)	Santos et al. 2001a
Bottlenose dolphin (*Tursiops truncatus*)	Santos et al. 2001b, 2005a
Common dolphin (*Delphinus delphis*)	González et al. 1994, Meynier 2004, Santos et al. 2004
Harbour porpoise (*Phocoena phocoena*)	Santos et al. 2005b
Fishes	
Hake (*Merluccius merluccius*)	Daly et al. 2001
Squids	
Veined squid (*Loligo forbesi*)	Pierce et al. 1994c, Rocha et al. 1994
European squid (*Loligo vulgaris*)	Pierce et al. 1994c, Rocha et al. 1994

There may be several distinct spawning events each year. For example, in the English Channel, there are three spawning groups of female *A. subulata* that spawn in spring, summer and autumn, with two recruitment events in spring and summer. The pattern in adult males is more complex, with no regular pattern observed (Rodhouse et al. 1988). In the Irish Sea, spawning occurs mainly in spring and summer, with only a possible minor event in autumn (Nyegaard 2001). In the North Sea, the spawning season is restricted to June–July, with hatchlings appearing in plankton samples towards the end of July (Yau 1994). In early summer, male and female *A. subulata* arrive together inshore. Spawning probably occurs earlier off the west coast of Scotland than in the North Sea (Yau 1994).

Alloteuthis subulata is an important species in coastal ecosystems since it appears to be an abundant predator of small fish species and is itself preyed on by a number of larger marine animals. The main prey of *A. subulata* is reported to be clupeid fish and crustaceans (Nyegaard 2001). Nyegaard (2001) showed that, although *A. subulata* was associated with the distribution of its main prey species, the squid at stations with high prey abundance did not seem to have been more frequently engaged in feeding activity than those at other stations (based on stomach fullness). This could indicate that *A. subulata* feeds in the pelagic zone rather than close to the bottom. Indeed both sandeel and sprat, which are important prey of *Alloteuthis*, undertake vertical migrations and were found in higher abundances in the pelagic zone than near the bottom during the day in the North Sea (Pedersen 1999). The observed co-occurrence of *Alloteuthis* and its prey near the seabed may thus be due to other factors.

A number of marine mammals, fish and larger squid species are reported to prey on *A. subulata* (Table 2). It is the most commonly recorded cephalopod species in stomach contents of demersal fish in U.K. waters (Hislop et al. 1991, Daly et al. 2001) and is also an important item in the diet of demersal fish in Spanish waters (Velasco et al. 2001).

Loligo forbesi

Biogeographic distribution The veined squid *Loligo forbesi* (Steenstrup, 1856) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is distributed in the north-eastern Atlantic from the Azores (20°N) to the Faroes and the north-western coast of Norway (63°N). It also occurs in the North Sea between Scotland and Norway and to a lesser extent the Mediterranean (Roper et al. 1984). It is relatively rare south of the Bay of Biscay (45°N). In U.K. waters, *L. forbesi* is often relatively abundant in the English Channel (Holme 1974), Irish Sea (Collins et al. 1995b), off Rockall Bank and the Scottish west coast (Pierce et al. 1994a) and in the Moray Firth (Young et al. 2006). Since the early 1990s, there has been a dramatic decline in catches of *L. forbesi* off the Iberian Peninsula (Chen et al. 2006). At the same time, abundance in northern waters (around Scotland) has increased. According to Chen et al. (2006), this apparent northerly shift in the range of *L. forbesi* may be associated with increasing seawater temperatures.

The main population in U.K. waters is distributed over the continental shelf and shelf edge, mostly 50–250 m in depth and within about 200 km of the coast (Pierce et al. 1994b). Mangold-Wirz (1963) described the vertical distribution of *L. forbesi* as between 15 and 150 m in the North Sea and eastern Atlantic and 150 and 400 m in the Mediterranean. Moreno et al. (1994) reported *L. forbesi* to occur in depths of 100–200 m in Portuguese waters. At Rockall, survey catches were mostly in shallow waters less than 150 m (Pierce et al. 1998). Recent data collected in U.K. waters showed that the depth distribution seemed to be correlated to season, with squid predominantly found in deeper waters along the shelf edge (100–200 m) at the beginning and the end of the spawning season (November and March) while during the peak of spawning most squid were caught in waters shallower than 50 m (Stowasser et al. 2005). The maximum recorded depth for the species is 700 m but in the Azores the fished population occurs in water depths greater than 1000 m (Martins 1982, Salman & Laptikhovsky 2002). Where its distribution overlaps with that of its congener *L. vulgaris*, it tends to be in slightly deeper water and at greater depths than the other species.

Migratory patterns are known but relatively poorly understood. Generally, this squid moves inshore during winter months for breeding where populations are at their most highly aggregated and where they may be targeted for fishing. Pierce et al. (1994c, 1998) found the spatial pattern of abundance of *L. forbesi* for the North Sea and the north-eastern Atlantic to vary with season, with highest abundances in coastal waters occurring in October and November and most landings from offshore waters (Rockall, north-eastern Atlantic) occurring in July and August. Horizontal migrations of *L. forbesi* are also known to occur in the southern range of its distribution, in spring–summer to shallow waters of the north, and in autumn–winter to deeper waters of the south (Holme 1974, Roper et al. 1984, Sims et al. 2001). Holme (1974) found *L. forbesi* to hatch in the western English Channel and migrate eastwards, appearing in trawls off Plymouth around May. After a few months of rapid growth in the English Channel and the southern North Sea (some summer spawning), squid moved back to the western English Channel to spawn and die during the following December–January.

Recent studies on temporal trends in abundance of *L. forbesi* showed that both the timing of migration into the English Channel and winter abundance in the North Sea are influenced by sea-surface temperature (SST) (Pierce et al. 1998, Waluda & Pierce 1998, Sims et al. 2001, Pierce & Boyle 2003). Its distribution in the North Sea in winter seemed also to be strongly correlated to sea bottom temperatures and to a lesser extent salinity (i.e., more squid in more saline waters), generally not being found in temperatures below 8.5°C (Pierce et al. 1998). Peak squid abundances in the English Channel occurred when bottom temperature measured 13°C independent of time of year (Sims et al. 2001). Zuur & Pierce (2004) found strength of the North Atlantic Oscillation (NAO) and SST to be key factors influencing squid abundance. It was concluded that both the inflow of Atlantic water (with associated nutrients, prey organisms and squid) and favourable growth conditions (i.e., temperature) are important in determining abundance. Georgakarakos et al. (2002) found a positive correlation between loliginid landings and SST in nutrient-rich areas. Pierce et al. (2008a) have recently reviewed cephalopod-environment interactions.

Morphometric and genetic studies of *L. forbesi* have found no evidence of distinct inshore stocks (Pierce et al. 1994d, Brierley et al. 1995, Collins et al. 1997a, 1999, Shaw et al. 1999). There is some evidence that the offshore population found on Rockall Bank may be distinct from the coastal population. By contrast, the unique morphometric and genetic characteristics exhibited by exploited Azorean *L. forbesi* stock indicate that they belong to a highly isolated population, based on an introductory event up to 1 million yr ago (Shaw et al. 1999). Based on allozyme data, Brierley et al. (1995) suggested that the Azorean population should be regarded as a separate subspecies.

Biology and ecology *Loligo forbesi* is an annual, semelparous species (Holme, 1974) showing extended breeding seasons with one, two or several pulses of recruitment. *Loligo forbesi* in Scottish waters spawns mainly from December to February, although breeding animals are also recorded in May. Two main pulses of recruitment appear in April and August to November, with small numbers of recruits present throughout most of the year (Lum-Kong et al. 1992, Boyle & Pierce 1994, Pierce et al. 1994b, Collins et al. 1997a). Early work on *L. forbesi* in the English Channel by Holme (1974) indicated the existence of distinct winter and summer breeding populations of *L. forbesi* in U.K. waters. Examination of Scottish fishery data suggests that since the 1970s, the summer breeding population has declined in Scottish waters and the winter population now dominates and breeds later than was previously the case (Pierce et al. 2005).

Loligo forbesi is a relatively large loliginid squid. It matures over a range of sizes, with males achieving a larger maximum size than females (although some males mature at much smaller sizes). In U.K. waters, maximum lengths and weights of 61 cm ML and 2.87 kg for males and 42 cm ML and 1.54 kg for females, respectively, have been recorded (unpublished data). The largest *L. forbesi* have been caught around the Azores, with reported maximum values of 94 cm ML and 8.31 kg for males and 46 cm ML and 2.18 kg for females (Martins 1982), although the Azores population may belong to a distinct subspecies (Brierley et al. 1995). A number of techniques have been used to determine the growth characteristics of *L. forbesi*, including observations of captive squid in aquaria (Forsythe & Hanlon 1989), length-frequency analyses (Pierce et al. 1994a), statolith increment estimations (Collins et al. 1995a) and gladius increment estimations (Hughes 1998). Daily statolith increments in *L. forbesi* have been validated by aquarium-based studies (Hanlon et al. 1989) and supported by length-frequency analyses of fishery data (Collins et al. 1995a). The growth pattern of *L. forbesi* is influenced by a number of factors, including sex, maturation, season and reproduction (Hughes 1998, Smith et al. 2005). Although precise age determinations of cephalopods are difficult, it is generally accepted that *L. forbesi* lives for a maximum of 9–23 mo (Rocha & Guerra 1999, Cordes 2002).

Modal progression analyses of length-frequency data have revealed the presence of two or three size modes at maturity in males (Holme 1974, Boyle & Ngoile 1993, Pierce et al. 1994a, Boyle et al. 1995, Collins et al. 1995a). Boyle et al. (1995) suggested three possible models that could explain these: squid of mixed growth, squid of mixed age or squid of mixed stock. Temperature is known to influence development time of squid embryos (von Boletzky 1987). A development time of 75 days at 12.5°C has been reported for *L. forbesi* (Hanlon et al. 1989). Boyle et al. (1995) suggested that *L. forbesi* eggs may be held in stasis over winter in low temperatures (8–10°C), thus generating two cohorts from a single breeding population in Scottish waters. By analogy with other loliginids, male squid maturing at a small size may become ‘sneakers’ on the spawning grounds (Hanlon & Messenger 1998).

The two recruitment periods identified for Scottish waters produce distinctive microcohorts of two or three different size classes in female and male squid, respectively (Collins et al. 1997a, 1999). Genetic evidence exists for separate offshore (Rockall and Faroe banks) and shelf stocks in Scottish waters (Shaw et al. 1999). Mature squid are recorded throughout Scottish waters in winter and eggs of *L. forbesi* have been recorded in trawls off Shetland (Lum-Kong et al. 1992) and are regularly found on creel lines along the Scottish mainland coastline. Although spawning grounds have not yet been documented it has been suggested from the analysis of spatial patterns in fishery data that *L. forbesi* move from the West Coast of Scotland into the North Sea to spawn (Waluda & Pierce 1998, Pierce et al. 2001). However, a more comprehensive recent analysis by Viana (2007) suggests that the pattern is considerably more complicated. Two general, seasonal migrations of *L. forbesi* in Scottish waters were apparent, a movement inshore during summer/autumn and offshore during winter/spring. One subpopulation may in fact reside in inshore waters, whereas another appears to migrate offshore during winter/spring. Squid abundance appeared to be closely related to SST, bottom depth and distance offshore, with optimal values of 11°C, 200 m and 30 km, respectively, reported for *L. forbesi* (Viana 2007). Potential spawning areas have been modelled based on survey and market sample data on squid distribution and size at maturity data (Stowasser et al. 2005).

Loligo forbesi has an annual reproductive cycle and is semelparous (Lum-Kong et al. 1992, Pierce et al. 1994a, Collins et al. 1995a). It exhibits intermittent, terminal spawning, in which the females lay eggs in batches and die shortly after spawning (Rocha et al. 2001). However, an extended spawning pattern, with different seasonal peaks has been reported (Roper et al. 1984, Lum-Kong et al. 1992, Boyle & Ngoile 1993, Guerra & Rocha 1994, Moreno et al. 1994, Pierce et al. 1994a, Boyle et al. 1995, Collins et al. 1995a). The timing of peak spawning activity varies across its range and secondary peaks have been observed in some areas (Pierce et al. 1994a). Depending on the area and season, one or more associated pulses of recruitment occur. In the North Atlantic, concentrations of *L. forbesi* are usually found west of Scotland and Ireland in autumn and gradually shift from offshore to inshore waters as spawning progresses. By the following spring (January to March), the highest abundances are found in the Minch and Moray Firth areas and further south along the east coast of England. In summer, mature specimens are only found in the English Channel (Stowasser et al. 2005). It is not clear how long an individual squid can remain in spawning condition and it is likely that extended seasonal peaks represent a series of microcohorts maturing out of phase with each other, while secondary peaks may indicate distinct winter and summer breeding populations.

Although they are a short-lived species, fecundity in loliginid squids is surprisingly low, with female *L. forbesi* apparently producing only a few thousand eggs in their lifetime (Boyle et al. 1995). Mature females exhibit permanent oocyte maturation, with several types of oocytes found at various stages of development (Ngoile 1987, Collins et al. 1995a). The potential fecundity of *L. forbesi* females is estimated to range from 1,000 to 23,000 eggs (Boyle at al. 1995). A weakly positive relationship between size (ML) and fecundity has been reported for this species, although small mature females may have relatively more oocytes than larger females (von Boletzky 1987, Hanlon et al. 1989, Guerra & Rocha 1994, Boyle et al. 1995, Collins et al. 1995a). Fecundity does not appear to be related to the timing of maturity during the spawning season (Guerra & Rocha 1994).

The eggs of *L. forbesi* are relatively large and contain large quantities of yolk (von Boletzky 1987, Hanlon et al. 1989). They are usually packed together in layers of gelatinous substances produced by the oviducal and nidamental glands and wrapped into finger-like egg strings (Lum-Kong et al. 1992). The number of egg strings in a cluster is variable and a cluster may contain egg strings deposited by one or several females. Even egg strings deposited by single females may be multipaternal since they could be fertilised by different males (Shaw & Boyle 1997). Clusters of egg strings are typically attached to submerged, fixed substrata, including macrophytes, shells, rock crevices and various types of fishing gear. Records of egg clusters of *L. forbesi* originate primarily from shallow, inshore areas. Collins et al. (1995a) recovered egg clusters from static fishing gear over rocky ground at 10–50 m depth off the south coast of Ireland. Lum-Kong et al. (1992) and Martins (1997) found egg clusters attached to creel lines in Scottish waters and Holme (1974) reported egg clusters attached to fishing boats, rope moorings and crab pots off the coast of Devon. Along the west coast of Scotland, egg clusters of *L. forbesi* were found on creels set on both muddy and rocky grounds, at 40–110 m depth (Craig 2001). Along the Moray Firth, egg clusters have been found on moorings and piers as shallow as 2 m depth.

There are also, however, a small number of records from deeper, offshore waters. Egg clusters were found in the Celtic Sea, between France and Ireland, at depths of 135–507 m (Lordan & Casey 1999). Salman & Laptikhovsky (2002) reported egg clusters in the Aegean Sea at 720–740 m depth. In other parts of the Mediterranean, *L. forbesi* eggs have been found at 150–200 m depth (lo Bianco 1909). According to Lum-Kong et al. (1992), however, most spawning may occur in relatively deep waters since the majority of spawning squid reported are usually captured by commercial fleets working offshore. The lack of egg data could be due to non-reporting or the possibility that spawning squid prefer areas of rocky substrata that are inaccessible to demersal trawling (Holme 1974, Lordan & Casey 1999).

The rate of development and timing of hatching of *L. forbesi* are influenced by egg size and water temperature (Paulij et al. 1990, Gowland et al. 2002). Size at hatching is inversely related to temperature and is significantly reduced at 16°C compared to 8°C. The duration of the embryonic phase decreases as temperature increases, for example, 140 days at 8°C, 60 days at 12°C and 36 days at 16°C (Martins 1997, Gowland et al. 2002). The possibility that eggs may remain unhatched for several months could give rise to a complex pattern of 12-, 18- and 24-mo life cycles as discussed in Boyle & von Boletzky (1996). The incidence of deformities in hatchlings is reported to increase at extreme temperatures (Martins 1997, Gowland et al. 2002), indicating a small temperature range for normal hatching development. Craig (2001) found hatchlings to emerge from egg strings over several days, but only during hours of darkness. Detailed descriptions of the embryonic stages of *L. forbesi* are provided by Segawa et al. (1988).

Loligo forbesi is a highly mobile, opportunistic predator that will attack and consume any potential prey that it can overcome. A large number of prey species, including various polychaetes, molluscs, crustaceans and fish have been identified in *L. forbesi* stomachs (Table 3). Across its geographical range, fish was found to be the main prey type, with crustacean, cephalopod and polychaete species present in the diet to varying degrees. The most prominent fish species present in the diet belong to families Gadidae, Clupeidae, Ammodytidae and Gobiidae (Collins et al. 1994, Rocha et al. 1994, Collins & Pierce 1996, Pierce & Santos 1996). Pierce et al. (1994c) observed that crustaceans were relatively more important in the diet of small squid whilst larger squid preyed predominantly on fish. In Spanish waters, cephalopods also become a larger component of the diet, as the squid grow larger (Rocha et al. 1994). Cannibalism in *L. forbesi* appears to be limited to large squid (>15 cm ML) feeding on much smaller squid (2–5 cm ML) (Collins & Pierce 1996).

The same broad prey taxa are important in the diet of *L. forbesi* throughout its geographic range (Pierce et al. 1994c). However, regional differences in the prey composition of the diet have been identified. For example, in Scottish waters, whiting (*Merlangius merlangus*), *Trisopterus* spp. and sandeels (Ammodytidae) were the principal prey species (Pierce et al. 1994c) whereas in Irish waters, sprat (*Sprattus sprattus*) and *Trisopterus* spp. were predominant (Collins et al. 1994). There is some evidence that prey composition may vary seasonally, probably due to changes in prey availability (Collins et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Collins & Pierce 1996). Howard (1979) observed seasonal differences in stomach emptiness, with a higher frequency of empty stomachs found in winter. Gaard (1987) noted that *L. forbesi* probably feeds mainly by day since stomach fullness was greatest and the state of digestion was less when squid were caught in the evening.

Recent investigations using fatty acid and stable isotope analyses indicates that *L. forbesi* is mainly associated with the benthic food web and that prey type and prey variability changed with body size (Stowasser et al. 2005). Captive rearing studies have shown that *L. forbesi* paralarvae feed predominantly on copepods, juvenile mysids and palaemonid larvae (Forsythe & Hanlon 1989, Hanlon et al. 1989).

Loligo forbesi is itself included in the diets of a number of marine predators. Large demersal fish and some marine mammals have been reported to prey on *L. forbesi* (Table 4). Identification of stomach contents in the majority of published reports on predatory fish and marine mammals however remains at the level of family (Loliginidae). Beaks have been identified from the stomachs of pygmy sperm whale (*Kogia breviceps*), northern bottlenose whale (*Hyperoodon ampullatus*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleolba*), bottlenose dolphin (*Tursiops truncatus*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melaena*) and Risso's dolphin (*Grampus griseus*; Santos et al. 2004, De Pierrepont et al. 2005). The great skua (*Catharacta skua*) is the only reported bird species from north-eastern Atlantic waters with beaks of *Loligo* sp. found in the stomach (Furness 1994). None of these species, however, were considered by the investigators to be a major cause of mortality of *Loligo* sp.

Table 3 List of identified prey types and species from *Loligo forbesi* stomach contents

		Geographic area						
Group	Taxonomic description	Northwest Spain	Ireland	Scotland	England	Faroes	Portugal	Azores
Fish	*Agonus cataphractus*		•					
	Ammodytes sp.	•	•	•	•		•	
	Anthias anthias							•
	Anthias minuta	•	•	•				
	Argentina sp.		•	•			•	
	Argentina sphyraena	•	•					
	Atherina sp.	•						
	Belone belone							•
	Boops boops							•
	Callionymus sp.	•	•	•	•		•	
	Callionymus lyra							•
	Callionymus maculatus	•	•	•	•	•		
	Capros aper		•	•				
	Cepola macrophthalma		•					
Crustacea	Amphipoda							•
	Brachyura	•						•
	Caridea	•						
	Copepoda			•				
	Calanoidea	•		•				
	Crangonidae		•					
	Crustacea	•	•	•	•	•	•	•
	Decapoda Natantia							•
	Dichelopandalus bonnieri		•					
	Euphasiacea	•		•				•
	Gnathia sp. (larvae)		•					
	Hippolytidae	•						
	Maia sp.							•
	Meganyctiphanes norvegica		•					
	Mysidacea	•						
	Nephrops norvegicus		•					
	Oplophoridae		•					
	Paguridae		•					
	Palaemonidae		•					
	Pandalidae			•				
	Pasiphaea sivado		•					
	Processidae	•						
Mollusca	*Alloteuthis* sp.	•						
	Alloteuthis subulata	•		•				
	Bivalvia	•						
	Cephalopoda	•	•	•	•	•	•	•
	Eledone cirrhosa	•						
	Loliginidae		•					
	Loligo forbesi	•		•	•			
	Loligo sp.	•						
	Loligo vulgaris	•						

(continued on next page)

Table 3 (continued) List of identified prey types and species from *Loligo forbesi* stomach contents

		Geographic area						
Group	Taxonomic description	Northwest Spain	Ireland	Scotland	England	Faroes	Portugal	Azores
	Octopodidae		•	•				•
	Octopus vulgaris	•						
	Sepioidea							
	Sepiolidae		•	•				
	Teuthoidea							•
Polychaeta	*Nereis pelagica*		•					•
	Nereis sp.							
	Polychaeta			•				
	Sternaspid							•
Chaetognatha	*Sagitta* sp.							•

Source: Compiled from Martins 1982, Collins et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Stowasser et al. 2004.

Table 4 Reported predators of *Loligo forbesi*

Type/species	Geographic area	References
Demersal fish		
Gadus morhua	Scotland	Daly et al. 2001
Lophius piscatorius	Scotland	Daly et al. 2001
Seals		
Halichoerus grypus	Scotland	Pierce et al. 1991
Phoca vitulina	Scotland	Brown & Pierce 1998
Cetaceans		
Phocoena phocoena	Netherlands	Santos et al. 2005b
Physeter macrocephalus	Scotland, Denmark	Santos et al. 1999
	Iceland, Norway	Santos et al. 2002

Loligo vulgaris

Biogeographic distribution The European squid *Loligo vulgaris* (Lamarck, 1798) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from South Africa (20°S) to north-western Scotland (57°N). It also occurs in the southern North Sea and the Mediterranean (Roper et al. 1984). It is most abundant in waters between southern Portugal (36°N) and the English Channel (52°N); in this area there appears to be a gradual increase in abundance with decreasing latitude (Cunha et al. 1995). It is also found in Madeiran waters (Clarke & Lu 1995). It is widely distributed in the Mediterranean, particularly in the Catalan Sea (Sánchez & Martin 1993), the Adriatic (Flamigni & Giovanardi 1984), Greek seas (Lefkaditou et al. 2001) and the Levantine Basin (Ruby & Knudsen 1972). In U.K. waters, it is moderately abundant only in the English Channel (Robin & Boucaud-Camou 1993). It is relatively scarce in the Irish Sea and southern North Sea, although it often appears in mixed catches with *L. forbesi* during late spring and summer. In Scottish waters it is typically very rare, with only one or two individual *L. vulgaris* appearing sporadically in samples from *L. forbesi* catches during certain years (Pierce et al. 1994a).

Loligo vulgaris is typically a benthic spawner and attaches egg clusters to hard substrata. At other times, it is more pelagic in behaviour, for example hunting in the water column in the circumlittoral and upper bathyal regions (Worms 1983). Off the Portuguese coast and in the Mediterranean, it occurs in shallow waters (<100 m deep) (Sánchez & Martin 1993, Cunha et al. 1995, Salman et al. 1997, Sánchez et al. 1998). Smaller numbers are also found over the continental slope (200–300 m), especially near coasts with steep bottom slopes in Algerian waters (Mangold-Wirz 1963) and the Ionian Sea (Lefkaditou et al. 2001).

In the North Sea, *L. vulgaris* usually appears in small numbers in late spring–summer, occasionally reaching the Kattegat and western Baltic (Jaekel 1937, Muus 1959, Hornborg 2005). Large population fluctuations have been reported in some areas (Amaratunga 1983) and changes in SST may be involved (Chen et al. 2006). Adult and juvenile squid inhabit waters with temperatures ranging from 12.5 to 20°C and are often associated with relatively low salinities (Mangold-Wirz 1963). In the North Atlantic this species has been reported at salinities of 30–36‰ (Tinbergen & Verwey 1945) and it has also been found in brackish conditions in the Sea of Marmar (Unsal et al. 1999) and the River Tagus estuary (unpublished data). However, in the Mediterranean, it has also been recorded in much higher salinities of 37.7–38.15‰ (Salat et al. 1978), indicating that it may be able to adapt to local conditions.

Biology and ecology *Loligo vulgaris* is an annual, semelparous species (Mangold 1987) showing extended breeding seasons with one, two or several pulses of recruitment, depending on locality. At the northern and eastern edges of its range, in the North Sea, English Channel and central Mediterranean, the spawning period is relatively short (Tinbergen & Verwey 1945, Moreno et al. 2002, Sifner & Vrgoc 2004). Further south and west, *L. vulgaris* spawns throughout the year, in Atlantic waters between north-western Spain and Africa (Baddyr 1988, Coelho et al. 1994, Guerra & Rocha 1994, Moreno et al. 1994, Rocha 1994, Bettencourt et al. 1996, Villa et al. 1997, Raya et al. 1999, Moreno et al. 2002) and the western Mediterranean (Mangold-Wirz 1963, Worms 1983). The timing of spawning also varies with locality. In the English Channel, *L. vulgaris* spawns in winter (November to April, peaking in February; Moreno et al. 2002). In Portuguese waters and on the Saharan Bank, it spawns all year but with two peak periods, in autumn–winter and late spring (Moreno et al. 1994). Further east, in the Adriatic and Greek seas, this species spawns during winter–spring (January to May and November to May, respectively) peaking in April (Mangold-Wirz 1963, Worms 1983).

Loligo vulgaris is a relatively large loliginid squid, very similar in size and appearance to *L. forbesi*. It also matures over a range of sizes, with males generally growing bigger than females (although again, some males mature at small sizes). In the north-western Atlantic, maximum lengths of 55 cm ML for males and 37 cm ML for females have been recorded (unpublished data). The largest *L. vulgaris* have been caught off the West African coast, with reported maximum values of 64 cm ML for males and 54 cm ML for females (Raya et al. 1999).

The reproductive system of *L. vulgaris* is identical to that of *L. forbesi*; a detailed description is provided by van Oordt (1938). Fertilisation is internal; during mating, the male seizes a female by the head and transfers spermatophores to a buccal receptacle via the penis and hectocotylus. Oogenesis is asynchronous and mature ovaries exhibit polymodal oocyte size distribution, indicating a reproductive strategy of ‘intermittent terminal spawning’, where oocyte maturation and egg-laying occur as a number of discrete events during an extended spawning season (Rocha 1994). During spawning, female *L. vulgaris* secrete a protective mucous coating around their eggs, forming egg strings 6–16 cm long (Worms 1983). Female squid are known to lay egg strings close to others, forming ‘clusters’ containing up to 40,000 eggs, probably as a result of visual or chemical stimuli (Mangold-Wirz 1963). The sizes of mature oocytes of *L. vulgaris* appear to vary according to location, with the largest values (2.3–2.8 mm) found in Galician and north-western Mediterranean waters (Mangold-Wirz 1963, Guerra & Rocha 1994, Sifner & Vrgoc 2004) and the smallest values (1.9–2.2 mm) found off southern Portugal and the North African coasts (Coelho et al. 1994, Laptikhovsky 2000). The potential fecundity of female *L. vulgaris*, based on the total numbers of developing and mature oocytes in the ovary and oviducts, ranges from 10,000 to 42,000 eggs (Baddyr 1988, Coelho et al. 1994, Guerra & Rocha 1994, Laptikhovsky 2000). Maximum fecundity, based on mature oocytes only, is reported to be only about 7000 eggs per individual (Worms 1983) but this could be an underestimate if several egg batches mature sequentially.

Egg clusters are found throughout the year, but more frequently between June and August, during a peak in spawning activity, with some geographic variation (Baddyr 1988, Villa et al. 1997). They are typically attached to hard substrata in shallow water (6–120 m depth) over sand and silt bottoms (Worms 1983, Baddyr 1988). There are no confirmed records of *L. vulgaris* eggs in U.K. waters, although spawning is thought to occur in the English Channel. Further south, confirmed records in northern French, Galician and Portuguese waters (15–80 m depth) were reported by Pereira et al. (1998). Fixed egg clusters of *L. vulgaris* have been reported as shallow as 2 m (Villa et al. 1997).

The rate of embryonic development of *L. vulgaris* is influenced by water temperature and oxygen content (Worms 1983). For example, development times of 40–45 days at 12–14°C, 30 days at 17°C and 26–27 days at 22°C have been reported (Mangold-Wirz 1963, von Boletzky 1979). Photoperiod also appears to impact embryonic development, with most embryos hatching after a fixed light period ends (Paulij et al. 1990). Sen (2004) reported a 100% hatching success rate for a 12-h light plus 12-h dark regime but only a 52% success rate for a 24-h light regime. However, the duration of embryonic development did not appear to be affected by photoperiod.

There are no confirmed records of *L. vulgaris* paralarvae in U.K. waters, although they are likely to be included in the *Loligo* sp. collected in plankton samples in the English Channel (Collins et al. 2002). They have not been found in the cooler neritic waters around Scotland, in the northern North Sea or the Rockall Trough area (Yau 1994). Further south, records of *L. vulgaris* paralarvae from samples off Galicia and Portugal have been reported (Moreno & Pereira 1998, Piatkowski 1998, González et al. 2005, Moreno et al. 2009). They appear to overwinter offshore, move inshore during summer (Moreno & Sousa Reis 1995, Moreno et al. 2009) and undergo diurnal vertical migrations, appearing near the surface during the night (Sousa Reis 1989). SST ranges of 11–20°C have been reported for *L. vulgaris* paralarvae (Mangold-Wirz 1963, Moreno & Sousa Reis 1995, Moreno & Pereira 1998), with optimum values at 13–15°C (Moreno et al. 2009).

The early juvenile stages of *L. vulgaris* feed mainly on planktonic crustaceans, particularly copepods, mysids, euphausids and shrimp larvae (Nigmatullin 1975, Worms 1983). As the squid grow larger, fish become a greater proportion of the overall diet (Rocha et al. 1994). Adult *L. vulgaris* also prey, to a lesser degree, on polychaetes, cephalopods and crustaceans (Coelho et al. 1994, Guerra & Rocha 1994, Pierce et al. 1994c, Rocha et al. 1994). The ranges of observed prey species and types of *L. vulgaris* are similar to those reported for *L. forbesi* (Pierce et al. 1994c, Rocha et al. 1994). There is also evidence that the prey composition of *L. vulgaris* may vary seasonally due to changes in prey availability (Rocha et al. 1994).

Short-fin squids (family Ommastrephidae)

Short-fin or flying squids (ommastrephids) belong to the Suborder Oegopsina and are characterised by lacking a membrane of tissue over their eyes. Ommastrephid squids are typically medium-sized, muscular, powerful swimmers and have high-quality flesh suitable for human consumption. A number of species are of commercial importance. They are typically oceanic, deep-water squids although a few species sometimes venture occasionally into shallow waters. Many ommastrephid species exhibit diurnal vertical migratory behaviour, inhabiting deep waters during the day and moving to surface waters to feed at night. Four genera and four species of ommastrephid squid are found in the north-eastern Atlantic.

Illex coindetii

Biogeographic distribution The broadtail short-fin squid *Illex coindetii* (Verany, 1839) is an oceanic, benthopelagic species occurring in subtropical/temporate, offshore and coastal waters and continental slope areas and is widely distributed in the eastern Atlantic to 30°W and from South Africa (17° S) to the North Sea (60°N) (Clarke 1966, Lu 1973). It is quite common in the Mediterranean (Mangold & von Boletzky 1987) and Galician waters (González et al. 1994) and is also found in the western Atlantic Ocean, from the Caribbean Sea (9°N) to the eastern seaboard of North America (37°N). The limit of its southern distribution is undefined (Roper et al. 1984). In U.K. waters, *I. coindetii* is often found in the Celtic Sea, south-west of Cornwall (Arvanitidis et al. 2002).

Illex coindetii occurs over a considerable depth range, from surface waters down to greater than 800 m. The optimal depth range, where maximum concentrations of this squid have been observed, is reported to be 100–400 m and 100–600 m depending on locality (Sánchez et al. 1998). It is usually found close to soft (mud/sand/detritic) bottoms, often covered by *Funiculina* sp., in the lower sublittoral and upper bathyal zones (Mangold-Wirz 1963, Roper et al. 1984). The occurrence of *I. coindetii* has also been associated with decapod crustaceans, for example *Parapenaeus longirostris*, certain fish species, including *Merluccius merluccius* and *Micromesistius poutassou* (Jereb & Ragonese 1991a, Rasero et al. 1996, Dawe & Brodziak 1998) and another short-fin squid, *Todaropsis eblanae* (Mangold-Wirz 1963, Rasero et al. 1996). Adult squid are known to undergo diurnal vertical migrations in the water column, from close to the seabed during daylight hours to just below the surface at night (Ragonese & Bianchini 1990, Sánchez et al. 1998). The distribution and abundance of *I. coindetii* in certain areas appears to be influenced by particular hydrographic conditions and frontal zone movements (Jereb et al. 2001).

Biology and ecology In the wild, *Illex coindetii* exhibits extended spawning periods, ranging from a few days to several weeks, and it is considered to be an 'intermittent spawner' (González et al. 1996a). Variable seasonal peaks in maturation and spawning activity occur, depending on locality. For example, in the Mediterranean, maturity peaks in spring and autumn are apparent (Sánchez et al. 1998, Belcari et al. 1999), whereas in the north-eastern Atlantic, a summer (July–August) peak has been observed (González et al. 1996a). According to Hernández-Garcia (2002), water temperature is the main factor influencing the timing of reproduction. Correlations between the timing of peak spawning activity and environmental conditions (e.g., temperature, food availability) have also been observed in populations of *I. coindetii* in the Mediterranean (Arvanitidis et al. 2002).

Illex coindetii is a relatively small ommastrephid squid. It matures over a range of sizes, with females generally growing larger than males. Unusually large specimens (>25 cm ML) are occasionally reported in the Atlantic (Roper & Mangold 1998) and Mediterranean (Arvanitidis et al. 2002). Across its range, however, the majority of mature *I. coindetii* are typically far smaller (<20 cm ML). Estimates of longevity based on length-frequency and statolith analyses indicate maximum life spans of 6–18 mo for this species, depending on locality (Sánchez 1982, González et al. 1994b, Jereb & Ragonese 1995, Arkhipkin 1996).

Fecundity in ommastrephid squids is relatively high. Female *I. coindetii* are typical in this respect, being capable of producing 50,000–200,000 mature eggs. A maximum of 800,000 oocytes was reported by Sánchez et al. (1998). The eggs are relatively small, ranging from 0.8 to 1.3 mm (von Boletzky et al. 1973, Hernández-Garcia 2002). Although egg masses of *Illex* spp. have never been found in nature, observations of the closely related *I. illecebrosus* 'spawning' in captivity, producing gelatinous egg masses whilst swimming in open water (Durward et al. 1980, O'Dor & Balch 1985), indicate that species of the genus *Illex* may be pelagic spawners. According to O'Dor & Balch (1985), the gel coating appears to function as a buoyancy mechanism, regulating the sinking rate of the eggs in accordance with ambient conditions, particularly temperature. As a result, *Illex* eggs could be suspended in the mesopelagic zone for days, perhaps maintaining them at optimal temperatures for embryonic development, a possible explanation for why ommastrephid eggs are seldom found in nature (O'Dor & Balch 1985). The eggs of *I. illecebrosus* require temperatures above 13°C for successful embryonic development (O'Dor et al. 1982).

The diet of *Illex coindetii* includes various fish, crustacean and cephalopod species, in decreasing order of importance. The main components are usually related to local prey abundance and availability, but they are also influenced by the size of the feeding squids. Crustaceans are relatively more important in the diet of smaller squid, with cephalopods and fish becoming increasingly important as the squids grow larger (Castro & Hernández-García 1995). Small, juvenile squids exhibit a larger proportion of euphausids in the diet, an indication of pelagic feeding, whereas adult squid seem to take both pelagic and benthic species (Castro & Hernández-García 1995). Prey species taken include myctophids, anchovies, pearlside, blue whiting and mackerel (Sánchez 1982, Ovcharov et al. 1985, Chesalin 1987, Rasero et al. 1996, Lordan et al. 1998, Sánchez et al. 1998, Lelli et al. 2005). *Illex coindetii* is also cannibalistic, particularly at high densities (Dawe 1988) and where fish and other prey species are scarce (Dawe & Brodziak 1998). *I.coindetii* is in turn preyed on by a number of marine mammal species, including *Delphinus delphis*, *Tursiops truncatus* and *Stenella coeruleoalba* (González et al. 1994, Santos et al. 2004, 2005a).

Ommastrephes bartramii

Biogeographic distribution The red flying squid *Ommastrephes bartramii* (Lesueur, 1821) is an oceanic, mesopelagic species occurring in temperate/subtropical coastal waters and continental slope areas. It has a discontinuous, circumglobal distribution, being absent from the tropics. In the South Atlantic, it is found at 14–27°S off Africa (Roeleveld 1989) and at 27–45°S off South America (Brunetti et al. 1999). In the North Atlantic, it is found at 44–65°N, as far north as Iceland, although it is rarely caught in the North Sea and the Mediterranean (Roper et al. 1984). It appears to be particularly abundant in the eastern Atlantic off North Africa, between the Azores and the Canary Islands (Pinchukov 1975).

Although *O. bartramii* is very widely distributed, reproduction has only been reported in, and may be limited to, warm equatorial and subtropical waters, between 40°S and 25°N, with squids migrating elsewhere to feed (Aleksandronetz et al. 1983). Zuev et al. (1976) suggested a thermal range of 14–17°C for this species. It is believed to undergo considerable diurnal vertical migrations, from 560 to 1050 m depth during hours of daylight to less than 100 m depth at night (Moiseev 1987, 1991). Upwards migration speeds of 5 m.min^{-1}, and overall migration times of up to 2.5 h have been reported, depending on the starting depth (Moiseev 2001). During the night, *O. bartramii* appears to avoid shallow waters above seamounts (Moiseev 2001) and tends to group together in small shoals of fewer than 30 individuals (Zuev & Nigmatullin 1975).

Biology and ecology *Ommastrephes bartramii* is a medium-sized ommastrephid squid. Females generally mature at greater than 40 cm ML and can reach 69 cm, growing much larger than males (36 cm). Very little biological information is available on *O. bartramii* in the North Atlantic. Based on research on Pacific stocks, it appears that *O. bartramii* is an annual species and that females grow faster than males (Yatsu et al. 1997, Yatsu 2000).

Reproduction in *O. bartramii* is an annual event, with timing depending on location. For example, spawning occurs in late summer/early autumn in the Atlantic and in spring in the North Pacific. There are no confirmed records of *O. bartramii* egg masses in nature. Sakurai et al. (1995) developed an artificial fertilization technique for observing embryonic development in *O. bartramii*. Females are thought to produce more than 300,000 eggs, arranged in floating ribbons. The eggs and newly hatched rynchoteuthis paralarvae measured about 1 mm (ML) (Nigmatullin 1987). The latter inhabit open water 0–250 m deep (Zuev & Nesis 1971). Excellent descriptions of *O. bartramii* paralarvae were provided by Young & Hirota (1990).

Nigmatullin (1987) suggested five developmental changes in the ecological niche of *O. bartramii* (Table 5). *O. bartramii* is considered to be an important food resource for a number of marine

Table 5 Developmental and ecological changes in *Ommastrephes bartramii*

Size (mantle length, cm)	Developmental stage	Habitat	Prey
0.1	Egg mass	Plankton	N/A
0.1–0.8	Paralarva	Plankton	Macroplankton
1.0–2.5	Juvenile	Plankton	Mesozooplankton
3.0–8.0	Juvenile	Micronekton	Macrozooplankton
>15.0	Subadult/adult	Necton	Fish and squid

Source: From Nigmatullin 1987.

predators, including large fish (Bello 1991, 1996, Carrassòn et al. 1992), seabirds (den Hartog & Clarke 1996) and marine mammals (Carlini et al. 1992, Clarke et al. 1993, Hernández-Garcia 2002).

Todarodes sagittatus

Biogeographic distribution The European flying squid *Todarodes sagittatus* (Lamarck, 1798) is a neritic and oceanic, pelagic species occurring in temperate/subarctic/arctic, deep offshore, coastal waters and continental slope areas and is widely distributed in the eastern Atlantic to 40°W and the Arctic Ocean to 13°S (Guerra 1992). It is also found in the North Sea and is common in the Mediterranean (Roper et al. 1984). *Todarodes sagittatus* is found in both shallow coastal and deep oceanic environments. It has been recorded from surface waters to estimated depths of 4500 m (Collins et al. 2001) although most specimens have been caught in waters less than 1000 m deep (Roper et al. 1984). In common with other ommastrephids, it is known to undergo considerable diurnal vertical migrations, occurring at depths down to 2500 m during hours of daylight to surface waters at night (Mangold-Wirz 1963, Clarke 1966, Korzun et al. 1979, Nesis 1987). Significant strandings of this species sometimes occur at various beaches (Berdar & Cavallaro 1975). Spawning depths of 70–800 m have been reported for *T. sagittatus* in Portuguese waters (Anonymous 2005).

In the northern Atlantic, *T. sagittatus* is known to undergo extensive seasonal feeding and spawning migrations (Shimko 1989). Between early June and December, large aggregations of these squid appear around Iceland and the Faroe Islands and off the north-western coast of Norway (Wiborg 1972, Sundet 1985). It is often caught in deep waters west of Scotland and Ireland (Boyle et al. 1998, Lordan et al. 2001) but less commonly in shallow coastal waters. In certain years, however, huge aggregations of this species have been observed in the North Sea, around Shetland and just off the Scottish coast (Stephen 1944, Joy 1990). Large-scale strandings of *T. sagittatus* also occur during these events (Berdar & Cavallaro 1975). By late December, the squid have started migrating into the deeper, offshore waters of the continental slope where they overwinter and spawn. Elsewhere, migratory patterns are highly variable, depending on the geographic area. For example, in fishing grounds around Madeira and elsewhere in the eastern central Atlantic, *T. sagittatus* are only caught in large numbers between March and May (Borges & Wallace 1993, Piatkowski et al. 1998, Arkhipkin et al. 1999). However, no evidence of similar migrations of this species has been found in the Mediterranean (Quetglas et al. 1998a).

Biology and ecology *Todarodes sagittatus* is generally considered to be an annual species (Rosenberg et al. 1990, Arkhipkin et al. 1999), although a 2-yr life cycle has also been suggested (Lordan et al. 2001). Breeding seems to be protracted, with two peaks occurring, in spring and in autumn (Wiborg & Beck 1984, Roper et al. 1984, Rosenberg et al. 1990, Lordan et al. 2001). According to Borges & Wallace (1993), there is evidence of at least two *T. sagittatus* populations coexisting in north European waters. In years of abundance, *T. sagittatus* moves inshore during summer and autumn, when it is caught in large numbers (Wiborg & Gjøsæter 1981, Sundet 1985, Joy 1989, Lordan et al. 2001). Catches in northern coastal waters are made up mainly of immature female specimens, which suggests that inshore migration is mainly carried out by females, probably for feeding (Wiborg et al. 1982, Sundet 1985, Joy 1989, Borges & Wallace 1993, Boyle et al. 1998).

Todarodes sagittatus is a medium- to large-sized ommastrephid squid. It is reported to reach 75 cm ML, with females growing larger than males (Roper et al. 1984). Confirmed maximum sizes of 49 and 64 cm in the North Atlantic and 39 and 60 cm in the Mediterranean have been reported for this species (Cuccu et al. 2005). According to Nesis (1987), individual *T. sagittatus* larger than 50 cm ML may be at least 2 yr old.

Age at maturity in this species is thought to be 12–15 mo. Annual spawning events of *T. sagittatus* are thought to occur in deep waters adjacent to the continental slopes. These occur in late winter–spring in north European waters, around March–April in the Bay of Biscay, mainly between October and December in Portuguese waters and September–November in the western Mediterranean (Roper et al. 1984, Piatkowski et al. 1998, Quetglas et al. 1998a, Arkhipkin et al. 1999, Lordan et al. 2001). Females always outnumber males in fished samples. Mature males are relatively scarce but are usually found throughout the year, while mature females are more abundant but only found during the spawning season. Female *T. sagittatus* may produce 12,000–18,000 eggs (Laptikhovsky & Nigmatullin 1999).

Todarodes sagittatus is an opportunistic and aggressive, highly mobile squid that will consume any potential prey it can overpower. Its diet is typically composed of fish, crustaceans and cephalopods, in decreasing order of importance. Cannibalism is also relatively common in this species. In the North Atlantic, *T. sagittatus* feeds voraciously on a variety of small fish, particularly young herring (*Clupea harengus*) and cod (*Gadus morhua*) (Brieby & Jobling 1985, Joy 1990, Piatkowski et al. 1998, Quetglas et al. 1998a. *Todarodes sagittatus* is itself preyed on by a number of fish and marine mammal species (Table 6).

Todaropsis eblanae

Biogeographic distribution The lesser flying squid *Todaropsis eblanae* (Ball, 1841) is a neritic, demersal species occurring in subtropical/temporate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from South Africa (40°S) to the North Sea (61°N). It has also been reported in the Mediterranean (Mangold-Wirz 1963, Quetglas et al. 2000). A distinct population also occurs in the Indo-Pacific region (Nesis 1979), off the south coast of Australia (Lu 1982, Roper et al. 1984). *Todaropsis eblanae* appears to be primarily a benthic species, associated with soft (mud-sand) bottoms, mainly in the lower sublittoral and upper bathyal zones of the continental shelf (Clarke 1966). Unlike other ommastrephid species, there is no evidence that it regularly ascends to the surface or approaches shorelines. It occurs in waters of 9–18°C and depths of 20–780 m (Guerra 1992). In Italian waters, a depth range of 30–700 m has been reported (Belcari et al. 1999).

Todaropsis eblanae is commonly caught in Galician waters (González et al. 1994), in the Celtic Sea, south-west of Ireland (Lordan et al. 1998), in Portuguese waters and in the Bay of Biscay (Robin et al. 2002). In some years, it can be very widespread and abundant in the north-eastern Atlantic, second only to *Loligo forbesi* in overall squid catches (Stephen 1944, Lordan et al. 2001). Further north, this species is relatively scarce, although huge aggregations do occur infrequently in the northern North Sea, around Shetland and just off the Scottish coast (Stephen 1944, Hastie et al. 1994). These historical phenomena may be linked to hydrographical anomalies such as incursions of high-salinity Atlantic seawater into the North Sea (Hastie et al. 1994).

Biology and ecology *Todaropis eblanae* is a relatively small ommastrephid squid. It is thought to live for 1–2 yr and matures over a range of sizes, with females generally growing larger than males. Maximum sizes of 22 and 29 cm ML have been reported for males and females, respectively (Robin et al. 2002). Estimates of size at maturity for this species range from 12 to 13 cm ML for males and from 14 to 20 cm ML for females, depending on the locality (González et al. 1994, Hastie et al. 1994). Total potential fecundity estimates of female *T. eblanae* range from 28,000 eggs in Scottish

Table 6 Recorded marine predators of selected cephalopod species found in U.K. waters

	Predator[a]	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Illex coindetii*	*Ommastrephes bartramii*	*Todarodes sagittatus*	*Todaropsis eblanae*	*Architeuthis* spp.	*Brachioteuthis riisei*	*Galiteuthis* spp.	*Gonatus* spp.	*Gonatus fabricii*	*Histioteuthis* spp.	*Histioteuthis bonnellii*	*Histioteuthis reversa*	*Onychoteuthis* spp.	*Teuthowenia* spp.	*Teuthowenia megalops*	*Neorossia* spp.	*Redeletiola* spp.	*Rossia macrosoma*	*Sepiola atlantica*	*Sepia officinalis*	*Sepia elegans*	*Eledone cirrhosa*	*Haliphron atlanticus*	*Octopus vulgaris*
Cephalopods																												
Loligo forbesi	X	X	X																						X		X	
Loligo vulgaris	X	X	X																					X				
Illex coindetii	X	X		X		X	X					X									X				X			
Onychoteuthis banksii								X																				
Todarodes sagittatus						X																						
Fishes																												
Alepisaurus ferox							X	X																				
Beryx splendens						X																						
Centroscymnus coelolepis					X	X		X																				
Conger conger				X																							X	
Coryphaenoides armatus												X																
Echiichthys vipera			X																									
Gadus morhua		X										X													X			
Galeus melastomus						X																						
Heptranchias perlo				X																								
Isurus oxyrinchus								X																				
Lamna nasus						X							X															
Lophius piscatorius		X																							X			
Melanogrammus aeglefinus																									X			
Merluccius merluccius	X																											
Micromesistius poutassou				X																								
Molva molva																									X			
Muraena helena																											X	

(continued on next page)

Table 6 Recorded marine predators of selected cephalopod species found in U.K. waters

	Predator[a]	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Illex coindetii*	*Ommastrephes bartramii*	*Todarodes sagittatus*	*Todaropsis eblanae*	*Architeuthis* spp.	*Brachioteuthis riisei*	*Galiteuthis* spp.	*Gonatus* spp.	*Gonatus fabricii*	*Histioteuthis* spp.	*Histioteuthis bonnellii*	*Histioteuthis reversa*	*Onychoteuthis* spp.	*Teuthowenia* spp.	*Teuthowenia megalops*	*Neorossia* spp.	*Redeletiola* spp.	*Rossia macrosoma*	*Sepiola atlantica*	*Sepia officinalis*	*Sepia elegans*	*Eledone cirrhosa*	*Haliphron atlanticus*	*Octopus vulgaris*
Mustelus mustelus			X																				X					
Phycis blennoides				X																								
Pollachius virens				X																								
Prionace glauca						X	X	X															X		X			
Reinhardtius hippoglossoides												X																
Sebastes marinus												X																
Seriola lalandi							X																					
Seriola dumerili			X									X																
Sphyrna zygaena								X																				
Somniosus spp.								X																				
Thunnus alalunga						X		X																				
Thunnus albacares				X																								
Torpedo spp.			X																									
Xiphias gladius			X	X	X	X		X																				
Zeus capensis							X																					
Birds																												
Calonectris diomedea					X																							
Diomedea spp.								X																				
Fratercula arctica												X																
Fulmarus glacialis												X																
Phoebetria fusca								X																				

Mammals																												
Arctocephalus pusillus																							X					
Balaenoptera musculus												X																
Cysophora cristata												X																
Delphinus delphis	X		X	X		X	X				X		X									X			X		X	
Globicephala macrorhynchus						X																						
Globicephala melas			X	X		X						X										X			X		X	
Grampus griseus						X	X															X	X		X		X	
Halichoerus grypus		X																										
Hyperoodon ampullatus	X					X	X					X																
Kogia breviceps		X			X	X			X					X	X													
Monachus monachus																							X					
Monodon monoceros												X																
Phoca groenlandica						X						X																
Phoca vitulina		X																							X			
Phocoena phocoena	X	X	X																			X			X			
Physeter macrocephalus		X			X	X		X			X	X	X	X				X							X	X	X	
Pseudorca crassidens					X																							
Stenella attenuata								X																				
Stenella coeruleoalba						X																						
Tursiops truncatus	X		X	X		X	X																		X		X	
Ziphius cavirostris					X	X						X																

Sources: Grimpe 1925, Hjort & Ruud 1929, Grieg 1930, Nesis 1965, Scott & Tibbo 1968, Dexter 1969, Clarke & Stevens 1974, Macalaster 1976, Wiborg 1980, Martins 1982, Sánchez 1982, Amaratunga 1983, Bergström & Summers 1983, Kristensen 1984, Clarke & Pascoe 1985, Ovcharov et al. 1985, Chesalin 1987, Dawe 1988, Lydersen et al. 1989, Bello 1991, 1996, Castley et al. 1991, Hislop et al. 1991, Carrasson et al. 1992, Falk et al. 1992, Clarke et al. 1993, Clarke & Goodall 1994, González et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Castro & Hernández-Garcia 1995, Hernandez-Garcia 1995, Matallanas et al. 1995, den Hartog & Clarke 1996, Klages 1996, Pierce & Santos 1996, Rasero et al. 1996, Clarke & Pascoe 1997, Martin & Christiansen 1997, Potelov et al. 1997, Hanlon & Messenger 1998, Lordan et al. 1998, MacNaughton et al. 1998, Sánchez et al. 1998, Hjelset et al. 1999, Santos et al. 1999, 2001a, 2002, 2004, 2006a, Brown et al. 2001, Daly et al. 2001, Velasco et al. 2001, López 2002, Hernandez-Garcia 2002, Salman et al. 2002, Cherel & Duhamel 2004, Garthe et al. 2004, Lelli et al. 2005, De Pierrepont et al. 2005,

[a] Not all predator species found in north-eastern Atlantic waters.

waters (Hastie et al. 1994) to 275,000 eggs in west African waters (Laptikhovsky & Nigmatullin 1999). Up to 10,000 mature eggs, ranging in size from 0.8 to 2.5 mm, have been observed in individual female squids (Mangold-Wirz 1963). The reported maximum number of eggs spawned ranges from 13,200 to 34,400 per female (Hastie et al. 1994, Laptikhovsky & Nigmatullin 1999).

Spent females are rarely found in the wild, indicating that *T. eblanae* is a terminal spawner. Annual spawning events, between spring and autumn (possibly peaking in summer), have been reported in the North Atlantic and Mediterranean (Mangold-Wirz 1963, González et al. 1994, Hastie et al. 1994, Arkhipkin & Laptikhovsky 2000, Robin et al. 2002).

The diet of *T. eblanae* includes, in decreasing order of importance, fish, crustaceans and other cephalopods. Cannibalism has also been reported in this species (Rasero et al. 1996, Lordan et al. 1998). *Todaropis eblanae* is itself preyed on by a number of fish and marine mammals (Table 6).

Other squid species

In addition to the commercially important ommastrephid squids, there are a number of other oegopsid species of various sizes found in the north-eastern Atlantic. At present, none of these are exploited commercially, although certain species are widespread and abundant, suitable for human consumption and are considered to have fishery potential. Five families, six genera and seven species of squid in this category are found in the north-eastern Atlantic:

Architeuthis dux

Biogeographic distribution The giant squid *Architeuthis dux* (Steenstrup, 1857) and its congeners are oceanic, cosmopolitan mesopelagic species found in relatively high abundance in subtropical/temporate, deep, offshore waters in the Atlantic and Indo-Pacific (Roper et al. 1984). Very few specimens of *Architeuthis* spp. in good condition have ever been found and consequently little is known about their taxonomy, biology and ecology. Based on 34% of verified worldwide reports (115 specimens), it is assumed that they are relatively abundant in the north-eastern Atlantic (Guerra et al. 2004). In U.K. and Irish waters, specimens are very occasionally caught by fishers or washed up on the coastlines of the northern North Sea, particularly Scotland (Ritchie 1918, 1920, 1922, Rae & Lamont 1963, Boyle 1986, Collins et al. 1997b, Collins 1998, Guerra et al. 2004a). Collins (1998) lists 25 known *Architeuthis* strandings and by-catches in the U.K. and Ireland.

Biology and ecology *Architeuthis dux* is one of the largest invertebrates known, with the only other possible contenders being other *Architeuthis* spp. and the Antarctic colossal squid *Mesonychoteuthis hamiltoni* (Robson, 1925). Maximum sizes of 6 m ML and 20 m total length (TL) have been reported for this species (Roper et al. 1984). Around the world, juvenile architeuthids are known to be predated by a number of marine mammals (notably the sperm whale *Physeter macrocephalus*, but also *Stenella attenuata*) (Clarke & Pascoe 1997, Robertson & Chivers 1997), seabirds (*Diomedea* spp., *Phoebetria fusca*) (Roper & Young 1972, Rodhouse et al. 1987), fish (*Alepisaurus ferox*, *Centroscymnus coelolepis*, *Isurus oxyrinchus*, *Prionace glauca*, *Somniosus* spp., *Sphyrna zygaena*, *Thunnus alalunga* and *Xiphias gladius*) (Roper & Young 1972, Toll & Hess 1981, Arkhipkin & Nigmatullin 1997) and other squid (*Onychoteuthis banksii*) (Arkhipkin & Nigmatullin 1997). The only confirmed predator of adult *Architeuthis* spp. is the sperm whale *Physeter macrocephalus* (Clarke & Pascoe 1997, Santos et al. 2002). Remains of large architeuthids have also been found in the stomachs of deep-water sleeper sharks (*Somniosus* spp.), although it is not known whether the squid were actively predated or already dead when scavenged on the seabed (Cherel & Duhamel 2004).

Brachioteuthis riisei

Biogeographic distribution The common arm squid *Brachioteuthis riisei* (Steenstrup, 1882) is an oceanic, cosmopolitan mesopelagic species found in deep, cool waters in all oceans except the

North Pacific and Gulf of Mexico. It is also present in the Mediterranean (Yau 1994). Larval and juvenile *Brachioteuthis* spp. are relatively common in plankton samples taken from waters west of Ireland (Collins et al. 2001). A depth range of 0 to 3000 m is reported for this species, with paralarvae found in the upper 200 m and subadults and adults occurring much deeper (Zuev & Nesis 1971, Clarke & Stevens 1974).

Biology and ecology Roper et al. (1984) report a maximum size of 4 cm ML for this species, but this is based on a few records. Young et al. (1985) provided descriptions of the eggs and larvae of a *Brachioteuthis* sp. from Hawaiian waters. In the North Atlantic, young stages of *B. riisei* are present from May to August and in February (Massy 1909). Paralarvae and juveniles are also abundant in the Rockall Trough area during May–June, indicating that hatching occurs throughout the year (Clarke 1966). Certain marine mammals are known to prey on *B. riisei*, including *Globicephala melaena*, *Hyperoodon planifrons* and *Ziphus cavirostris* (Clarke & Goodall 1994, Santos et al. 2001a). Remains of *B. riisei* have also been found in the stomachs of stranded pygmy sperm whales (*Kogia breviceps*) (Santos et al. 2006a).

Galiteuthis armata

Biogeograpic distribution The armed cranch squid *Galiteuthis armata* (Joubin, 1898) is an oceanic, bathypelagic species found in subtropical/temperate waters of the Atlantic, from Florida and the Gulf of Guinea (11° N) to Rockall Trough (60° N). It is also found in the Mediterranean but appears to be absent from the North Sea (Yau 1994). It has been recorded in Atlantic waters west of Scotland (Russell 1909).

Biology and ecology Roper et al. (1984) reported maximum sizes of 8 cm ML and 39 cm total length TL for this species, but these are based on a few records. Certain marine mammals are known to prey on *G. armata*, including *Globicephala melaena*, *Hyperoodon planifrons* and *Ziphus cavirostris* (Clarke & Goodall 1994, Santos et al. 2001a). Remains of galiteuthid squid have been found in the stomachs of sperm whales (Clarke & Pascoe 1997).

Gonatus fabricii

Biogeographic distribution The boreoatlantic armhook squid *Gonatus fabricii* (Lichtenstein, 1818) is an oceanic, mesopelagic species found in subarctic/arctic, deep offshore waters of the Arctic and North Atlantic, from Newfoundland Basin to the Norwegian Sea. The recorded southerly limits of this species are considered to be around 40°N in the western Atlantic, on the eastern seaboard of North America and 55°N in the eastern Atlantic, west of Scotland (Roper et al. 1984). It is found over a considerable depth range, from surface waters at night to depths of 3000 m during daylight hours (Kristensen 1983). According to Collins et al. (2001), juvenile *G. fabricii* are very common in plankton samples taken from waters around the United Kingdom.

Biology and ecology *G. fabricii* is a relatively small semelparous oegopsid, with males and females reaching maximum lengths of 35 and 38 cm ML, respectively (Roper et al. 1984). Maturity in both sexes occurs at about 20 cm ML. The potential fecundity of female *G. fabricii* is estimated to be approximately 10,000 eggs per individual (Bjørke & Gjøsæter 2004). Females undergo considerable morphological degeneration before spawning, including tentacle loss, arm sucker loss and swelling of arm and mantle tissues; they appear to lose ability for active locomotion and their swollen bodies may act as gelatinous floats for their egg masses that remain attached (Bjørke et al. 1997, Arkhipkin & Bjørke 1999, Bjørke & Gjøsæter 2004). In the Norwegian Sea and off Greenland, spawning occurs pelagically, possibly at great depths, between late winter and summer and hatching events occur from late March to July (Kristensen 1984, Bjørke & Gjøsæter 2004).

Juvenile *Gonatus fabricii* feed on planktonic invertebrates, including copepods, euphausids, amphipods, pteropods and chaetognaths. When the squid reach 2.5 cm ML, they develop characteristic tentacle hooks and fish become an important dietary component. Adult *G. fabricii* are apparently capable of overcoming prey larger than themselves and their diet includes, in decreasing order of importance, crustaceans, fish (*Mallotus villosus*, *Sebastes marinus*) and other cephalopods. Cannibalism has also been reported in this species (Nesis 1965, Wiborg 1980, Kristensen 1984).

Gonatus fabricii is an abundant food source that is exploited by a large number of marine predators in the Arctic and North Atlantic (see Bjørke 2001 for a review). These include several species of whale (*Globicephala melaena*, *Hyperoodon ampullatus*, *Monodon monoceros*, *Physeter macrocephalus*, *Ziphius cavirostris*) (Hjort & Ruud 1929, Grimpe 1925, Nesis 1965, Santos et al. 1999, 2001a, 2002), seals (*Cysophora cristata*, *Phoca groenlandica*) (Potelov et al. 1997, Lydersen et al. 1989), seabirds (*Fratercula arctica*, *Fulmaris glacialis*) (Falk et al. 1992, Garthe et al. 2004), fish (*Coryphaenoides armatus*, *Gadus morhua*, *Histiobranchus bathybius*, *Sebastes marinus*, *Seriola dumerili*, *Reinhardtius hippoglossoides*) (Grimpe 1925, Nesis 1965, Matallanas et al. 1995, Martin & Christiansen 1997, Dawe & Brodziak 1998) and other squid (*Illex illecebrosus*) (Amaratunga 1983) (Table 6). In certain offshore areas of the North Atlantic, particularly around the Faroes and Norwegian Sea, puffins (*Fratercula arctica*) have been observed feeding almost exclusively on *G. fabricii* (Falk et al. 1992).

Gonatus steenstrupi

Biogeographic distribution The Atlantic gonate squid, *Gonatus steenstrupi* (Kristensen, 1981) is an oceanic, mesopelagic species found in boreal/subarctic, deep offshore waters of the North Atlantic, from Newfoundland Basin and the Bay of Biscay (40°N) to south-eastern Greenland and Iceland (65°N). It is found off the west coast of the British Isles but appears to be absent from the North Sea (Roper et al. 1984).

Biology and ecology *Gonatus steenstrupi* is very similar in morphology and biology to its congener *G. fabricii* and the two species co-occur in many areas and are often confused. Falcon et al. (2000) provided valuable descriptions of the early life stages of both species. These species are highly sympatric, with overlapping ranges and a considerable amount of further research is required to distinguish them properly.

Histioteuthis bonnellii

Biogeographic distribution The umbrella squid *Histioteuthis bonnellii* (Férussac, 1835) is an oceanic, mesopelagic species found in subtropical/temperate/subarctic waters of the Atlantic, from the west coast of Africa (20°S) to Greenland (65°N). It is also present in the southern Indian Ocean (30°S) and the Mediterranean, but is absent from the Gulf of Mexico and Caribbean Sea (Yau 1994). It is widely distributed in northern waters (Clarke 1966) and has been recorded off the Irish coast (Collins et al. 1997b). A depth range of 240–2200 m has been reported for this species, with mature specimens typically occurring below 1000 m (Yau 1994).

Biology and ecology Roper et al. (1984) reported a maximum size of 33 cm ML for this species, but this is based on a few records. A large mature female specimen, measuring 23 cm ML, was caught off the west coast of Ireland (Collins et al. 1997b). *Histioteuthis bonnellii* is preyed on by various species of whale (*Physeter macrocephalus*, *Hyperoodon ampullatus*, *Ziphius cavirostris*) and fish (*Prionace glauca*, *Xiphias gladius*) (Bello 1991, Hernández-Garcia 1995, Santos et al. 2001a). Sperm whales and porbeagle sharks (*Lamna nasus*) are known to feed on several histioteuthid squid species (Clarke & Pascoe 1997, Clarke & Roper 1998, Cherel & Duhamel 2004). Remains of *Histioteuthis bonnellii* have been found in the stomachs of stranded pygmy sperm whales (*Kogia breviceps*) (Santos et al. 2006a).

Histioteuthis reversa

Biogeographic distribution The reverse jewel squid *Histioteuthis reversa* (Verrill, 1880) is an oceanic, mesopelagic species found in moderately warm waters of the Atlantic, from South Africa (45° S) to south of Iceland and Newfoundland Bank (52° N). It is also present in the southern Indian Ocean (to 30° S) and the Mediterranean. It is absent from the Gulf of Mexico and rare in the Caribbean Sea (Yau 1994). According to Voss (1969), *H. reversa* occurs in greatest abundance over deep bottom slopes, near land masses and oceanic ridges.

Biology and ecology Little is known about the biology and ecology of *Histioteuthis reversa*. In the North Atlantic, young specimens (2–4 cm ML) were captured near the continental shelf, indicating spawning over the continental slope (Clarke 1966). Remains of *H. reversa* have been found in the stomachs of stranded pygmy sperm whales and sperm whales (Santos et al. 2006a,b).

Onychoteuthis banksii

Biogeographic distribution The common clubhook squid *Onychoteuthis banksii* (Leach, 1817) is an oceanic, epipelagic species with a circumglobal distribution in deep, tropical, subtropical and temperate waters, between 45°S and 65°N (Roper et al. 1984). It has not been recorded in the Mediterranean. In U.K. waters, it has been caught in the North Sea, off the Scottish coast and near the Isle of Man in the Irish Sea. According to Arkhipkin & Nigmatullin (1997), *O. banksii* is one of the most abundant epipelagic squid species found in the oceans. Paralarvae and juveniles occur mainly near the surface (<30 m), whereas larger adults are generally found 30–150 m deep (Degner 1925, Arkhipkin & Nigmatullin 1997) and are occasionally encountered as deep as 4000 m (Clarke 1966).

Biology and ecology A maximum size of 30 cm ML is reported for *Onychoteuthis banksii* (Roper et al. 1984), but this is based on a few records. The larvae are abundant in the eastern Atlantic, particularly from January to March (Roper et al. 1984). There are no records of predation on this species in U.K. waters, although specimens have been found in the stomachs of blue sharks (*Prionace glauca*) caught in Irish waters (MacNaughton et al. 1998). In other parts of the world, *O. banksii* is apparently predated by petrels (*Pteroderma* spp.) (Imber et al. 1995), fur seals (*Arctocephalus* spp.) (Klages 1996) and dolphins (*Stenella* spp.) (Fiscus 1993).

Teuthowenia megalops

Biogeographic distribution The Atlantic cranch squid *Teuthowenia megalops* (Prosch, 1847) is an oceanic, bathypelagic species found in deep, cool subarctic waters of the North Atlantic, from the Canary Islands (24°N) to Greenland (66°N). It is absent from the North Sea and Mediterranean (Yau 1994). It is reported to be widely distributed and abundant (Nesis 1987). Juvenile *T. megalops* have been recorded in plankton samples off the west coasts of Ireland, Scotland and northern Portugal (Collins et al. 2001, Santos et al. 2001c, Moreno et al. 2009).

Biology and ecology According to Nixon (1983), the lifespan of *T. megalops* is probably 2–3 yr and it can reach a size of 35 cm ML. No eggs of this species have been found in the wild. A potential fecundity of 70,000–80,000 eggs is reported based on a few preserved specimens (Nixon 1983). Hatching probably occurs at greater than 1000 m deep, followed by ontogenetic ascent (Yau 1994). Paralarvae of *T. megalops* (<1 cm ML) have been found at 1000 m and larger specimens (1–6 cm ML) at 200–300 m. There is some evidence of diel vertical migrations for juvenile and adult *T. megalops* (Yau 1994). A peak in abundance of paralarvae occurred in spring (May–June) in the Rockall Trough and in winter (February–March) in northern Portugal. Remains of *T. megalops* have been recovered from the stomachs of large fish (*Prionace glauca*, *Xiphias gladius*) (Hernández-Garcia 1995, MacNaughton et al. 1998) and stranded whales (*Globicephala melaena*, *Hyperoodon ampullatus*, *Physeter macrocephalus*, *Ziphius cavirostris*) (Clarke & Goodall 1994, Santos et al. 2001a, 2002) (Table 6).

Sepiolids

Bobtails (sepiolids), also known as dumpling or stubby squids, are a group of small-sized decapods closely related to cuttlefishes. They tend to have shorter, round mantles and possess no cuttlebone. Bobtails have a symbiotic relationship with bioluminescent bacteria that help to conceal their silhouettes from below by matching the amount of light hitting their mantles from above. In U.K. waters, sepiolids are considered to be too small to exploit and are often overlooked in catches, although certain species may be very abundant (Stephen 1944). During deep-water benthic surveys in the north-eastern Atlantic, Collins et al. (2001) found that sepiolids were predominant in cephalopod catches taken from upper continental slope stations (150–500 m deep) Four sepiolid genera and eight species are found in the north-eastern Atlantic: *Neorossia caroli, Rondeletiola minor, Rossia glaucopis, Rossia macrosoma, Sepietta neglecta, Sepietta oweniana, Sepiola atlantica* and *Sepiola aurantiaca*.

Neorossia caroli

Biogeographic distribution The carol bobtail *Neorossia caroli* (Joubin, 1902) is a deep-water, benthic species found in the eastern Atlantic, from the equator to 40–50°N (Roper et al. 1984, Nesis 1987). Further north, in U.K. waters it is very rare, although significant numbers have been caught in 400–1540 m in the Porcupine Seabight, south-west of Ireland (Collins et al. 2001).

Biology and ecology There is very little published information available about the biology and ecology of *N. caroli*. A maximum size of 6 cm ML has been reported for this species (Roper et al. 1984, Collins et al. 2001).

Rondeletiola minor

Biogeographic distribution The lentil bobtail *Rondeletiola minor* (Naef, 1912) is a neritic, nectobenthic species occurring in moderately warm, shallow coastal waters and continental shelf areas in the eastern Atlantic and Mediterranean. Its geographic range has not been determined (Roper et al. 1984). It is common in the Mediterranean and in Portuguese waters (Nesis 1987, Villanueva 1995). Further north, in U.K. waters it is very rare, although significant numbers have been caught in 150–280 m in the Porcupine Seabight, south-west of Ireland (Collins et al. 2001). It is typically found over muddy bottom substrata, at depths of 80–100 m (Roper et al. 1984).

Biology and ecology Very little is known about the biology and ecology of *R. minor*. It is a very small sepiolid species, with a maximum size of about 2 cm ML reported (Reid & Jereb 2005).

Rossia glaucopis

Biogeographic distribution The stout bobtail *Rossia glaucopis* (Lovén, 1845) is a neritic, nectobenthic species occurring in cool, coastal waters and continental shelf areas of the Arctic and North Atlantic, off Greenland, Iceland and Sptizbergen. It is found over a considerable depth range, from 10 to 1500 m, but is most common at a depth of 120 m (Yau 1994). The southerly limit of *R. glaucopis* appears to be around the northern North Sea (60°N) and it is rarely found in Scottish waters (Yau 1994).

Biology and ecology A maximum size of 4 cm ML has been reported for this species (Yau 1994). The eggs of *R. glaucopis* are relatively large (~7 mm diameter) and are laid singly but attached in clusters to empty shells, stones and other hard substrata. Hatchlings measure about 5–6 mm ML. In Scottish waters, juveniles appear in plankton samples from spring to autumn, with peak abundances in the spring, although data are scarce (Yau 1994). Adult *R. glaucopis* are hardly ever found in U.K. waters, the last confirmed record from Scottish waters being 1926 (Yau 1994).

Rossia macrosoma

Biogeographic distribution The stout bobtail *Rossia macrosoma* (delle Chiaje, 1829) is a neritic, nectobenthic species occurring in moderate and cool, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Senegal (15°N) to Greenland and the Norwegian Sea (65°N). It is also found in the North Sea (Nesis 1987) and the Mediterranean (Villanueva 1995). It has been found in waters all around the United Kingdom (Nesis 1987), although in Scottish waters it is apparently more common on the west coast than the east coast, at around 50 m deep (Yau 1994). It is usually found over sand-mud substrata (Roper et al. 1984). A maximum depth of 515 m was reported by Collins et al. (2001).

Biology and ecology Current knowledge of *R. macrosoma* is largely based on observations made in the western Mediterranean and laboratory studies. It is a relatively large sepiolid, sometimes exceeding 8 cm ML, but usually less than 6 cm ML (Jereb & Roper 2005). Longevity is apparently 1–1.5 yr (von Boletzky & von Boletzky 1973). Mangold-Wirz (1963) reported seasonal spawning migrations to shallow inshore waters, with an extended spawning season from March to November. Migrations are apparently partitioned by size, with the largest individuals arriving first in spring, followed by smaller individuals in summer (Jereb & Roper 2005). Maturation begins at 3 cm ML (age 7 mo) and 3.5 cm ML (age 8 mo) for males and females, respectively. The eggs, which measure 7–8 mm, are laid in clusters of 30–40 and covered by a violet-red coat. These are usually deposited on bivalve shells or other hard substrata on the seabed. Embryonic development lasts about 45 days at 16°C (Mangold-Wirz 1963). In Scottish waters, juvenile *R. macrosoma* are found in the summer and early autumn (Yau 1994). *R. macrosoma* preys on decapod shrimps such as *Leander serratus* but does not appear to feed on mysids or crabs (von Boletzky & von Boletzky 1973). Unlike other sepiolids, it does not bury itself in bottom substrata but prefers to sit on the surface or hide in crevices (von Boletzky & von Boletzky 1973).

Sepietta neglecta

Biogeographic distribution The elegant bobtail *Sepietta neglecta* (Naef, 1916) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Morroco (25°N) to the northern North Sea (63°N). It is also found in the Mediterranean. This species appears to prefer muddy bottom substrata, at depths of 25–500 m (Jereb & Roper 2005).

Biology and ecology *Sepietta neglecta* rarely exceeds 3 cm ML (Jereb & Roper 2005). Little is known about its biology and ecology. It is thought to spawn throughout the year and is often associated with the bobtails *Rossia macrosoma* and *Sepietta oweniana*. It closely resembles the latter species and it is often difficult to distinguish between them (Jereb & Roper 2005).

Sepietta oweniana

Biogeographic distribution The common bobtail *Sepietta oweniana* (d'Orbigny, 1841) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Mauritania (20°N) to the Faroe Islands and

Norwegian Sea (63°N). It is also found in the North Sea and Mediterranean, in depths of 20–600 m (Mangold-Wirz 1963). In Scottish waters, it is most common in 80–90 m (Yau 1994). This species appears to prefer bottom substrata of mud or muddy sands (Mangold-Wirz 1963).

Biology and ecology *Sepietta oweniana* is a relatively large sepiolid, reaching 7 cm ML (Norman 2000). It is a short-lived species; longevity ranges from 6 to 9 mo in the Mediterranean (Mangold & Froesch 1977). However, it does appear to be a multiple spawner (Bello & Deickert 2003). In the western Mediterranean, spawning migrations of *S. oweniana* to shallow inshore waters, with an extended spawning period from March to November, have been reported (Mangold-Wirz 1963). According to Salman (1998), in the Aegean Sea peaks in spawning activity occur during April–May and October–November. In Scottish waters, spawning occurs from September to February (Yau 1994). Batch size ranges from 50 to 100 eggs per female (Bello & Deickert 2003). Embryonic development is related to temperature, taking for example, 67 days at 14°C and 84 days at 12°C. Juvenile *S. oweniana* (measuring up to 9 mm ML) have been found in plankton samples between March and September (Yau 1994).

Juvenile *S. oweniana* prey on mysids (*Praunus* spp.), amphipods and large copepods, whilst the adults prey on larger crustaceans (*Meganyctiphanes norvegica*, *Palaemon elegans*, *Crangon crangon*) (Bergström & Summers 1983, Bergström 1985). Newly hatched juveniles actively forage during the day until they reach 10 wk old at 15–18 mm ML (Bergström & Summers 1983). The adults are ambush predators, remaining buried in soft substratum and feeding during dawn and dusk (Bergström 1985). Predators of *Sapietta oweniana* include species of demersal fish (*Gadus morhua*, *Melanogrammus aeglefinus*) (Bergström & Summers 1983).

Sepiola atlantica

Biogeographic distribution The Atlantic bobtail *Sepiola atlantica* (d'Orbigny, 1839) is a neritic, nectobenthic species occurring in moderate and cool, shallow coastal waters and continental shelf areas and is distributed in the eastern Atlantic, from North Africa (20°N) to the Faroe Islands, Iceland and the Norwegian Sea (65°N). It is also found in the North Sea and is reported to be very common in U.K. waters (Yau & Boyle 1996) but is either rare or absent in the Mediterranean (Yau 1994). *S. atlantica* is found from the sublittoral zone to a depth of 150 m and is most common in clean, sandy bottoms at 50–120 m deep (Yau 1994).

Biology and ecology Although *S. atlantica* is a very common nearshore species, few studies have been carried out on this species (Yau 1994, Yau & Boyle 1996). It is a small species, with both sexes measuring less than 2 cm ML maximum (Roper et al. 1984, Yau 1994). The eggs of *S. atlantica* measure 2–3 mm (Yau & Boyle 1996) and are usually laid in clusters attached to hard surfaces on the seabed (Yau 1994). Mature females carry 40–130 ova prior to spawning (Yau & Boyle 1996). Males and females mature at about 1.3 and 1.6 cm ML, respectively. In Scottish waters, mature individuals are found from March to August, with a peak in maturity observed in June, indicating an extended spawning season (Yau & Boyle 1996). Size at hatching is unknown; a minimum size of less than 2 mm ML has been recorded in plankton samples (Yau 1994).

The main prey of *S. atlantica* are mysids and decapod shrimps, usually taken near the seabed during dawn and dusk (Yau 1994). *Sepiola atlantica* appears to be the most common cephalopod recorded in the diet of harbour porpoises (Santos et al. 2004, 2005b).

Sepiola aurantiaca

Biogeographic distribution The golden bobtail *Sepiola aurantiaca* (Jatta, 1896) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is distributed in the eastern Atlantic and North Sea, from the French coast (45°N) to southern Norway

(60°N) (Yau 1994). It occurs in shallow to moderate depths of 0–150 m, most common around 40 m depth.

Biology and ecology A maximum size of 2 cm ML has been reported for *S. aurantiaca* (Yau 1994). The precise timing of spawning is unknown, but juveniles have been found during August–September in Scottish waters, suggesting a similar pattern to *S. atlantica*, which spawns during summer months (Yau 1994). Occasionally, large numbers of *S. aurantiaca* are caught in demersal trawls, in association with foliaceous (flustridian) bryzoans (Yau 1994).

Cuttlefishes

Cuttlefishes (Sepiida) are small- to medium-sized decapods of commercial importance. They possess a unique, internal porous structure known as cuttlebone, which is used to regulate buoyancy by adjusting its internal gas-liquid ratio. Cuttlefish have highly developed eyes capable of perceiving polarised light. One genus and three species of cuttlefish are found in the north-eastern Atlantic.

Sepia elegans

Biogeographic distribution The elegant cuttlefish *Sepia elegans* (Blainville, 1827) is a neritic, demersal species occurring in moderately warm shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Namibia (21°S) to the west coast of Scotland (55°N). It is also found in the southern North Sea and throughout the Mediterranean (Roper et al. 1984). It is a sublittoral species, inhabiting soft (sand-mud) bottoms at depths of up to 600 m, although records deeper than 400 m are rare and depth may be a limiting factor for the species (Ward & von Boletzky 1984).

Biology and ecology *Sepia elegans* is a relatively small cuttlefish, with males and females measuring up to 7 and 8 cm ML, respectively, and weighing 50–60 g (Adam 1952). Male and female *S. elegans* begin to mature at 2 and 3 cm ML, respectively (Guerra & Castro 1989). However, most of the population matures at a greater size, at an age of about 1 yr. Mature females carry about 250 eggs and spawn at temperatures of 13–18°C (Mangold-Wirz 1963). The eggs are relatively large (0.5 cm) and usually attached to hard substrata (sea fans, shells corals) on muddy bottoms (Mangold-Wirz 1963). Juvenile *S. elegans* are benthic immediately after hatching.

Mature individuals (both sexes) are present throughout the year, indicating that spawning and recruitment events may be continuous for this species, although small peaks in recruitment have been observed in some Mediterranean waters (Jereb & Ragonese 1991b). In some areas in the Mediterranean, male and female *S. elegans* overwinter in deep water (>200 m) and migrate into shallower waters in spring–summer to spawn (Mangold-Wirz 1963, Guerra 1992, Belcari 1999). However, in other areas, no seasonal migratory patterns have been observed (Jereb & Ragonese 1991b). *Sepia elegans* has also been recorded in brackish, estuarine environments of low salinities (18–25%), indicating a relatively high degree of tolerance (Guerra 1992, Unsal et al. 1999).

Sepia elegans is a small but efficient benthic predator, feeding on small fish, crustaceans and polychaetes (Reid & Jereb 2005). No size or seasonal effects on diet composition have been observed for this species (Guerra 1985, Castro & Guerra 1990), although males and females appear to have slightly different feeding rates and habits (Bello 1991).

Sepia officinalis

Biogeographic distribution The common cuttlefish *Sepia officinalis* (Linnaeus, 1758) is a neritic, demersal species occurring in moderately warm, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (16°N) to the North Sea (60°N). However, it is typically found only in the southern North Sea and further south (<55°N). It also occurs throughout the Mediterranean (Roper et al. 1984). In the English Channel and Bay of Biscay, *S. officinalis* undertakes considerable seasonal migrations, wintering in deep offshore waters (<200 m) and moving inshore to shallow grounds during spring–summer to spawn (Mangold-Wirz 1963, Gi Leon 1982, Najai 1983, Wang et al. 2003). It is currently the most important exploited cephalopod in British waters, with the fishery being primarily located in the English Channel (Anonymous 2005).

Biology and ecology *Sepia officinalis* has a lifespan of up to 2 yr, depending on the timing of the reproductive cycle. It is a relatively large sepioid, with males growing larger than females and measuring up to 49 cm ML and weighing up to 4 kg. Specimens caught in the English Channel typically range from 10 to 22 cm ML. *Sepia officinalis* is semelparous and spawns intermittently, in shallow waters, typically at depths less than 30 m (von Boletzky 1983, Boucaud & Daguzan 1990, Boucaud-Camou et al. 1991). Male and females mature over considerable size ranges, at 6–14 and 11–25 cm ML, respectively. Female *S. officinalis* produce between 150 and 4000 eggs, depending on their size at maturity. Most individuals spawn during spring and summer, although there is also some winter spawning activity in the North Atlantic. Hatching follows from midsummer to autumn (von Boletzky 1983, Le Goff & Daguzan 1991, Dunn 1999). Mature males and large mature females (~18 mo old) move inshore during early spring to reproduce. These are later followed in summer by smaller mature females (14–16 mo old). Adult cuttlefish concentrate in coastal spawning grounds, mainly along both sides of the English Channel and on the French Atlantic coast.

Cuttlefish eggs are black and relatively large (measuring 12–14 mm) and are attached in grape-like clusters to various substrata fixed on the seabed. Embryonic development in this species varies with temperature and ranges from 40 to 45 days at 20°C and 90 to 90 days at 15°C. *Sepia officinalis* hatchlings range in size from 6 to 9 mm ML (von Boletzky 1983). In late autumn, juveniles migrate from inshore nursery grounds to deeper waters offshore, where they overwinter. Recent studies indicate that English Channel and Bay of Biscay cuttlefish may be genetically distinct and therefore should be considered as separate stocks (Le Goff & Daguzan 1991, Pawson 1995, Dunn 1999).

Sepia officinalis actively preys on small crabs, shrimps, demersal fishes, other cephalopods and polychaetes. Individuals change from feeding on mainly crustaceans to more fish as they grow larger. Cannibalism occurs at all sizes. Daily feeding rates range from 5 to 30% of body weight, depending on size and temperature (Castro & Guerra 1990, Guerra 1992). *Sepia officinalis* is itself consumed by a large number of marine predators. It has, for example, been found in the stomachs of cetaceans (e.g., *Grampus griseus*) (Clarke & Pascoe 1985), pinnipeds (e.g., *Monachus monachus* (Salman et al., 2002), *Arctocephalus pusillus* (Castley et al. 1991)) and sharks (e.g., *Prionace glauca*) (Clarke & Stevens 1974), *Mustelus mustelus* (Morte et al. 1997)) (Table 6).

Sepia orbignyana

Biogeographic distribution The pink cuttlefish *Sepia orbignyana* (Férussac, 1826) is a neritic, demersal species occurring in moderately warm, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from southern Angola (17°S) to the west coast of Scotland (55°N). It is also found in the southern North Sea and throughout the Mediterranean (Roper et al. 1984). A maximum depth range of 15–565 m has been reported for this species (Belcari & Sartor 1993, Cuccu et al. 2003), although records outside the 25- to 450-m range are extremely rare (Jereb & Ragonese 1991b, Casali et al. 1998). It is particularly abundant over sand-mud bottoms at depths of 50–250 m (Mangold-Wirz 1963, Jereb & Ragonese 1991b, Casali et al. 1998).

Biology and ecology *Sepia orbignyana* is a relatively small cuttlefish, with males and females measuring up to 10 and 12 cm ML, respectively (Mangold-Wirz 1963). There have been no reports of *S. orbignyana* reproducing in U.K. waters. In the Mediterranean, the spawning period is continuous, with peaks of intense activity observed between spring and autumn (Jereb & Ragonese 1991b, Wurtz et al. 1991, Belcari & Sartor 1993). Mature female *S. orbignyana* carry around 400 eggs (Roper et al. 1984). The eggs measure 7–9 mm, are off-white or grey in colour and more elongate than those of *S. officinalis* (Mangold-Wirz 1963). Based on aquarium studies, the newly hatched juveniles measure 6 mm ML and become benthic immediately, either swimming just above the bottom or crawling over short distances (von Boletzky 1988). Recruitment appears to be continuous throughout the year, with peaks in spring–autumn (Jereb & Ragonese 1991b, Wurtz et al. 1991). Female *S. orbignyana* grow slightly faster than males, rates of 2.9 and 3.0 mm ML per month have been reported for males and females, respectively (Jereb & Ragonese 1991b). Maturation occurs at about 3.5 and 6.5 cm ML for males and females, respectively (Belcari & Sartor 1993). *Sepia orbignyana* feeds on small crustaceans and fish (Auteri et al. 1988).

Incirrate octopods

Incirrate (non-finned) octopods are highly developed, small- to large-sized cephalopods, characterised by eight arms and lacking the paired head fins, tentacles and rigid internal supporting structures found in decapods (squid, bobtails, cuttlefish). Octopus arms are usually equipped with rows of suckers. Unlike squid suckers, octopus suckers lack rings or hooks and perform as simple suction cups. Incirrate octopods dominate the benthic cephalopod fauna at depths of 500–1500 m (Collins et al. 2001). Six genera and six species of incirrate octopods are found in the north-eastern Atlantic:

Bathypolypus arcticus

Biogeographic distribution The spoonarm octopus *Bathypolypus arcticus* (Prosch, 1847) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic. It is known to occur over a wide geographic area, between 25 and 80°N, at depths of 250–2700 m (Collins et al. 2001). In U.K. waters, it has been recorded in Rockall Trough and the Faroe-Shetland Channel (Collins et al. 2001).

Biology and ecology *Bathypolypus arcticus* is a relatively small octopod; the largest specimens recorded are 10 cm ML, but most are less than 6 cm ML (Roper et al. 1984). In the wild, *B. arcticus* is known to feed on a wide range of invertebrates, including various bivalves, crustaceans, cumaceans, foraminiferans, gastropods, polychaetes and sipunculids (von Boletzky & Hanlon 1983). In laboratory studies, it has been maintained on a diet of polychaetes and amphipods (*Gammarus* spp.) (von Boletzky & Hanlon 1983). *Bathypolypus arcticus* is itself preyed on by a number of fish species, including *Anarhichas lupus*, *Coryphaenoides berglax*, *Gadus morhua*, *Merluccius merluccius*, *Melanogrammus aeglefinus*, *Reinhardtius hippoglossoides*, *Sebastes marinus*, *Xiphias gladius* (Grieg 1930, Scott & Tibbo 1968, Dexter 1969, Macalaster 1976) and seals (*Erignathus barbatus*, *Phoca groenlandica*) (Klages 1996, Hjelset et al. 1999).

Benthoctopus piscatorum

Biogeographic distribution The octopus *Benthoctopus piscatorum* (Verrill, 1879) (no common name) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic, between 39 and 78°N. It has been recorded in Scottish waters (Boyle et al. 1998), around the Faroe-Shetland channel (Russell 1922) and in the Rockall Trough (Collins et al. 2001). In the last, a depth range of 1400–2520 m was reported for this species (Collins et al. 2001).

Biology and ecology A maximum size of 4 cm ML is reported for this species (Roper et al. 1984), but this is based on limited information. Collins et al. (2001) identified three putative species of *Benthoctopus* (possibly including *B. piscatorum*) from samples taken in deep waters around Rockall Bank. Remains of *B. piscatorum* have apparently been found in the stomach contents of two predatory fish species (*Melanogrammus aeglefinus*, *Gadus morhua*) (Grieg 1930).

Eledone cirrhosa

Biogeographic distribution The curled octopus *Eledone cirrhosa* (Lamarck, 1798) is a neritic, nectobenthic species occurring in warm and cool shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Morocco (25°N) to the Norwegian Sea (67°N). It is also found throughout the Mediterranean (Roper et al. 1984). Collins et al. (2001) reported depth records of down to 450 m, but it is generally found 50–300 m deep on a variety of seabed types, ranging from soft muds to rocky bottoms (Boyle 1983). In British waters, it appears to be very common in shallow coastal waters to the west of Scotland.

Biology and ecology *Eledone cirrhosa* is a small- to medium-sized octopus. Individuals of about 18 cm ML have been reported in the Mediterranean and occasionally in Portuguese waters (Belcari & Sartor 1999, unpublished data). Elsewhere, sizes greater than 16 cm ML are rare for this species. Females tend to grow larger than males; the latter may reach more than 13 cm ML but generally reach less than 12 cm ML. Although *E. cirrhosa* is a short-lived, semelparous species (Mangold-Wirz 1963, Guerra 1992), it exhibits considerable plasticity in its life cycle throughout its geographic range. In the North Sea, a combination of 1- and 2-yr cycles, based on individual growth and maturation rates, has been proposed (Boyle & Knobloch 1983, Boyle et al. 1988). In the Mediterranean, however, 2- and 3-yr cycles have been proposed for this species based on individual growth and maturation studies and length-frequency analyses of different local stocks (Mangold-Wirz 1963, Lefkatidou & Papaconstantinou 1995, Cuccu et al. 2003, Orsi Relini et al. 2006).

Eledone cirrhosa exhibits seasonal maturation patterns that vary with locality (Belcari et al. 1990). In the Mediterranean, sexual maturity occurs earlier (spring–summer) in western waters than further east (summer–autumn) (Belcari & Sartor 1999, Lefkatidou et al. 2000). In the North Sea, sexual maturity is observed from July to September, with spawning occurring shortly thereafter (Boyle 1983, Boyle & Knobloch 1983). In Portuguese waters spawning occurs from May to August at a mean size of 12 cm (unpublished data). Fecundity estimates for *E. cirrhosa* range from 2000 to 9000 eggs, depending on locality (Boyle et al. 1988). Few spent females have been recovered after spawning, indicating post-reproductive mortality (Mangold-Wirz 1963, Guerra 1992, Tursi et al. 1995). Fertilised eggs hatch after 3–4 mo, usually during April–July, in temperatures of 14–18°C. Young *E. cirrhosa* are less than 5 mm ML and are planktonic for several weeks before settling on the seabed (Mangold et al. 1971).

The diet of *E. cirrhosa* is composed mainly of decapod crustaceans, particularly alpheids and brachyurans (Auteri et al. 1988, Sánchez 1981, Boyle & Knobloch 1983). Cephalopod eggs and other molluscs are occasionally found in stomach contents of *E. cirrhosa*, and cannibalism has also been reported (Moriyasu 1981, Guerra 1992). A number of marine mammal and fish species are considered to be important predators of *E. cirrhosa* (Santos et al. 1999, Brown et al. 2001, Velasco et al. 2001) (Table 6). *Eledone cirrhosa* is an important component of the summer diet of harbour seals in the Moray Firth in some years (Tollit et al. 1998) as well as a prominent component of the diet of some cetaceans (e.g., *Grampus griseus* and to a lesser extent *Hyperoodon ampullatus*) (Pierce et al. 2007).

Graneledone verrucosa

Biogeographic distribution The octopus *Graneledone verrucosa* (Verrill, 1881) (no common name) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic, between 30°S and 62°N. It occurs in depths of 950–2500 m. It has been recorded in Scottish waters, the Faroe-Shetland Channel, Rockall Trough, Porcupine Seabight and off the coast of Norway (Grieg 1930, Boyle et al. 1998, Collins et al. 2001).

Biology and ecology Virtually nothing is known about the biology and ecology of *G. verrucosa*. A maximum size of 10 cm ML is reported for this species (Robson 1932), but this is based on a few records. There is no published information available on the prey or predators of *G. verrucosa*.

Haliphron atlanticus

Biogeographic distribution The seven-arm octopus *Haliphron atlanticus* (Steenstrup, 1861) is a cosmopolitan, deep-water, benthic species occurring in the temperate and tropical oceanic waters of the central and northern Atlantic, between the equator and 65°N (Norman 2000). Small numbers of *H. atlanticus* have been recorded off the coasts of Ireland, Shetland and Norway at depths of 100–200 m (Collins et al. 1995b, 1997b).

Biology and ecology Virtually nothing is known about the biology and ecology of *H. atlanticus*. Maximum sizes of 40 cm ML and 200 cm TL have been reported for this species (Norman 2000), but these are based on a few records. In U.K. waters, remains of *H. atlanticus* have been recovered from the stomachs of stranded sperm whales (Clarke & Pascoe 1997, Santos et al. 2002). In other parts of the world, *H. atlanticus* is sometimes predated by the wandering albatross (*Diomedea exulans*) (Xavier et al. 2003) and the Hawaiian monk seal (*Monachus schauinslandi*) (Goodman-Lowe 1998).

Octopus vulgaris

Biogeographic distribution The common octopus *Octopus vulgaris* (Cuvier, 1797) is a neritic, nectobenthic species occurring in abundance in moderately warm, shallow coastal waters (<200 m deep) and continental shelf areas of the north-eastern Atlantic and Mediterranean. It has a huge geographic range (presently undefined) and may in fact be a cosmopolitan species, with records in the South Atlantic and Pacific. Its northern limit appears to be the southern North Sea (55°N) (Roper et al. 1984).

Biology and ecology *Octopus vulgaris* is a relatively large-sized semelparous species, measuring up to 40 cm ML (with arms up to 140 cm in length) (Norman 2000). Maximum lifespans of 15–20 mo for males and 12–17 mo for females have been reported for this species, varying depending on locality (Sánchez & Obarti 1993, Domain et al. 2000). Captive *O. vulgaris* have recently been successfully reared through a complete life cycle, with excess food provided and a temperature range of 17–23°C maintained; a male and female achieved 1.6 kg in 339 days and 1.8 kg in 356 days, respectively (Iglesias et al. 2004).

The spawning season of *O. vulgaris* varies according to locality. In the north-eastern Atlantic populations, spawning extends throughout the year with peaks between February and July (Otero et al. 2005, Moreno et al. 2009). In Galician (north-western Spain) and north-western Portuguese waters, the spawning season is thought to be linked to the regional dynamics of coastal upwelling, so that hatchlings benefit from the greatest abundance of zooplankton but avoid the most advective months (Otero et al. 2005, Moreno et al. 2009). In the Mediterranean, the main spawning event occurs in June–July (Mangold 1987, Sánchez & Obarti 1993). The total potential fecundity of *O. vulgaris* is reported to be 70,000–600,000 oocytes per mature female (Silva et al. 2002). Mature eggs are oval shaped and relatively small, measuring 2.5 mm along the longest axis (Mangold-Wirz 1963). During spawning, female *O. vulgaris* attach eggs to hard substrata and care for them for considerable periods until they hatch. The duration of incubation for *O. vulgaris* eggs is temperature dependent, ranging from 20 to 30 days at 25°C to 100–120 days at 13°C (Mangold & von Boletzky 1987).

The duration of the early, planktonic, post-hatching phase is also influenced by temperature, ranging from 33 days at 25°C to 60 days at 21°C. *Octopus vulgaris* juveniles are still very small when they become benthic, typically at about 0.1 cm ML and weighing less than 0.2 g. *Octopus vulgaris* exhibits rapid, highly variable, non-asymptotic growth patterns (Alford & Jackson 1993, Domain et al. 2000) that appear to be partly influenced by temperature and diet (Forsythe & van Heukelem

1987, Aguado & García 2002). Individuals raised in aquaria can reach body weights of 0.5–0.6 kg within 6 mo of hatching (Itami et al. 1963, Imamura 1990, Villanueva 1995, Iglesias et al. 2004).

Octopus vulgaris paralarvae feed on zooplankton and the abundance of this food source is thought to be a limiting factor affecting stock recruitment success. Nevertheless, according to Iglesias et al. (2006), greater prey densities have not produced a greater number of attacks under culture conditions. Therefore, to reduce time and economise on costs, it is advisable to fit the prey quantity to the effective consumption of paralarvae. Iglesias et al. (2007) concluded that satisfactory results at around 1 mo culture were attained using *Artemia* enriched with *Nannochloropsis* sp. Adult and juvenile *Octopus vulgaris* are active hunters and prey on a wide variety of fish, crustaceans, molluscs and polychaetes. Table 7 lists recorded prey of *O. vulgaris* from the north-eastern Atlantic. A large number of different prey items have also been recorded for the Mediterranean (Guerra 1978, Sánchez & Obarti 1993, Quetglas et al. 1998b). Significant predators of *O. vulgaris* include various marine mammals, birds and other cephalopod species (Hanlon & Messenger 1998). Mammal predators include *Delphinus delphis*, *Grampus griseus*, *Globicephala melas* and *Tursiops truncatus* (Blanco et al. 2001, López 2002, Santos et al. 2004). Certain fish species, including *Trisopterus* spp., Sparidae and Serranidae are significant predators of the planktonic stages of *Octopus vulgaris*, whilst others, including *Conger conger* and *Muraena helena*, prey on the benthic juvenile and adult stages (Table 6). Available literature on the biology of the planktonic stages of *Octopus vulgaris* and other incirrate octopod species was recently reviewed by Villanueva & Norman (2008).

Cirrate octopods

Cirrate (finned) octopods are highly specialised deep-water cephalopods that are poorly understood (Collins & Villanueva 2006). They are characterised by possession of eight arms and paired head fins. They include some of the largest invertebrates in the bathyal and abyssal megafauna (Gage & Tyler 1991). Although cirrate octopods are usually found in depths greater than 300 m and dominate the benthic cephalopod fauna at depths greater than 1500 m (Collins et al. 2001, Collins & Villanueva 2006), very little is known about their biogeography, biology and ecology. A few behavioural studies of cirrate octopods, using deep-water video cameras, have been undertaken (Vecchione 1987, Vecchione & Young 1997, Villanueva et al. 1997, Villanueva 2000, Collins & Villanueva 2006). They are apparently predated by certain marine mammal species (Santos et al. 2001a,b). At present, they are not considered to be marketable and there are no known conservation issues. Four genera and five species of cirrate octopods have been recorded in the north-eastern Atlantic (Table 8).

Opisthoteuthis grimaldii

Biogeographic distribution The cirrate octopus *Opisthoteuthis grimaldii* (Joubin 1903) is an oceanic, benthic species that appears to be relatively common in deep waters west of Scotland, where it has been recorded from 210 to 2300m (Collins et al. 2001). It is a regular by-catch in benthic trawls from the 800–1200 m depth range (Daly et al. 1998, Boyle & Daly 2000).

Biology and ecology *Opisthoteuthis grimaldii* is a relatively small species, with maximum sizes of 5 cm ML and 25 cm TL reported (Collins et al. 2001), but these are based on a few records. Body weights of 0.6–3 kg are reported for mature females (Daly et al. 1998). Boyle & Daly (2000) estimated a maximum potential fecundity of about 3000 eggs per female for this species. Based on observations of female maturation patterns and egg size distributions, Boyle & Daly (2000) concluded that, west of the Hebrides, mature female *O. grimaldii* spawned continuously throughout their growth period. No seasonal differences in female maturation during spring, autumn and winter have been observed, indicating that the timing of spawning is not closely related to season (Daly et al. 1998).

Table 7 Identified prey types and species from *Octopus vulgaris* stomach contents (Nigmatullin & Ostapenko 1976, Guerra 1978)

		Geographic area	
Group	Taxonomic description	NE Atlantic	Sahara Bank
Fish	Blenniidae	•	•
	Boops boops		•
	Decapterus sp.		•
	Dentex sp.		•
	Dentex macrophthalmus		•
	D. filosus		•
	Gobiidae	•	
	Labridae	•	
	Pagellus acarne		•
	P. canariensis		•
	Sardinella sp.		•
	Serranidae	•	
	Soleidae		•
	Trachinus sp.		•
	Trachurus sp.		•
	Triglidae	•	
Crustacea	Amphipoda		•
	Atelecyclus sp.	•	
	Cancer pagurus	•	
	Carcinus maenas	•	
	Eriphia verrucosa	•	
	Inachus sp.	•	
	Isopoda		•
	Liocarcinus puber	•	
	Liocarcinus sp.	•	
	Macropodia sp.	•	
	Maia squinado	•	
	Ostracoda		•
	Pachygrapsus marmoratus	•	
	Palaemon sp.	•	
	Polybius henslowii	•	
	Stomatopoda		•
Mollusca	*Alloteuthis subulata*		•
	Cymbium sp.		•
	Ensis ensis	•	
	Loligo vulgaris		•
	Mytilus galloprovincialis	•	
	Octopus vulgaris	•	
	Octopus sp.		•
	Sepia sp.	•	•
Polychaeta	Aphroditidae		•
	Polychaeta		•

Opisthoteuthis spp. feed on a variety of small, slow-moving benthic polychaetes and crustaceans. They in turn appear to be preyed on by large fish, sharks and marine mammals (Collins & Villanueva 2006).

Table 8 Cirrate octopod species recorded in U.K. waters

Species	ML[a] (cm)	TL[a] (cm)	Area record[b]
Cirroteuthis massyae (Grimpe, 1920)	19	30	Rockall Trough
Cirroteuthis muelleri (Eschricht, 1836)	8	150	West of Shetland
Grimpoteuthis wulkeri (Grimpe, 1920)	12	40	Rockall Trough
Opisthoteuthis grimaldii (Joubin, 1903)	5	25	Rockall Trough
Stauroteuthis syrtensis (Verrill, 1879)	9	N/A	Rockall Trough

Notes: ML = mantle length; TL = total length.

[a] *Source:* Roper et al. 1984, Nesis 1987, Voss & Pearcy 1990.

[b] *Source:* Collins et al. 2001.

Other species

Virtually nothing is known about other cirrate octopod species inhabiting the deep waters of the north-eastern Atlantic. According to Collins et al. (2001), the following species often dominate cephalopod catches from waters west of Ireland and Scotland: *Opisthoteuthis massyae* (Grimpe, 1920) (870–1400 m deep), *Stauroteuthis syrtensis* Verrill 1879 (1400–3100 m), *Cirroteuthis muelleri* (Eschricht, 1836) (700–4900 m), *Cirrothauma murrayi* (Chun, 1911) (2400–4900 m), and *Grimpoteuthis wulkeri* (1800–4900 m). Reported maximum sizes of these species are provided in Table 8. Available literature on the taxonomy, ecology and behaviour of cirrate octopods around the world was recently reviewed by Collins & Villanueva (2006).

Warm-water cephalopods

Besides the 30 species listed for the north-eastern Atlantic, several other species typical of the Mediterranean and the tropical-to-subtropical eastern Atlantic have their northern distribution encroaching north-eastern Atlantic waters. Examples include the sepiolids *Sepietta obscura* (Naef 1916) and *Sepiola ligulata* (Naef, 1912) both endemic of the Mediterranean Sea (Mangold & von Boletzky 1987) and reported off the west Iberian shelf by Pereira (1996) and Guerra (1985), respectively. The deep-water octopods *Bathypolypus sponsalis* (Fischer and Fischer, 1892), *Benthoctopus ergasticus* (Fischer and Fischer, 1892), *Pteroctopus tetracirrhus* (Chiaie, 1830) and *Scaeurgus unicirrhus* (Chiaie, 1839–1841 in Férussac and D'Orbigny, 1834–1848), and the histioteuthid squids *Histioteuthis corona* (Voss and Voss, 1962), *H. hoylei* (Goodrich, 1896) and *H. meleagroteuthis* (Chun, 1910) are also recorded occasionally to the west of Iberia. On the other hand, the octopods *Octopus salutii* Verany, 1839, *Octopus defilippi* (Verany, 1851), *Opisthoteuthis calypso* (Villanueva et al. 2002) and especially *Eledone moschata* (Lamarck, 1798) are presently fairly common in Portuguese waters as well as the sepiolid *Sepiola rondeletii* (Leach, 1834) and the enoploteuthid squid *Abralia veranyi* (Rüppell, 1844) (this species only since 1998). In addition, many tropical and subtropical oceanic species, mostly cranchiids and enoploteuthids, approach the rich Iberian waters for spawning and their early stages may be found in the vicinity of the Portuguese continental shelf (listed in Moreno et al. 2009). Given that temperature is a determinant in the biogeographic distribution, many southern species are likely to advance to higher latitudes in face of global warming, resulting in the near future in important changes in the biodiversity of the north-eastern Atlantic ecosystems.

Economic importance of cephalopods in the north-eastern Atlantic

A number of north-eastern Atlantic cephalopod species are highly valued for consumption, and substantial catches of these are taken each year. During the past decade, total cephalopod landings (all species) from the north-eastern Atlantic ranged from about 41,000 to 51,000 t (Table 9). Several species are exploited, although for (Food and Agricultural Organization, FAO and International

Table 9 Total annual (tonnes) cephalopod landings (1997–2006) in the north-eastern Atlantic; categories as used in official (FAO) fishery statistics (Anonymous 2008)

	Year									
Group	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Long-fin squid	11,519	11,245	11,049	10,253	8,234	9,939	8,472	12,562	9,420	7,800
Short-fin squid	6,145	5,841	7,693	5,607	4,260	2,571	1,483	2,114	2,536	1,282
Cuttlefish	16,652	20,275	20,210	23,754	18,034	22,614	19,492	30,928	21,371	21,513
Octopods	15,801	13,043	15,718	16,500	11,461	12,831	12,191	14,195	17,906	8,999
Total	50,117	50,404	54,670	56,114	41,989	47,955	41,638	59,799	51,233	39,594

Notes: FAO = Food and Agricultural Organization.

Council for the Exploration of the Sea, ICES) fisheries statistical records, they are conveniently grouped into four broad categories: long-fin squid, short-fin squid, cuttlefish (including sepiolids) and octopods. The main species caught and marketed in Europe are *Loligo forbesi*, *L. vulgaris*, ommastrephid spp., *Sepia officinalis*, sepiolid spp., *Octopus vulgaris* and *Eledone* spp. The bulk of European catches are landed by the French, Portuguese, Spanish and U.K. fleets. These four nations, in fact, account for more than 90% of the total north-eastern Atlantic cephalopod catch.

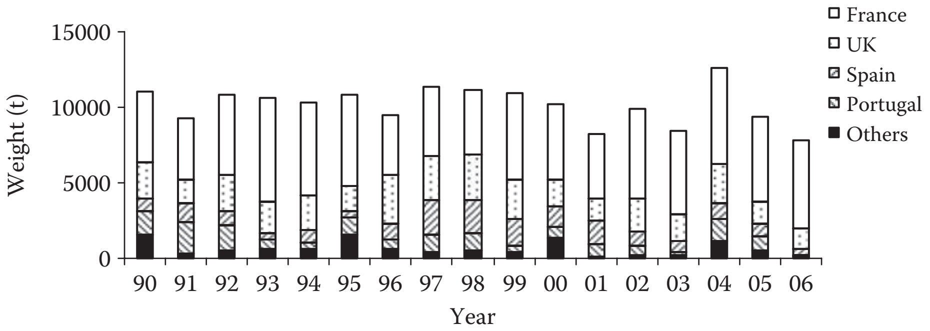
As with all commercially exploited marine species, fishery data are imperfect. Since no quotas are set in European cephalopod fisheries, deliberate misreporting or illegal landing of catches is not a major issue. However, the low taxonomic resolution of official landings statistics, the relatively high importance of poorly recorded artisanal landings, and indeed patchy reporting of commercial landings from some ports, are issues.

Exploitation of long-fin squid

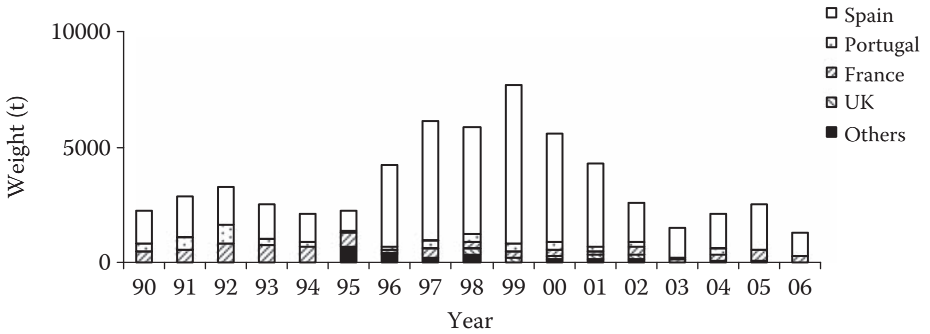
Total landings of long-fin squid (Family Loliginidae) from the north-eastern Atlantic (ICES Area) ranged from about 8,000 to 11,000 t per annum during the past decade (Table 10). The four main fishing fleets involved, based in France, Portugal, Spain and the United Kingdom, currently account for 90–95% of total landings (Figure 1a). A large portion of the total long-fin squid catch (40–50%) was landed by the French fleet. The geographical distribution of French and U.K. (1999–2002) catches is provided in Figure 2.

Table 10 Total annual long-finned squid (f. Loliginidae) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Loligo forbesi*, *L. vulgaris* and *Alloteuthis subulata*) (Anonymous 2008)

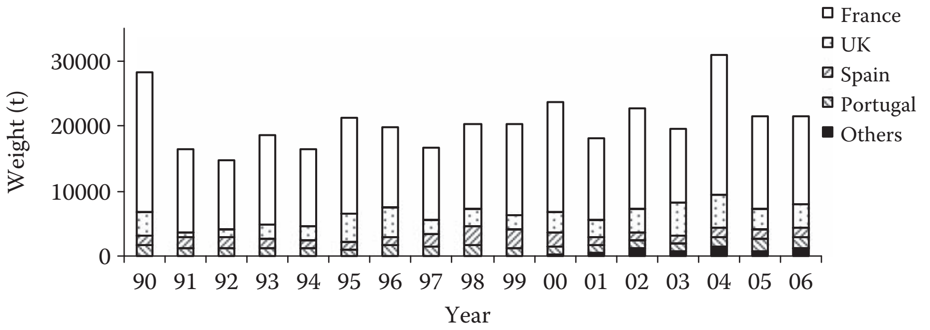
	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	155	253	222	463	51	137	132	106	73	81
Denmark	22	48	50	20	0	0	0	0	0	0
France	4,560	4,275	5,759	5,039	4,243	5,963	5,523	6,292	5,621	5,829
Germany	4	11	6	5	0	0	58	38	24	15
Ireland	217	216	178	101	14	40	0	245	264	115
Netherlands	0	0	0	773	0	0	0	238	176	168
Portugal	1,153	1,111	375	678	899	687	236	1,526	873	96
Spain	2,253	2,186	1,728	1,371	1,489	927	748	987	872	438
Sweden	1	1	1	+	0	0	0	5	3	10
United Kingdom	3,014	3,045	2,624	1,765	539	2,184	1,775	3,125	1,514	1,351
Total (ICES)	11,379	11,146	10,943	10,215	8,234	9,939	7,527	12,562	9,420	7,100



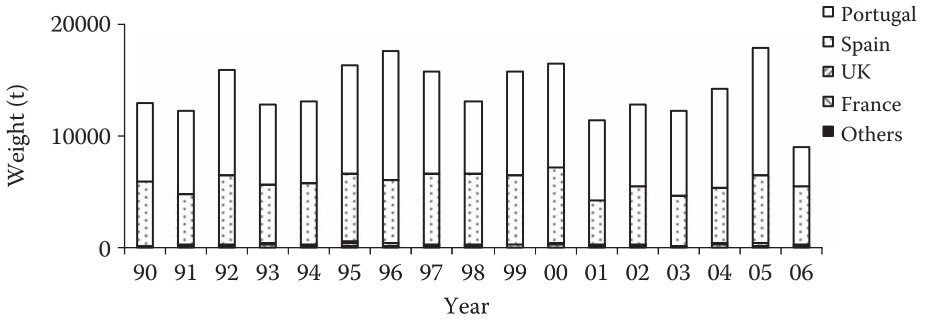
(A) Long-fin squid



(B) Short-fin squid

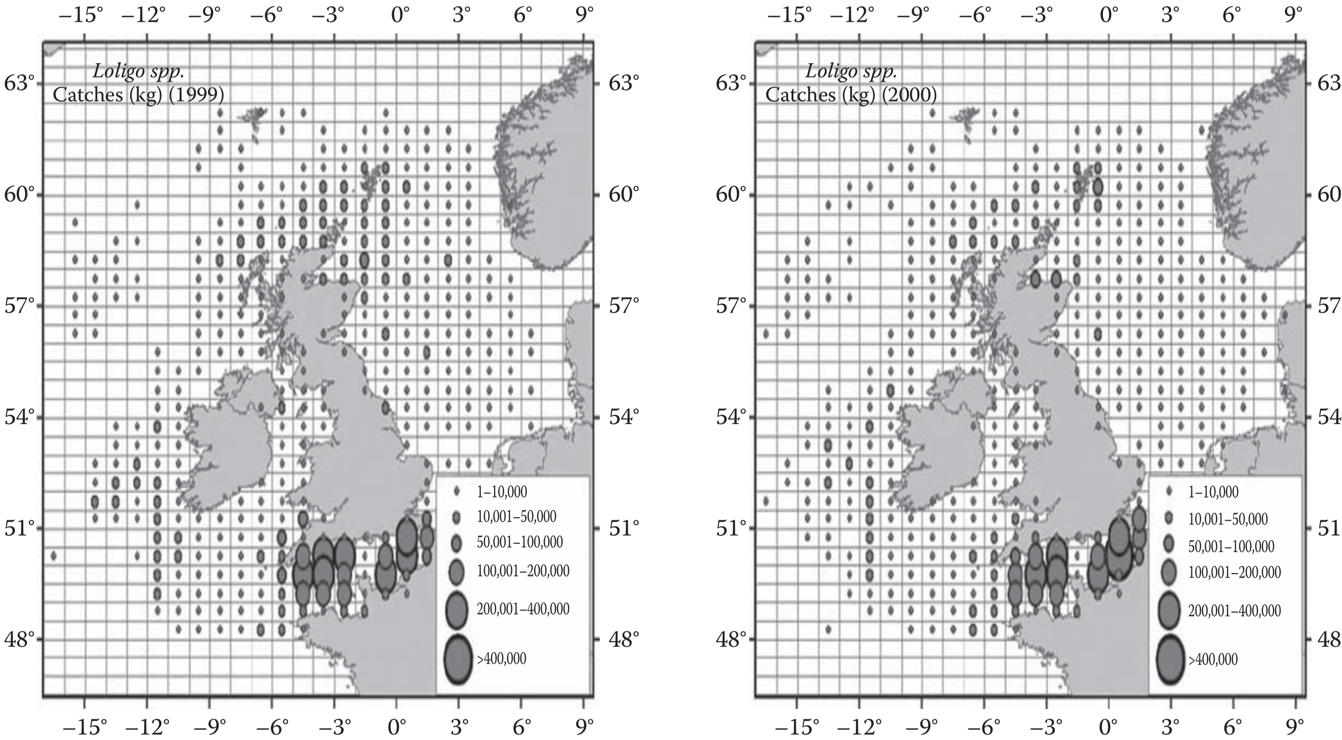


(C) Cuttlefish



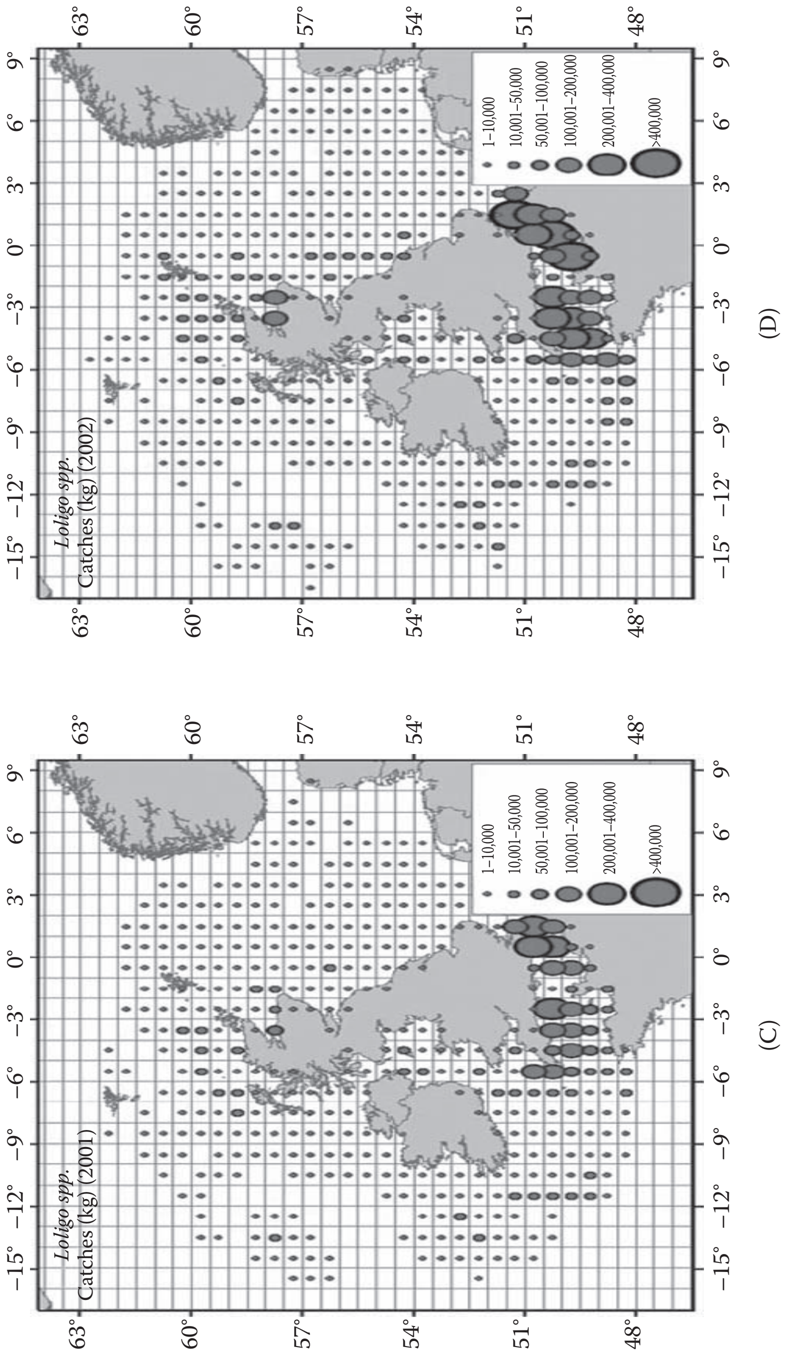
(D) Octopods

Figure 1 Total landings of cephalopods caught in the north-eastern Atlantic (International Council for the Exploration of the Sea [ICES] Area) by nation (1990–2006): (A) long-fin (loliginid) squid, (B) short-fin (ommastrephid) squid, (C) cuttlefish (including sepiolid) and (D) (incirrate) octopods (Anon. 2005, 2008).



(A) (B)

Figure 2 Maps showing distributions of annual long-fin (loliginid) squid catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005, 2008): (A) 1999, (B) 2000, (C) 2001, (D) 2002.



(C)

(D)

Figure 2 (continued).

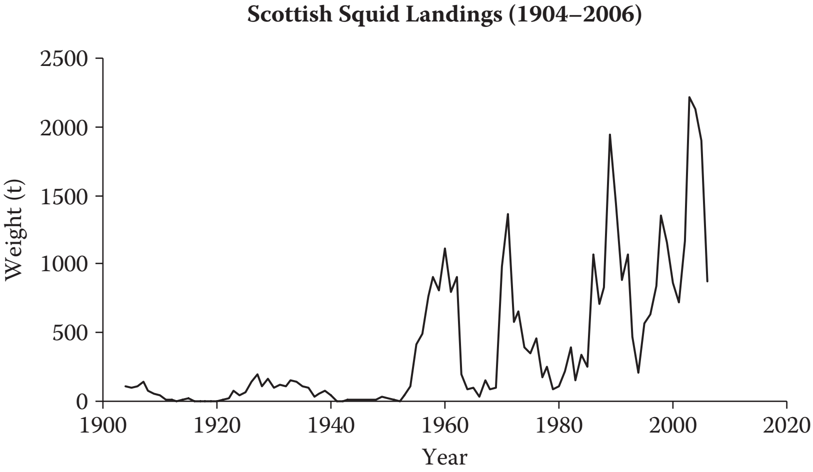


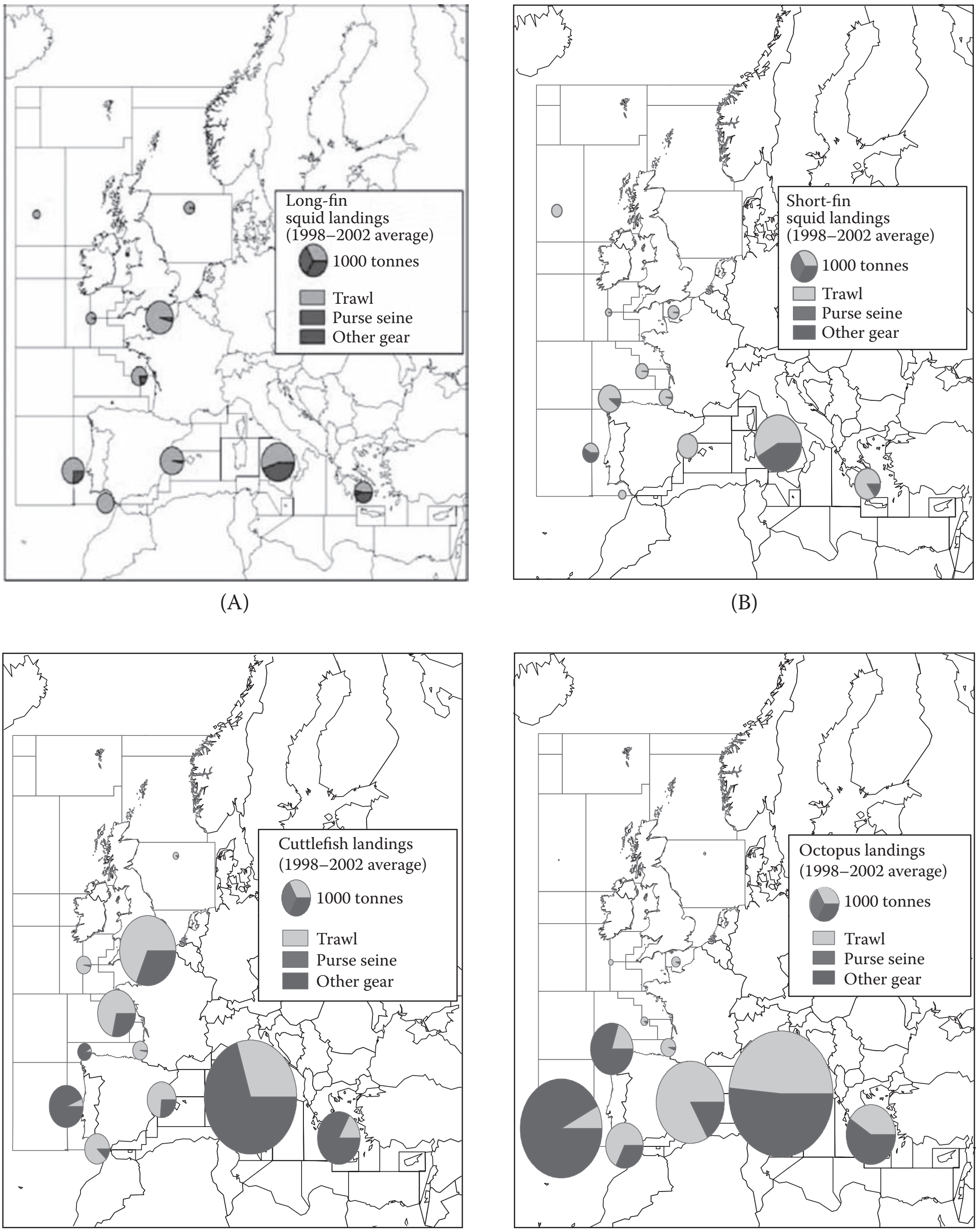
Figure 3 Scottish squid (*Loligo forbesi*) landings during period 1904–2006 (Scottish Sea Fisheries Database, Edinburgh).

Loligo forbesi is the most frequently caught squid species in U.K. waters where it forms the basis of a significant by-catch fishery (Pierce et al. 1994b), with annual landings as high as 3500 t (Collins et al. 1997a). Based on historical fishery data (Figure 3), this species appears to exhibit cyclical population trends on an appropriately decadal scale. At certain times *L. forbesi* is targeted, notably on Rockall Bank in summer (during the 1980s) Pierce et al. 1994a) and in the Moray Firth in autumn (Young et al. 2006). There is also some directed squid fishing, including jig fishing (as described by Hamabe et al. 1982), off the south coast of England, although it is not clear which species of *Loligo* is targeted. On the Spanish and Portuguese Atlantic coasts, inshore jigging catches mainly *Loligo vulgaris*, which is thought to generally occur closer inshore than *L. forbesi*, although it is also the case that *L. forbesi* is increasingly rare to the south (see Chen et al. 2006). Recently, squid fishing has attracted considerable attention in Scotland, and in 2005, small-scale directed squid fisheries were reported in several localities, including the Firth of Forth, off Aberdeen, off the islands of Skye and Lewis.

The main Scottish fishery for *L. forbesi* occurs in coastal waters and usually exhibits a marked seasonal peak around October and November, corresponding to the occurrence of pre-breeding squid (Howard 1979, Pierce et al. 1994c, Young et al. 2006).

Analysis of fishery data collected between 1980 and 1990 indicated that *L. forbesi* was widely distributed on the continental shelf and also occurred on offshore banks, notably Rockall (Pierce et al. 1994a,c). Data from trawling surveys confirm the wide distribution while also highlighting its patchy nature. Research trawling surveys record squid in U.K. waters in all seasons. Pierce et al. (1998) presented data from demersal trawl surveys along the west coast of Scotland during November (1990–1994), which showed that highest catches of *L. forbesi* occurred north of Ireland near the Stanton Bank area (~3200/h in one haul). Good catches occurred north and west of the Hebrides and in Donegal Bay, whereas catches south and west of Ireland were relatively poor. Data collected from research cruises carried out in 2004 showed highest catch numbers from waters to the west of the Isle of Man. Recent analysis of long-term trends in abundance points to the possible influence of oceanographic conditions on abundance of *L. forbesi* in Scottish waters (Pierce & Boyle 2003) and suggests that the relative importance of summer and winter breeding populations may show marked shifts on a decadal timescale (Zuur & Pierce 2004, Pierce et al. 2005).

Loligo vulgaris is also landed mainly as a by-catch of multispecies demersal and pelagic trawl fisheries in the north-eastern Atlantic and Mediterranean (Figure 4a). In U.K. waters, the English



(A) (B)

(C) (D)

Figure 4 Maps showing distributions of (A) cuttlefish, (B) octopods, (C) long-fin squid and (D) short-fin squid in the north-eastern Atlantic and Mediterranean by International Council for the Exploration of the Sea [ICES] division and fishing gear type (Freitas & Robin, WGCEPH Report, in Anon. 2008).

Channel and off the north-western coast of Spain, it is usually landed in mixed catches with *L. forbesi*. In these areas where the two species overlap, the landing statistics refer to *Loligo* spp. (Robin & Boucaud-Camou 1993). Therefore, the overall catch of *L. vulgaris* in U.K. waters is currently unknown, although it is believed to be significant. Further south, *L. vulgaris* is an important secondary target species in the Saharan Bank trawl fishery (Raya et al. 1999) and it is also targeted by a number of small, inshore, directed hand-jig fisheries operating from the coasts of Spain and Portugal (Guerra et al. 1994). Landings from the small-scale fisheries are poorly reported but in north-western Spain they may be of a similar order of magnitude to the trawl by-catch landings (Pierce 1999). In Greek and Portuguese waters, spawning aggregations of *L. vulgaris* are also targeted using beach seines, gill nets and trammel nets.

Substantial catches of *Alloteuthis* spp. are also landed in southern Spain, although they are often mixed with *Loligo* spp. and there are no separate, quantitative records currently available (Anonymous 2008).

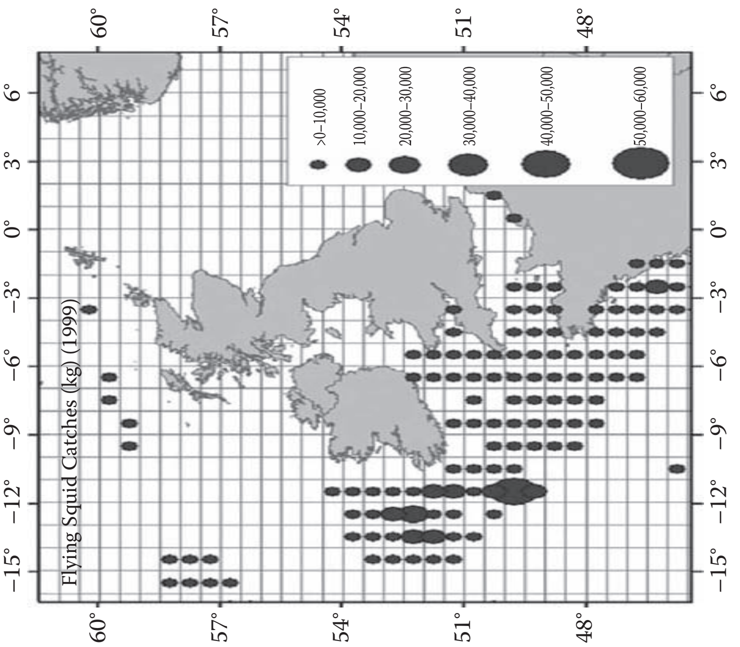
Exploitation of short-fin squid

Total landings of short-fin squid (Family Ommastrephidae) from the north-eastern Atlantic ranged from about 3000 to 10,000 t per annum during the past decade (Table 11). Landings have generally been sporadic, although landings from Spain and Portugal have been fairly consistent, at more than 1000 t per annum (Figure 1b). However, very large catches (>4000 t) were landed by the Danish and Norwegian fleets in 2004. French and U.K. landings of short-fin squid (1999–2002) are provided in Figure 5.

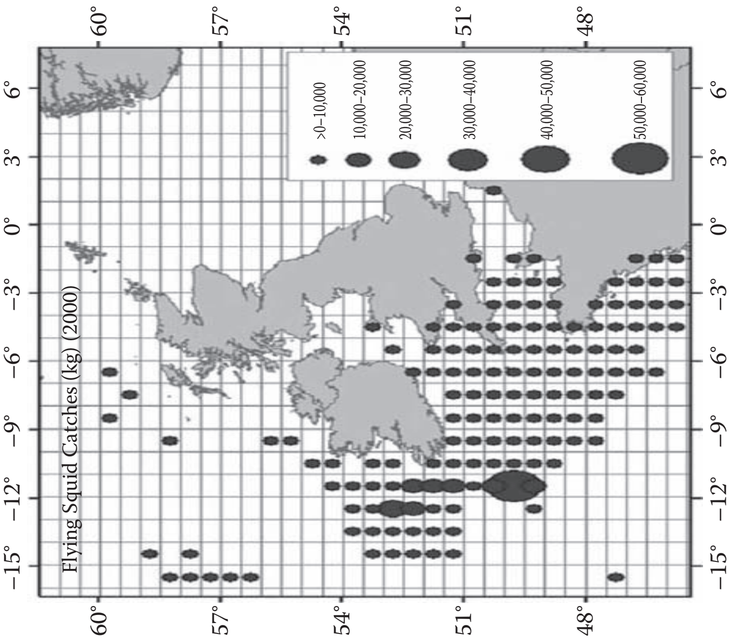
Ommastrephid squid stocks from the north-eastern Atlantic are harvested throughout the year by Spanish and other European fleets. Figure 4b shows the distribution of ommastrephid catches in the north-eastern Atlantic and Mediterranean. They are usually taken as by-catch during demersal and pelagic trawling operations and in gill and trammel nets, in depths of 100–400 m (Mangold & von Boletzky 1987, Jereb & Ragonese 1991a, González et al. 1994, González et al. 1996a). Different species (predominantly *Illex coindetii* and *Todaropsis eblanae*, occasionally *Ommastrephes bartramii* and *Todarodes sagittatus*) are often landed together as mixed 'short-fin' squid. Consequently, landings data for individual ommastrephid species are often unavailable. Nevertheless, ommastrephid

Table 11 Total annual short-fin squid (f. Ommastrephidae) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Illex coindetii*, *Todarodes sagittatus*, *Todaropsis eblanae* and *Ommastrephes bartramii*) (Anonymous 2008)

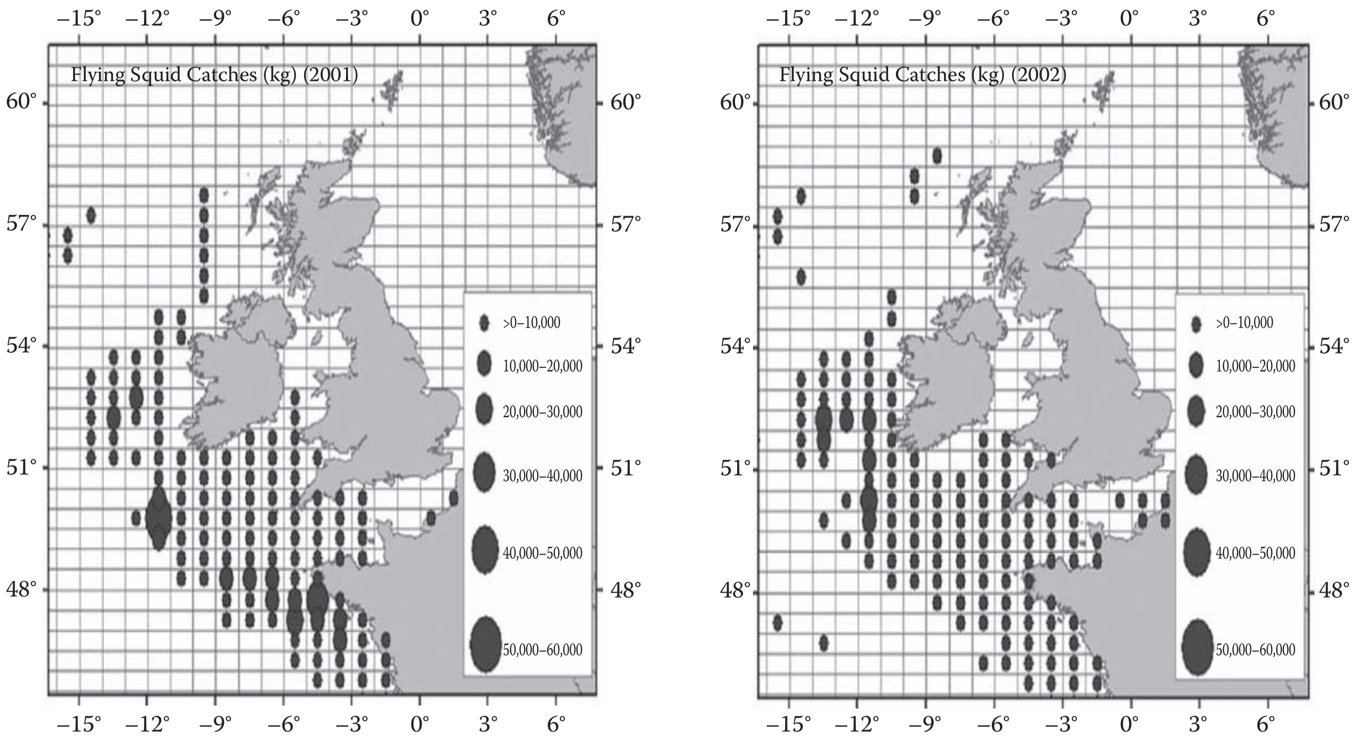
	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Denmark	0	0	0	0	0	0	16	4360	0	0
France	375	216	289	266	128	358	94	235	456	230
Iceland	5	4	3	1	0	0	0	1	0	0
Ireland	0	347	9	112	135	154	0	77	36	24
Norway	190	2	+	+	0	0	0	4642	0	0
Portugal	364	388	314	323	232	205	119	321	0	0
Spain	5185	4591	6874	4719	3573	1685	1253	1471	2023	1018
United Kingdom	26	293	204	186	193	169	1	27	20	10
Total (ICES)	6145	5841	7693	5607	4260	2571	1348	2114	2536	1282


Flying Squid Catches (kg) (1999)
>0–10,000
10,000–20,000
20,000–30,000
30,000–40,000
40,000–50,000
50,000–60,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(A)


Flying Squid Catches (kg) (2000)
>0–10,000
10,000–20,000
20,000–30,000
30,000–40,000
40,000–50,000
50,000–60,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(B)



(C)

(D)

Figure 5 Maps showing distributions of annual short-fin (ommastrephid) squid catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

squid stocks are now regarded to be a high-value fishery resource (Jereb & Ragonese 1995). During the past decade, the total ommastrephid catch in European waters has ranged from 3000 to 7000 t annually, with U.K. fleets accounting for up to 300 t per annum (Anonymous 2005).

A significant, directed fishery for *T. sagittatus* has previously been operated by north European countries, notably Norway, during 1980–1987. During this period, *T. sagittatus* invaded coastal waters of the Faroe Islands, south-western Iceland and north-western Norway in late summer and autumn, with some squids migrating into the North Sea (Sundet 1985). Large numbers of *T. sagittatus* were also taken as by-catch by demersal trawlers around Shetland at this time (Joy 1990). Very large numbers of *T. sagittatus* can be caught in U.K. waters on occasion, particularly around Shetland and off the west coast of Scotland. However, since there is no current market for this species in Scotland, it is usually discarded by Scottish fishing vessels (Joy 1989). The directed fishery in Norwegian waters has not operated since 1990 due to a decline in seasonal invasions, although catches of 352 and 190 t of short-fin squid, presumed to be *T. sagittatus*, were reported in 1995 and 1997, respectively (Anonymous 2005).

At present, *Illex coindetii*, *Ommastrephes bartramii* and *Todaropsis eblanae* are not exploited commercially by U.K. fleets and consequently there is little information available on their abundance in U.K. waters. However, reports from adjacent waters indicate that they can at times be widespread and abundant in the north-eastern Atlantic and may represent a significant potential fishery resource. The North Atlantic stock of *Ommastrephes bartramii* is estimated to be about 2.5 million t (Nigmatullin et al. 1991); this species is already exploited commercially in the Pacific (Bower & Ichii 2005). The occurrence of *Todaropsis eblanae* in the Irish Sea was reported by Collins et al. (1995a). This species was occasionally caught during research cruises carried out in the spring, summer and autumn of 1992 and 1993. Lordan et al. (2001) studied the distribution and abundance of cephalopod species caught during demersal trawls surveys west of Ireland and in the Celtic Sea. The most numerous species in catches was *Loligo forbesi* followed by *Todaropsis eblanae,* which was concentrated close to the shelf break in most years. However, in 1994 there were also large catches off the south coast of Ireland. It is also reported to be superabundant in the North Sea in some years, a phenomenon possibly linked to hydrographical anomalies such as influxes of warm high-salinity Atlantic seawater (Hastie et al. 1994).

Exploitation of other squid species

Aside from loliginids and ommastrephids, there are a number of other squid species in U.K. waters that may have some fishery potential. *Gonatus fabricii*, for example, is considered to be the most abundant squid of Arctic and subarctic waters (Nesis 1965, Kristensen 1984). Spawning concentrations of *G. fabricii* may be a valuable, exploitable resource, based on the large catches of subadults frequently taken by midwater trawlers operating in the Norwegian Sea (Wiborg et al. 1984, Bjørke & Gjøsæter 2004). Using a fishery production model, Bjørke & Gjøsæter (1998) estimated the spawning stock biomass of *G. fabricii* in the Norwegian Sea to be about 5 million t. Bjørke (2001) estimated the annual consumption of *G. fabricii* by sperm whales alone to be about 385,000 t. Santos et al. (1999) estimated the annual consumption of *Gonatus* spp. in Norwegian waters by sperm whale to be 400,000–520,000 t. In Greenland, Inuit fishermen use *G. fabricii* as bait in local cod and shellfish fisheries. It is also frequently taken as by-catch in shrimp trawls. The high lipid content of the digestive gland (>60%) makes this species potentially suitable for industrial use (Kristensen 1984). Although there are no British records of large spawning aggregations of *G. fabricii* or *G. steenstrupi*, juvenile gonatids are relatively common in U.K. waters based on the numbers found in plankton samples (Collins et al. 2001).

Table 12 Total annual cuttlefish (sepiids and sepiolids) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Sepia officinalis*, *Sepia* spp. and sepiolid spp.) (Anonymous 2008)

	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	17	26	24	59	261	742	569	819	599	729
Denmark	0	0	0	0	3	16	42	60	49	90
France	11,046	13,015	13,926	16,974	12,395	15,434	11,305	21,511	14,142	13,475
Netherlands	+	+	+	101	163	382	250	388	174	310
Portugal	1,423	1,734	1,161	1,365	1,348	1,368	1,208	1,727	1,857	1,859
Spain	1,956	2,720	2,819	2,154	1,154	125	1,287	1,418	1,531	1,456
United Kingdom	2,210	2,780	2,280	3,101	2,710	3,547	5,008	5,514	3,015	3,593
Total (ICES)	16,652	20,275	20,210	23,754	18,034	22,614	19,659	30,988	21,371	21,513

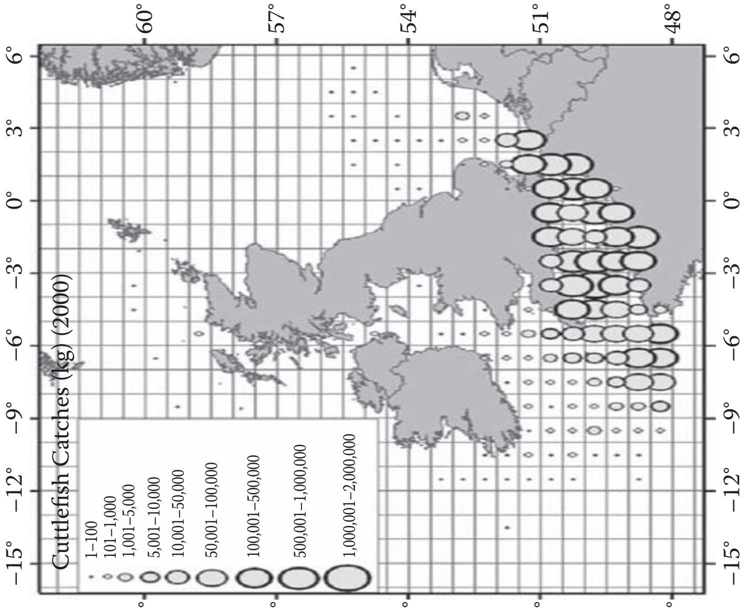
Exploitation of sepiolids

Small, bottom-living sepiolids are not presently considered to be of commercial value by U.K. fishermen and are usually discarded from catches. However, they may be very abundant in U.K. waters. Stephen (1944) reported a record of 256 specimens of *Sepiola atlantica* taken in a single haul, indicating fishery potential. In southern European waters of the Atlantic and Mediterranean, significant numbers of *Sepietta* spp., *Sepiola* spp. and *Rossia macrosoma* are often landed and marketed. No fisheries data for specific sepiolid catches are available, however, since these are currently recorded for fishery statistical purposes (together with commercial *Sepia* spp.) as ‘cuttlefish’ (Table 12).

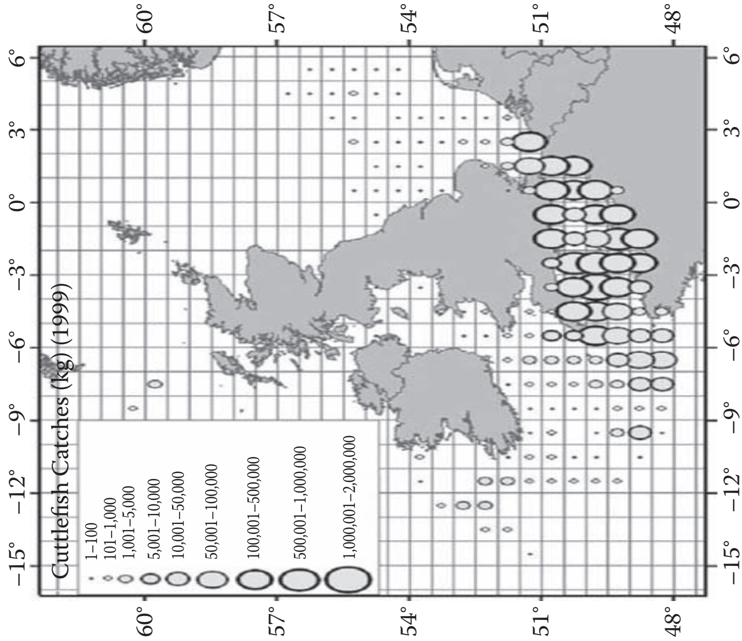
Exploitation of cuttlefishes

Total landings of cuttlefish (including sepiolids) from the north-eastern Atlantic (ICES Area) ranged from about 16,000 to 24,000 t per annum during the past decade (Table 12). The four main fishing fleets involved, based in France, Portugal, Spain and the United Kingdom, currently account for 95–99% of total landings (Figure 1c). The bulk of the total catch (60–65%) was in fact landed by the French fleet alone.

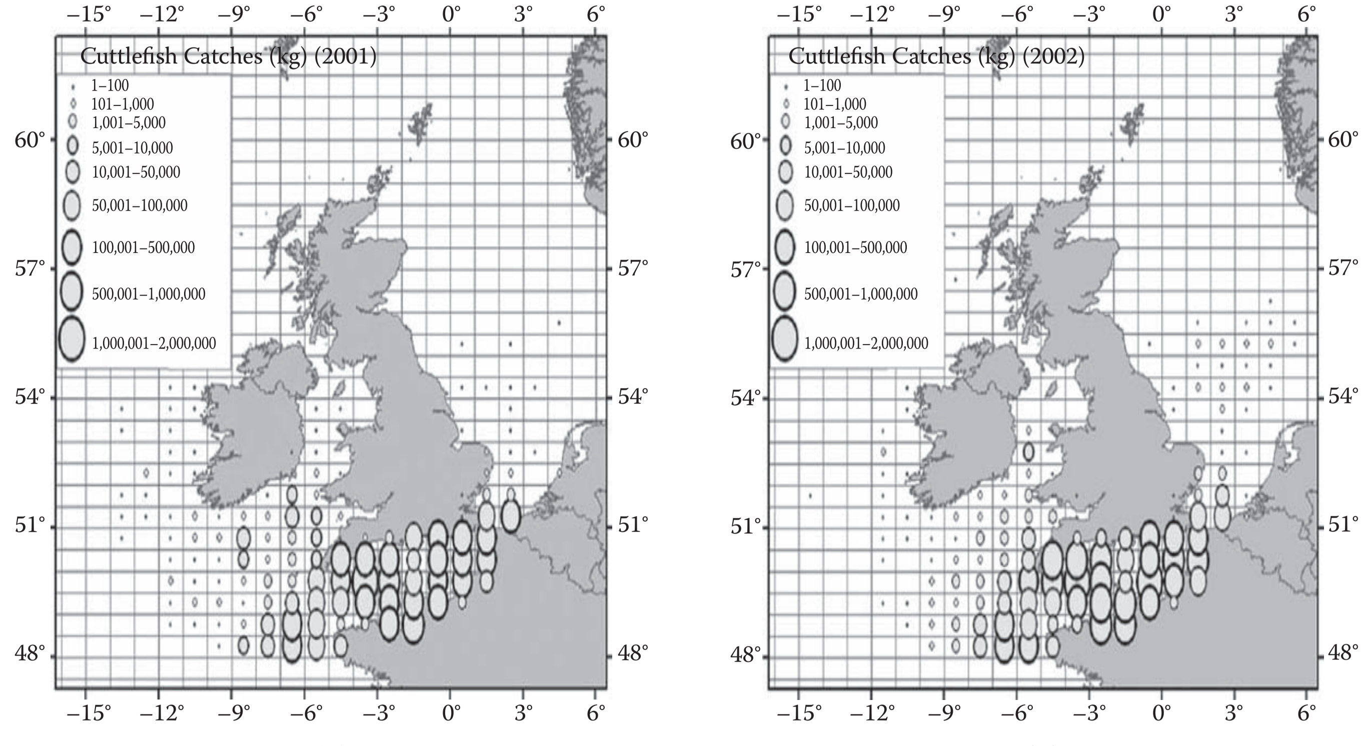
Sepia officinalis is an important commercial species that is exploited by a number of fisheries in Europe. The mean annual catch of this species (1993–2003) was about 41,000 t, taken more or less equally from the Atlantic and Mediterranean (Anonymous 2005). Figure 4c shows the distribution of cuttlefish catches in the north-eastern Atlantic and Mediterranean. The main fisheries for *S. officinalis* are currently based in France (Atlantic) and Italy (Mediterranean). U.K. fleets account for 2200–5100 t per annum, mostly from the English Channel (Anonymous 2005). In the United Kingdom and France, cuttlefish are landed by otter and beam trawlers, both as target species and as a by-catch of demersal fin fisheries. The main northern cuttlefish grounds are located in the English Channel and adjacent waters, the French Atlantic coast and the Bay of Biscay (Denis & Robin 2001; Figure 6). Further south, they are caught by a variety of artisanal gears, including gill nets, trammel nets, traps and jigs. Different cuttlefish species are grouped together in official catch statistics. Although the bulk of reported cuttlefish catches in European waters are *Sepia officinalis*, significant numbers of *S. elegans*, *S. orybignyana* and some sepiolid species (e.g., *Sepietta* spp. *Sepiola* spp., *Rossia macrosoma*) are also taken on occasion and marketed as ‘cuttlefish’ (Dunn 1999, Denis & Robin 2001, Reid & Jereb 2005).


Cuttlefish Catches (kg) (2000)
1–100
101–1,000
1,001–5,000
5,001–10,000
10,001–50,000
50,001–100,000
100,001–500,000
500,001–1,000,000
1,000,001–2,000,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(B)


Cuttlefish Catches (kg) (1999)
1–100
101–1,000
1,001–5,000
5,001–10,000
10,001–50,000
50,001–100,000
100,001–500,000
500,001–1,000,000
1,000,001–2,000,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(A)



(C) (D)

Figure 6 Maps showing distributions of annual cuttlefish (including sepiolid) catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

Table 13 Total annual octopod landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Octopus vulgaris and Eledone* spp.) (Anonymous 2008)

	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	45	47	41	44	29	70	0	51	22	27
France	93	90	216	205	98	81	33	221	154	132
Ireland	7	3	10	12	14	13	0	13	30	3
Netherlands	0	0	0	0	5	0	0	0	1	0
Portugal	9,217	6,446	9,266	9,280	7,284	7,369	7,550	8,840	11,484	3,441
Spain	6,291	6,347	6,133	6,824	3,867	5,119	4,471	4,882	6,031	5,238
United Kingdom	148	110	52	135	164	180	137	188	184	148
Total (ICES)	15,801	13,043	15,718	16,500	11,461	12,831	12,191	14,195	17,906	8,999

Exploitation of incirrate octopods

Total landings of octopods from the north-eastern Atlantic (ICES Area) ranged from 12,000 to 16,000 t per annum during the past decade (Table 13). Three main fishing fleets, based in France, Portugal and Spain, accounted for more than 90% of annual landings (Figure 1d), although relatively big landings (>100 t) were occasionally reported in Ireland and the United Kingdom.

Eledone cirrhosa is one of the most important commercial cephalopod species in southern Europe and is of high value, especially in the western Mediterranean (Mangold & von Boletzky 1987, Relini et al. 1998, Sartor et al. 1998). Figure 4d shows the distribution of octopod catches in the north-eastern Atlantic and Mediterranean. It is usually caught by bottom trawling and more than 90% of the catches in the western Mediterranean are landed (Sartor et al. 1998). Mediterranean catches of *E. cirrhosa* are often separated into two categories for marketing (Belcari et al. 1990, Belcari & Sartor 1999). Small specimens (<5 cm ML) are highly valued and a number of targeted fisheries for these operate in certain areas during spring and summer, coinciding with the annual peak in recruitment (Relini & Orsi Relini 1984, Belcari et al. 1990, Sánchez, et al. 2004). Juvenile *E. cirrhosa*, known as ‘popets’ in Catalonia and ‘moscardini” in Tuscany, are an important component of multispecies trawl fisheries in the Mediterranean (Belcari & Sartor 1999). At present, U.K. fleets account for only 50–230 t per annum (Anonymous 2005), probably reflecting the absence of local markets more than low abundance (Figure 7).

Octopus vulgaris is currently exploited as a target species in both the north-eastern Atlantic and Mediterranean, in depths of 20–200 m, by demersal trawl fleets and numerous small coastal fisheries (utilising hand jigs, pots, traps and trammel nets) operating in southern Europe and north-western Africa.

Conservation issues for cephalopods in the north-eastern Atlantic

Fishing pressure

There are particular problems for the fishery assessment and sustainable management of cephalopod stocks, largely associated with their general biology, short life histories and lack of knowledge for most species (Caddy 1983, Rosenberg et al. 1990, Pierce & Guerra 1994). The typical short life cycle of cephalopods provides little opportunity to adjust fishing effort on individual cohorts (Bravo de Laguna 1989) and renders them vulnerable to overfishing (Bravo de Laguna 1989). In U.K.

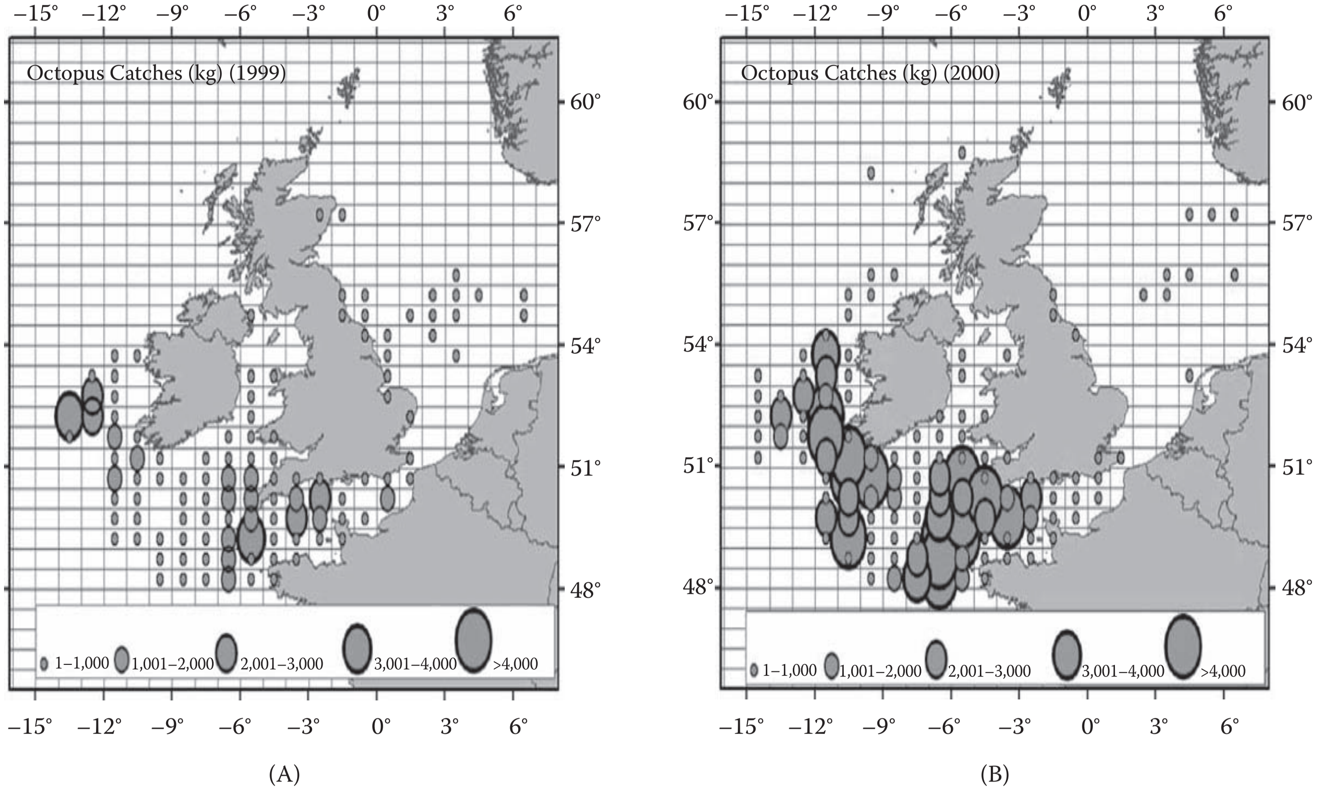


Figure 7 Maps showing distributions of annual (incirrate) octopod catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

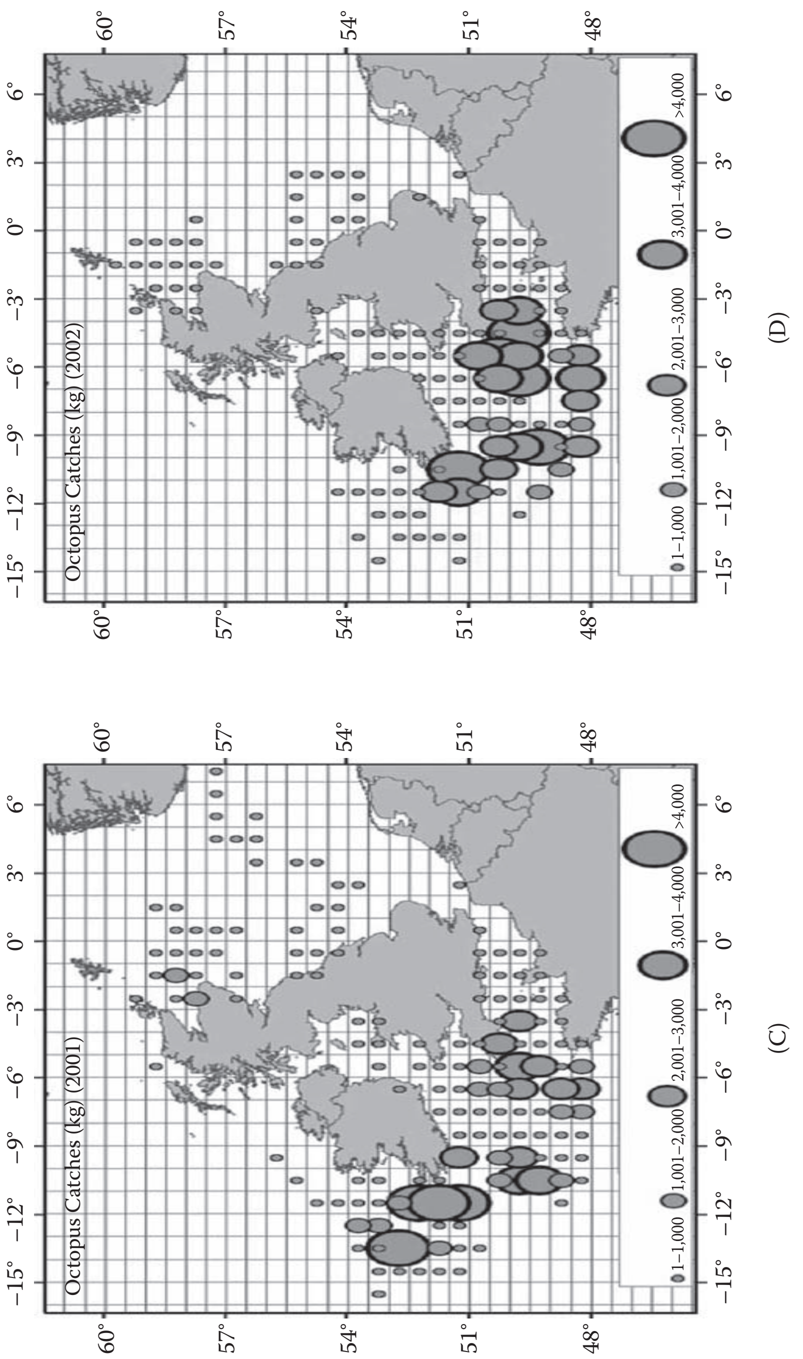


Figure 7 (continued).

waters, the by-catch fisheries take *Loligo forbesi* of a wide range of body sizes. Pierce et al. (1994a) observed that in Scottish catches of *L. forbesi*, mean ML at recruitment is no more than half that of fully mature animals. Thus growth overfishing may already be a problem in U.K. waters (Pierce & Guerra 1994). In the short term, recruitment overfishing may have more serious consequences for cephalopod stocks than for finfish stocks. In the long term, however, cephalopod stocks may be able to recover more quickly from overexploitation (Caddy 1983).

At present, there is very little or no management of cephalopod fisheries in European waters. In Galicia, north-western Spain, the Department of Fishing and Maritime Affairs of the Galician Autonomous Community (Xunta de Galicia) establish an annual ban on *Octopus vulgaris* fishing (from 9 May to 7 July for 2008) and there are seasonal weight restrictions on total catches landed in Spanish ports. Moreover, regional minimum size/weight restrictions are enforced on four species: *Loligo vulgaris* 10 cm, *Sepia officinalis* 8 cm, *Sepia elegans* 4 cm, *Octopus vulgaris* 1 kg (Xunta de Galicia 2007). In Portugal, minimum size/weight restrictions are also enforced for *Loligo vulgaris*, *Sepia officinalis* and *Octopus vulgaris*. A minimum weight restriction of 1 kg is also applied nationally to *Octopus vulgaris*. Squid (mainly *Loligo forbesi*) are largely by-caught by multispecies fisheries and represent a very small proportion of total U.K. fish landings (Pierce & Guerra 1994).

For most cephalopod species, abundance and geographic distribution vary widely from year to year and management options are currently constrained by procedures used to regulate target (whitefish) fisheries (Pierce & Guerra 1994). To date, there have been relatively few attempts to assess cephalopod stocks in the north-eastern Atlantic, and none are subject to routine assessment (Payne et al. 2006). A number of approaches have been employed with some success, including depletion models (Pierce et al. 1996, Young et al. 2004), modified cohort analysis (Royer et al. 2002, 2006), environmental predictors of recruitment (Robin & Denis 1999, Sims et al. 2001, Pierce & Boyle 2003, Zuur & Pierce 2004, Challier et al. 2005) and production models (FAO 1986, Payne et al. 2006). A considerable amount of fisheries-related research has been carried out on a few European stocks, including those of *Loligo forbesi* and *L. vulgaris* (Robin & Denis 1999, Pierce & Boyle 2003). However, most stocks have never been properly assessed (Pierce & Guerra 1994, Payne et al. 2006). Assessments of cephalopod stocks (utilising traditional techniques developed for fish stocks) have been difficult to implement for a number of reasons, including complex (within-year) recruitment patterns, insufficient (targeted) survey data and the susceptibility of distribution, abundance and life history of many species to environmental factors (Boyle & Pierce 1994, Payne et al. 2006, Pierce et al. 2008b).

Heavy metal contamination

Heavy metals, including arsenic, barium, cadmium, chromium, copper, iron, mercury, nickel, lead and zinc, reach the marine environment via rivers and certain marine operations, such as the exploitation of offshore resources and disposal of dredged materials. Highest concentrations of trace metals are found near freshwater outlets, with much lower levels in the open sea. Metallic contaminants are incorporated in the body of top marine predators via the food chain (Bustamante et al. 1998, Lahaye et al. 2005, Stowasser et al. 2005). Consequently, diet is the first factor controlling metal intake (Aguilar et al. 1999). Transfer of trace elements from prey to predator greatly depends on the bioavailability of the metal, which is determined by the detoxification processes in prey species. Metals located in the cytosolic fraction are readily available to higher trophic levels, whereas those bound to the insoluble subcellular fraction have a lower potential for transfer (Wallace & Lopez 1997). Consequently, the physicochemical forms of metals in different prey species appear to be a key factor that might control metal bioaccumulation in top marine predators. The most recent surveys of mercury levels in cephalopods from the north-eastern Atlantic indicated higher levels of mercury in demersal cephalopods than in pelagic species (Bustamante et al. 2006, Pierce et al.

2008b). Concentrations of cadmium were on average much higher in ommastrephid squid than loliginid squid (Pierce et al. 2008b).

As trace elements, certain metals (e.g., copper, selenium, zinc) are essential for the metabolism of organisms, but toxic in high doses. Other metals such as cadmium and mercury play no biological role. Cadmium, for example, derives its toxicological effect from the fact that it closely resembles zinc in its chemical properties and therefore is readily taken up by the body. The main danger of heavy metals to an organism lies in their tendency to be stored in the tissue faster than they can be broken down or excreted, that is, they bioaccumulate to harmful levels in the tissue.

Cephalopods represent an important link in marine food webs, being consumed by many top predators such as marine mammals, birds and fish (e.g., Clarke 1966, Croxall & Prince 1996, Smale 1996, Santos et al. 2001a, Stowasser et al. 2005). Studies of trace metal contents in cephalopod tissues indicated significant bioaccumulation in the digestive gland (hepatopancreas) (Martin & Flegal 1975, Schipp & Hevert 1978, Miramand & Bentley 1992, Caurant & Amiard-Triquet 1995, Bustamante et al. 1998, 2006, Stowasser et al. 2005). The availability of trace metals in cephalopods indicates their importance as vectors of contaminant transfer in the food chain.

Like many other molluscs, cephalopods rapidly accumulate high levels of cadmium, copper, mercury and zinc and other trace metals (Martin & Flegal 1975, Finger & Smith 1987, Stowasser et al. 2005). High levels of copper were found in the digestive gland of several cephalopod species (*Octopus vulgaris, Eledone moschata* and *Sepia officinalis*). Although copper is essential to marine molluscs, these studies revealed digestive gland copper levels 100 times higher than those of vertebrate liver and 105 times that of seawater (Rocca 1969). *Loligo opalescens* from Monterey Bay, California showed copper levels three orders of magnitude higher than concentrations found in other molluscs (Martin & Flegal 1975). Bustamante et al. (1998) found relatively low levels of copper but highly elevated levels of cadmium in the digestive gland of two octopod species in waters off the Kerguelen Islands. Since in molluscs in general copper and cadmium bind on the same metalloproteins in the digestive gland, some competition between the two metals may occur.

Cadmium, mercury and zinc have been shown to accumulate largely in the digestive gland of cephalopod species. High concentrations of cadmium have been found in the digestive glands of *Todarodes pacificus, Illex coindetii*, *Loligo opalescens*, *L. forbesi*, *Ommastrephes bartramii*, *Symplectoteuthis oualaniensis*, *Octopus salutii*, *Graneledone* sp., *Benthoctopus thielei* (Tanaka et al. 1983, Bustamante et al. 1998, Storelli & Marcotrigiano 1999, Craig & Overnell 2003, Stowasser et al. 2005, Pierce et al. 2008b). Even in areas like the Faroe and Kerguelen islands, which are relatively isolated from human activity, high cadmium concentrations were found in both cephalopods and their marine mammal predators (Caurant & Amiard-Triquet 1995, Bustamante et al. 1998). A study of *Sepioteuthis lessoniana* concluded that cadmium was accumulated from food rather than from surrounding seawater and that the digestive gland was the main retention organ in the body (Koyama et al. 2000). Cadmium and mercury levels in squid are highly variable between and within species (Table 14, see Stowasser et al. 2005, Pierce et al. 2008b). Spatial and temporal variations of

Table 14 Concentrations of cadmium (Cd) and mercury (Hg) recorded in four squid species caught in U.K. waters

Species	Sample size (*n*)	Cd concentration[a] (mean, µg.g^{-1} dwt ± SD)	Hg concentration[a] (mean, µg.g^{-1} dwt ± SD)
Alloteuthis subulata	20	9.48 ± 2.30	0.07 ± 0.01
Loligo forbesi	105	12.20 ± 9.92	0.22 ± 0.18
Todaropsis eblanae	23	25.10 ± 25.9	0.13 ± 0.10
Todarodes sagittatus	11	65.3 ± 61.1	0.28 ± 0.11

[a] Levels recorded in digestive gland tissues.

Source: From Pierce et al. 2008b.

Table 15 Monthly concentrations of cadmium (Cd) and mercury (Hg) recorded in *Loligo forbesi* in three geographic areas around the United Kingdom and Ireland

Area	Cd concentration[a] (mean μg.g^{-1} dwt ± SD)		Hg concentration[a] (mean μg.g^{-1} dwt ± SD)	
	Jan	Aug	Jan	Aug
Moray Firth	9.14 ± 3.57	14.9 ± 3.70	0.19 ± 0.06	0.08 ± 0.01
	Mar	Nov	Mar	Nov
Scottish west coast	28.8 ± 19.00	11.9 ± 10.30	0.31 ± 0.05	0.13 ± 0.08
	Apr	Nov	Apr	Nov
Irish west coast	18.10 ± 2.94	30.2 ± 8.18	0.36 ± 0.27	0.08 ± 0.01

Source: From Pierce et al. 2008b.

Table 16 Mean concentrations of trace metals in squid and whiting and median values recorded in piscivorous (porpoise, minke whale) and teuthophagous (Risso's dolphin, sperm whale) marine mammals in Scottish waters (mg/kg wet weight) (FRS, 1998)

	Cadmium	Copper	Lead	Zinc	Mercury	Arsenic
Squid	0.030	7.12	0.02	11.0	0.03	7.91
Whiting	0.001	0.14	<0.01	3.75	0.04	4.27
Risso's dolphin	5.00–8.73	4.18–9.09	0.10–0.89	26.7–46.2	1.47–5.22	—
Sperm whale	17.0	5.00	0.73	48.3	22.7	—
Porpoise	0.016	11.5	0.11	48.5	1.02	—
Minke whale	0.13	3.93	<0.07	87.4	1.84	—
FSC	0.02	20	2	50	0.5	—

Note: Limits set by the Food Standard Committee (FSC) are shown for comparison.

the concentrations of these metals in the tissues of *Loligo forbesi* were also observed, with the highest levels recorded west of Scotland during March (Table 15) although these may be confounded by seasonal migrations (Stowasser et al. 2005).

The potential for bioaccumulation and biomagnification of metals in the food chain is illustrated by results from a survey conducted by the U.K. Fisheries Research Services (FRS 1998). The mean concentrations of trace metals in squid (presumably *L. forbesi*), a fish (whiting) and various marine mammals are presented in Table 16. The Food Standards Committee's maximum recommended limits are also given for comparisons. In squid, levels of cadmium were 30 times those in whiting (*Merlangus merlangius*) and exceeded recommended safe limits for food. The presence of biomagnification could clearly be seen from highly elevated levels in cadmium in the marine mammals and the teuthophagous species compared to the piscivorous species.

Cephalopods are potentially an important (seafood) source of increased burdens of cadmium and mercury in human tissues (Pierce et al. 2008b). The viscera, containing elevated levels of these metals, are normally removed prior to consumption (thereby reducing exposure to contamination). However, in a number of countries, including Italy and Spain, small *Loligo* spp. and *Alloteuthis* spp. are often eaten whole (Shaw 1994). In Japan, the digestive gland is in fact considered to be a delicacy. Consideration of these 'high-risk' consumer groups is required, therefore, when evaluating the implications of heavy metal contamination of cephalopod tissue for public health (Pierce et al. 2008b).

Oil and gas production

At present, offshore oil and gas production is a major environmental issue in European waters, with important sedimentary basins in the North Sea, Irish Sea and north-eastern Atlantic (Pierce et al. 2002, Stowasser et al. 2004, Sacau et al. 2005). The main risks of oil pollution are currently from accidental spills, bunkering operations, fishing vessel casualties and tanker source spillages (Advisory Committee on Protection of the Sea [ACOPS] 1999). A wide variety of wastes is produced during oil and gas production. Some regulated discharge of wastes into the sea is permitted. These wastes include machinery cooling water, deck drainage, domestic sewage, drill cuttings, drilling fluids and produced waters. In addition, submerged structures and equipment may be protected against corrosion and fouling with sacrificial anodes and antifouling coatings that leach toxic metals (aluminium, copper, mercury, tin, zinc) into the water column (Sacau et al. 2005). Major discharges associated with drilling operations are drill cuttings and drilling fluids (Menzie 1983). Drill cuttings are particles of crushed, relatively inert sedimentary rock contaminated with drilling fluid residue and thus a potential source of several trace metal pollutants, including arsenic, barium, chromium, cadmium, copper, iron, lead, mercury, nickel and zinc (Neff et al. 1987). However, as noted in the previous section, the uptake of these elements by cephalopods is probably more of an issue for consumers of cephalopods than for the animals themselves.

There may also be problems for cephalopods associated with oil and gas exploration activities. Nine stranded giant squid (*Architeuthis* sp.) were recovered from Spanish waters during 2001–2003. On examination, no surface damage was observed but all specimens had massive internal injuries. These may have been caused by offshore seismic surveys for oil and gas that were being conducted in the vicinity during this time (Guerra et al. 2004b). Oil and gas production and exploration will continue in the north-eastern Atlantic for a considerable period.

Radionuclide contamination

Radionuclides discharged by the nuclear industry may also have a contaminating effect on marine biota. The main contribution to anthropogenic marine radioactivity is from global fallout from nuclear testing performed in the atmosphere. Due to global atmospheric transports and precipitation patterns the fallout is maximal at mid-latitudes between 30° and 60° and minimal at the equator and poles. Fewer nuclear tests in the Southern Hemisphere and the limited stratospheric exchange between hemispheres cause 76% of fallout to occur in the Northern Hemisphere (Aarkrog 2003).

In U.K. waters, the concentrations of anthropogenic radionuclides in the marine environment have also been significantly influenced by waterborne discharges from European nuclear reprocessing plants, notably Sellafield in the United Kingdom and Cap de la Hague in France (Livingston & Povinec 2000). Many radionuclides exhibit low solubility in seawater and high particle reactivity. This means in coastal regions they are rapidly removed from the water column and absorbed in sediments (Livingston & Povinec 2000). For example most of the plutonium discharged by Sellafield remains in a relatively narrow coastal zone incorporated into sediments. However initial discharges from Sellafield in the late 1970s were so large that suspended particles of plutonium could be measured in seawater at distances of hundreds of kilometres in the North Atlantic. Although recent years have seen the improvement of waste treatments, Sellafield is still a major source of potentially harmful radionuclides such as iodine and technetium. These are highly soluble in seawater, have very long half-lives, are transported over long distances from the source and readily accumulate in seafood (STOA 2001, Aarkrog 2003).

The danger of radionuclides lies in their accumulation in living tissues and the consequent transport and further concentration to toxic levels along the food chain. Studies of radionuclides in U.K. waters found that concentrations declined over the last decade and reflected decreasing emissions from the Sellafield plant in the same period (STOA 2001 and Table 7). Watson et al. (1999) found activity concentration of both plutonium and caesium in seals and porpoises to decrease with increasing distance from the source (Sellafield) and found elevated concentrations in animals of higher trophic levels and higher weights within the same species. Concentrations of plutonium and americium were found to be high and mainly unchanged over the course of 10 yr in shellfish (molluscs) from the Irish Sea. In contrast concentrations in fish were hardly detectable and low in crustaceans. Levels declined over the course of 10 yr for both taxa in concordance with decreasing emissions from the Sellafield reprocessing plant (Ryan et al. 1999).

A food web study from the Norwegian and Barents Sea found radiocaesium concentrations to be low for this area (Heldal et al. 2002). However, concentrations were found to multiply from lowest levels in krill and squid (*Gonatus fabricii*) by a factor of 10 to highest values found in harbour porpoise (*Phocoena phocoena*). Studies of naturally occurring radionuclides in marine organisms found polonium concentrations to be dependent of the diet of the organism (Cherry et al. 1989, Carvalho & Fowler 1994). High concentrations were found in benthic molluscs and marine mammals through bioaccumulation from lower trophic levels. Both fish and squid (*Loligo vulgaris*) showed lower levels than either other shellfish species or marine mammals (Cherry et al. 1989, Heyraud et al. 1994, Dahlgaard 1996, Betti et al. 2004). Contamination levels in molluscs seemed to be related to reproductive cycles in *Mytilus galloprovincialis* (Charmasson et al. 1994) and ontogenetic changes in feeding in the case of *L. vulgaris* (Heyraud et al. 1994).

Climate change

Cephalopods are highly sensitive to environmental conditions and change at a range of spatial and temporal scales (Pierce et al. 2008a). Two main types of relationship between cephalopod population dynamics and environmental conditions are recognised. These concern effects on the geographic distribution of species abundance and on critical biological processes such as egg survival, growth, recruitment and migration. Species-environment interactions are influenced by both large-scale atmospheric and oceanic processes and local environmental variations (Pierce et al. 2008a). Mobile pelagic species, such as ommastrephid squids, are directly affected by oceanographic conditions, whilst shallow-water, neritic species such as cuttlefish may be impacted by coastal variations in water quality and salinity that are influenced by rainfall and run-off. Climate change, therefore, is expected to have a significant effect on many cephaliopod species in the north-eastern Atlantic and elsewhere.

The embryonic development and hatching, growth and maturation, timing of reproduction and migration and biogeographic distribution of many cephalopod species are influenced by temperature (Boyle 1983). Observed changes in abundance of the squid *Loligo forbesi* in Scottish waters appeared to be related to climatic variation. Pierce & Boyle (2003) reported significant correlations between abundance of *L. forbesi* in coastal waters of the North Sea and a number of annual environmental indices, including winter NAO Index, average SST and sea-surface salinity. SST in particular appeared to influence recruitment strength.

North Atlantic climatic variation also appears to affect the timing of migration of *Loligo forbesi* in the English Channel. Analyses of historical research survey data by Sims et al. (2001) indicated that the eastwards migration of this species was earlier when water temperatures in the preceding months were higher, corresponding with warm (positive) phase of the NAO. The difference in timing of peak squid abundance between the warmest and coolest years was 120–150 days. Sea bottom temperature appeared to determine the extent of squid movement. It was also noted that these effects of water temperature and climatic fluctuations on the timing and extent of squid movements occurred irrespective of season (Sims et al. 2001). Since the early 1990s, marked declines in catches of *L. forbesi* in Iberian waters indicated a disappearance of this species from much of the southern part of its range, possibly linked to a rise in SST observed during this period (Chen et al. 2006).

Other loliginid species from different parts of the world also appear to be affected by climatic variations. On the Falkland Shelf, for example, seasonal changes in migratory patterns of Patagonian long-fin squid (*Loligo gahi*) have been associated with changes in water mass characteristics. A 5.5°C isotherm appeared to limit the distribution of *L. gahi* to deeper waters, irrespective of season, whilst the distribution of squid on the feeding grounds was associated with the warmest possible water layers (Arkhipkin et al. 2004). The extent of frontal waters and SST are affected by climate in the South Atlantic and these appear to directly influence annual recruitment success of an ommastrephid species, the Argentinian short-fin squid *Illex argentinus* (Waluda et al. 2001). As Robinson et al. (2005) pointed out, any significant long-term changes in these associated with climate change could therefore affect the distribution and abundance of *I. argentinus*.

Therefore, as mentioned, important changes in cephalopod biodiversity in the north-eastern Atlantic may occur within the next few decades. Global warming (sea temperature rise), for example, may result in the continued advance of a number of warm-water species into the north-eastern Atlantic and the simultaneous retreat of certain cold-water species to higher latitudes.

Another process associated with climate change that may affect cephalopods is the general rise in oceanic CO_2 concentration that has been observed in recent years. For example, ommastrephid squid such as *I. argentinus* are characterised by high metabolic rates and extremely pH-sensitive blood oxygen transport systems, and elevated CO_2 may affect their growth and reproduction (Pörtner et al. 2004).

Disturbance of spawning grounds

Another serious potential impact on cephalopod species in U.K. waters would be the physical disturbance of spawning grounds due to displacement of bottom sediments. Models of the distributions of mature adult *Loligo forbesi* in relation to habitat characteristics suggest that extensive areas of seabed within U.K. waters are potentially suitable spawning habitat for this species, although it remains unclear how many of these areas are actually used by squid (Stowasser et al. 2005). However, at present it is unclear how many of these areas are actually used by squid. Since *L. forbesi* is an annual species (Boyle et al. 1995), serious failure to reproduce and recruit in one year may endanger the survival of the population. In U.K. waters, spawning could occur over an extended area and the *L. forbesi* population is probably less dependent on specific spawning sites so that localised disturbance would not affect breeding success of the whole population. However, seasonal targeted fishing for squid, particularly in restricted areas where high concentrations of spawning activity occur, may have some impact on spawning success.

It is possible that drilling activities, dredging operations (gravel extractions) and extensive fisheries could have an impact on spawning grounds of *Loligo forbesi*. High turbidity is known to disrupt spawning behaviour in *L. vulgaris* in South African waters while low oxygen levels can limit distribution (Augustyn 1991). However cephalopod diversity is unlikely to be significantly affected by such disturbance since drilling operations are localised. Quantifying the effects of human activity on the marine ecosystem is problematic since no pristine 'baseline' marine habitats exist and historical data are sparse—and may still be impacted by historical activities (Frid et al. 2000).

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EXPLOITATION AND CONSERVATION OF ECHINODERMS

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Abstract The phylum Echinodermata contains some of the most charismatic benthic marine invertebrates and has become a symbol of marine life. However, growing global pressures on the collection of echinoderms for various commercial enterprises have put these enigmatic invertebrates under threat. This review summarises the demands on echinoderms from commercial fisheries, aquarium and souvenir trades, as part of the global search for bioactive compounds from marine organisms, and as experimental models in evolution and toxicology, and highlights the urgent need for an integrated global strategy for their protection and conservation. Sea urchins and sea cucumbers are fished commercially worldwide. Increased landings, limited information on population biology and lack of stringent management of the fisheries have resulted in a global decline of populations. In addition to being a target species for commercial fishing, many echinoderms form part of the significant by-catch produced from the general use of fishing hardware. Even when they are not caught directly, echinoderms may be damaged to varying degrees as the gear passes over them and may be affected indirectly by the physical disturbance caused by fishing gear to the seafloor. Echinoderms are gaining popularity with aquarists and account for about 17% of the global trade. Pharmaceutical companies are constantly screening marine organisms for biochemical compounds for potential use in medicine, traditional healing and industrial applications. The marine bioprospecting industry is not regulated and, although at an early stage of development, the huge potential of echinoderms to provide bioactive products highlights the need for urgent action to regulate this kind of activity. Echinoderm embryos and larvae have been used as experimental model systems in several lines of research for more than a century, leading to significant advances in the areas of developmental biology, cell biology and immunology. In addition, echinoderms are well known for their striking regenerative capacity and have provided a valuable experimental model to identify the genes involved in the process of neural regeneration. Sea urchin gametes, embryos and larvae have also been used for fast, low-cost and reliable screening of toxic substances, and for detailed studies of their mechanism of action. One way to mitigate the commercial exploitation of wild echinoderm stocks is to develop laboratory culture methods to produce individuals for reseeding exploited populations and this is being done with sea urchins and sea cucumbers. However, releasing large numbers of captive-bred animals into the wild will undoubtedly affect the genetic composition of local populations, giving rise to important ethical issues related to the loss of a genetically unique wild stock. To aid conservation, it is necessary to improve the collection of data to quantify the extent of harvesting echinoderms and to document the location and catch data by species. It is also necessary to develop a global database of echinoderm species to summarise information on biology, ecology, threats, monitoring and conservation. Beyond increasing the number of echinoderm species to be protected, it is important to improve the conservation management of already protected species.

Introduction

The phylum Echinodermata contains approximately 6500 living species and holds a unique phylogenetic position in Kingdom Animalia as the only major group of deuterostomous invertebrates (Ruppert & Barnes 1994). Echinoderms are stenohaline marine invertebrates and their limited osmoregulatory ability (Clark 1968) restricts the majority of species to the marine environment. As such, the phylum has become a symbol of marine life. Extant echinoderms include seastars (Asteroidea), brittlestars (Ophiuroidea), sea urchins (Echinoidea), crinoids/sea lilies (Crinoidea) and sea cucumbers (Holothuroidea).

Growing global pressures on the collection of echinoderms for various commercial enterprises have put these enigmatic invertebrates under threat, adding to the ongoing concern over the continued worldwide depletion of marine resources and, particularly, the ecological cascading effects of overfishing on the structure and functioning of entire ecosystems (Botsford et al. 1997, Thrush et al. 1998, Tegner & Dayton 2000, Chuenpagdee et al. 2003). Sea urchins and sea cucumbers are under high commercial fishing pressure, and various aspects of their biology are likely to compound the impact of overexploitation of wild populations. For example, recruitment of juvenile sea urchins and sea cucumbers is both sporadic and unpredictable (Kelly 2000, Harris et al. 2001, Lawrence 2001). Also, some species of sea urchin and sea cucumber are extremely long-lived, which tends to be an indicator of uncertainty in reproductive success (Ebert & Southon 2003). Temporal variability in population density is a common factor in sea urchins (Ebert 1998), even within populations of a single species (Himmelman 1978, Pearse & Cameron 1991, Lozano et al. 1995). This variability is explained by the fact that the reproductive cycle is determined by environmental cues (temperature, photoperiod, food availability and hydrodynamism), which are subjected to periodic cycles whose intensities and patterns vary according to geographical localities (Vaïtilingon et al. 2005). Sea urchins and sea cucumbers are susceptible to overexploitation also because of specific habitat requirements, such as a limited zone within reef habitats, algae, or seagrass beds (Bruckner et al. 2003), and a marked sedentary lifestyle (Kelly 2005), which make them an easy fishery target.

In addition to overfishing, the emerging global trade in the collection of echinoderms for home aquaria, souvenirs and biomedical products is at a critical stage and certain species of echinoderms are now listed as threatened species. This review summarises the demands on echinoderms from commercial fisheries, aquarium and souvenir trades, as part of the global search for bioactive compounds from marine organisms, and as experimental models in evolution and toxicology and highlights the urgent need for an integrated global strategy for their protection and conservation.

Commercial fisheries

Of the five extant classes of echinoderms, only sea urchins and sea cucumbers are heavily exploited (Kelly 2005). There is a limited, localised commercial fishery for seastars but reported global landings are small, unreliable and strongly dominated by the fishery for *Asterias rubens* in Denmark (Sloan 1985). The latter seastar is exported to West Germany as an additive to finfish meal for poultry feedstocks (Sloan 1985). In the United States, seastar fisheries are uneconomical due to high production costs and low product quality (Loosanoff 1961). Although Sloan (1985) considered that it was unlikely that seastars would become an object of appreciable new meal fisheries, there is an emerging demand for them in the Asian food markets but, unfortunately, the extent of this demand is not documented.

Male and female sea urchins are collected for their gonads, referred to as 'roe' (Kelly 2005), a food delicacy that fetches high prices in Asian and Mediterranean markets (Sloan 1985). Individuals are picked off the seabed by hand by divers operating in near-shore waters or are collected using dredges (Bergman & van Santbrink 1994). The quantity and quality of roe are vital to the market and are considered critical to the profitability of the processing operation. Because these roe attributes are not apparent externally, animals need to be cracked open, resulting in a high level of mortality and many discarded individuals (Kalvass & Hendrix 1997). There are established fisheries in Chile, northern Asia (Japan and Korea), Maine, California and Alaska (United States), Baja California (Mexico), Russia, and British Columbia, New Brunswick and Nova Scotia (Canada) (Andrew et al. 2002). Japan consumes more than 80% of the world's catch of sea urchin roe (Sonu 1995, Hagen 1996), followed by France (Hagen 1996). The growth of modern markets, particularly in Japan, has led to the development and expansion of new fisheries for sea urchin roe particularly around the Pacific Ocean and Mediterranean Sea (Williams 2002). Different sea urchin species are the target in different fishery regions (Table 1). World catches peaked in 1995 with global landings of 113,654 tonnes (t), representing a 3-fold increase in production over 25 yr (Williams 2002). As a supplier market, Chile landed some 54,600 t in 1995 making it the world's largest producer of sea urchins but this level of production was regarded as unsustainable (Jimmy et al. 2003). Smaller fisheries in Europe supply domestic markets in the main but Portugal, without a local market, exported 15 t of sea urchin in 2002 to the United States and Japan (Instituto Nacional de Estatistica 2003). The fishery statistics (Table 1) clearly demonstrate that most of the world's urchin fisheries are fully or overexploited and it is generally accepted that further sea urchin fishing grounds are unlikely to be discovered (Keesing & Hall 1998). Where appropriate management strategies have not been put in place, sea urchin fisheries in France (Mediterranean and Atlantic), Iceland, Ireland, South Korean (inshore) and the Philippines have collapsed (Williams 2002).

Table 1 Sea urchin species with a major contribution to the modern fishery

Species	Common name	Fishery distribution
Anthocidaris crassipina	—	Japan, Korea, China
Centrostephanus rodgersii	Purple crowned urchin	Australia, New South Wales
Echinometra spp.	—	Circumpolar–Caribbean
Evechinus chloroticus	Kina	New Zealand
Glyptocidaris crenulatus	—	China
Heliocidaris erythrogramma	Purple sea urchin	New South Wales
Heliocidaris tuberculata	—	New South Wales
Hemicentrotus pulcherrimus	—	Japan, Korea, China
Loxechinus albus	Erizo	Chile, Peru
Lytechinus variegatus	—	West Atlantic, Caribbean
Paracentrotus lividus[a]	—	Atlantic, Mediterranean
Pseudocentrotus depressus	—	Japan, Korea
Strongylocentrotus droebachiensis	Green sea urchin	Circumpolar–North
Strongylocentrotus franciscanus	Red sea urchin	Chile, Mexico, Northeast Pacific
Strongylocentrotus intermedius	—	Japan, Russia, Korea
Strongylocentrotus nudus	—	Japan, China
Strongylocentrotus pallidus	—	Russia
Strongylocentrotus polyacanthus	—	Russia
Strongylocentrotus purpuratus	Purple sea urchin	Mexico, Northeast Pacific
Tripneustes esculentus	—	Circumpolar–Caribbean
Tripneustes gratilla	—	Indian Ocean

[a] Species regulated in the Mediterranean by the Barcelona Convention. Adapted from Williams 2002.

About 42 species of sea cucumbers ('bêche-de-mer' or 'trepang') are fished commercially (Bruckner 2005, Conand 2005) for their proteinaceous body wall, which is boiled and dried. The Chinese have imported sea cucumbers for over 1000 yr from India, Indonesia and the Philippines but traders began gathering them from a wider area in the eighteenth and nineteenth centuries (Conand & Byrne 1993). During the 1990s, the number of producing countries (and species exploited) increased worldwide and holothurian fisheries became established in many non-traditional fishing areas such as Mexico, the Galapagos and North America (Bruckner et al. 2003). Growing evidence indicates that sea cucumber populations are declining worldwide, including Australia, India, Madagascar, Thailand, Papua New Guinea and the Galapagos (Conand 1997, Jaquemet et al. 1999, Bruckner et al. 2003).

In traditional cucumber fisheries of the Indo-Pacific, several species are targeted in the same fishing grounds. In other tropical fisheries, such as in the Indian Ocean, eastern Pacific and Caribbean, the fishery generally focuses on a few species that seldom occur in the same fishing area; temperate fisheries are monospecific (Conand 2004, 2005, Bruckner 2005). The stocks of many tropical and temperate species are reportedly overharvested (Lovatelli et al. 2004, Bruckner 2005, Uthicke & Conand 2005, Toral-Granda 2006) (Table 2). However, the exact contribution of each species to the total fishery is not known because sea cucumbers are rarely differentiated to species in trade reports. While there is substantial information on the main markets and trade routes, there is a lack of information regarding the location and volume of harvest years (Bruckner et al. 2003). A marked

Table 2 Sea cucumber species that contribute to the modern fishery

Species	Common name	Fishery distribution
Actinopyga echinites	Brownfish	South Pacific
Actinopyga lecanora	Stone fish	South Pacific
Actinopyga mauritiana	Surf red fish	South Pacific
Actinopyga miliaris	Black fish	South Pacific
Apostichopus japonicus	Thorn trepang	Pacific
Bohadschia argus	Leopard (tiger) fish	South Pacific, South-East Asia
Bohadschia graeffei	Orange fish	South Pacific, South-East Asia
Bohadschia marmorata marmorata	Chalky fish	South-East Asia, South Pacific, Red Sea
Bohadschia marmorata vitiensis	Brown sandfish	South-East Asia, South Pacific, Red Sea
Bohadschia vitiensis	Brown sandfish	South Pacific, Indian Ocean
Halodeima atra	Lolly fish	South Pacific
Halodeima edulis	Pink fish	South Pacific
Halodeima fuscogilva	White teatfish	South Pacific, South-East Asia, Indian
Halodeima nobilis	Black teatfish	South Pacific, South-East Asia
Halodeima scabra	Sandfish	South Pacific, South-East Asia, Indian
Halodeima scabra versicolor	Golden sandfish	South Pacific, South-East Asia
Holothuria fuscocinerea	Stone trepang	Pacific
Holothuria nobilis	Black teatfish	Pacific
Holothuria pervicax	Tiger spotted trepang	Pacific
Holothuria scabra	Sandy-fish	Pacific
Isostichopus fuscus	—	Indo and eastern Pacific
Parastichopus californicus	—	Canada
Stichopus chloronotus	Green fish	South Pacific, Indian
Stichopus hermanni	Curry fish	South-East Asia, South Pacific
Stichopus variegatus	Yellow meat	Pacific
Thelenota ananas	Prickly redfish	South Pacific
Thelenota anax	Amberfish	South Pacific

Adapted from Bruckner et al. 2003 and Chen 2003.

increase in landings and export of holothurians, combined with a limited amount of fishery data, a paucity of biological information on population parameters for commercially important species, and the existence of few management measures are all factors involved in the global decline of holothurian populations (Conand & Byrne 1993, Bruckner et al. 2003). Once sea cucumber density is reduced below a critical mass, populations may take as long as 50 yr to recover (Dalzell et al. 1996, Battaglene 1999, Bruckner et al. 2003). Most commercial sea cucumbers are detritivores and the bioturbation they cause during feeding plays a key role in nutrient cycling within the marine ecosystem (Bakus 1973, Uthicke & Klumpp 1998, Uthicke 1999, 2001). In addition, sea cucumbers consume and grind sediment and organic matter into finer compounds, turning over the top layers on the sea bed, allowing oxygen to enter the sediment. Basically, they are responsible for the extensive shifting and mixing of the substratum and recycling of detrital matter (Bruckner et al. 2003). This constant cycling prevents the accumulation of organic matter and may help control pathogens (Toral-Granda 2006). The consequences of sea cucumbers becoming locally ecologically extinct are not fully understood but cascade effects may be expected. For example, sea cucumbers such as *Isostichopus badionotus* rework the sediment (Webb et al. 1977) and are important in determining habitat structure for other species; their removal may result in the loss of these other benthic species (Lovatelli et al. 2004, Bruckner 2005). In some ecosystems, sea cucumbers represent a substantial portion of the ecosystem biomass (Bruckner et al. 2003) and their eggs, larvae and juveniles constitute an important food source for other marine species, including crustaceans, fishes and molluscs; rapid declines in sea cucumber populations may have serious consequences for the survival of other species that are part of the same complex food web. Finally, several species of sea cucumbers have unique symbionts such as bacteria, protozoans and metazoans, including molluscs and fishes, which may disappear on removal of the host (Bruckner et al. 2003).

Commercial fishing by-catch

All fishing hardware results in a significant by-catch (Roberts 1997) but the number of by-catch species collected is difficult to estimate because they are mostly not recorded in catches and are not regulated by quotas (Ryan et al. 1997). Discards from trawling are dumped at sea, sink to the bottom and decay where they reduce the oxygen levels in the benthic layer and make the habitat less suitable for many benthic organisms (Jones 1992). Although there is no global quantitative information on by-catch, it is likely that millions of corals, sponges, seastars and other invertebrates are caught each year around the world (Bergmann et al. 2002). Invertebrates account for up to 90% of the numbers of animals discarded and up to 73% of these are echinoderms (Pranovi et al. 2001). Over extensive regions of the eastern English Channel, Bristol Channel and Irish Sea, echinoderms are the dominant invertebrate component of beam trawl catches and account for approximately 29% of the biomass in each sample (Ellis & Rogers 2000). In the Clyde Sea (Scotland, U.K.) *Nephrops* fishery, 50–90% of the catch (by volume) is discarded (Bergmann et al. 2002).

Even when they are not caught by the gear, echinoderms may be damaged to varying degrees as demersal trawls pass over them (Wassenberg & Hill 1993, Kaiser & Spencer 1995, Kaiser 1996). For example, sea urchins are either damaged when tickler chains pass through the sediment or are crushed when dropped on to the deck (Bergman & Hup 1992). Seastars (*Asterias rubens*) and brittlestars (*Ophiura ophiura*) are the most abundant echinoderm species discarded in the Clyde Sea area and the Irish and North Seas (Fonds 1994, Kaiser & Spencer 1995, Bergman et al. 1998). Almost 60% of *Asterias rubens* and 100% of *Ophiura ophiura* caught by commercial trawls in the Clyde Sea area show signs of recent injury such as punctures in the epidermis, loss of arms, broken arms and damage to the oral disc (Bergmann & Moore 2001). Such injuries may be caused by physical contact with the fishing gear, interactions with other species in the catch, or handling by the crew. Alternatively, parts of arms or whole arms may be autotomised deliberately in attempts to escape or to reduce adverse effects after injury has occurred (Emson & Wilkie 1980, Pranovi et al. 2001). Injuries (loss of epidermis, autotomy) and trauma due to trawling can render seastars susceptible to bacterial infection (Bang & Lemma 1962, Pranovi et al. 2001). Echinoderms may be affected indirectly by the impacts of trawls and dredges on the benthic habitat, which include substratum alteration by scraping, ploughing or resuspension (Jennings & Kaiser 1998). The effects of these impacts vary according to the fragility of the habitat and severity of natural disturbance.

Echinoderms in the aquarium and souvenir trades

Many marine invertebrates, including echinoderms, are popular in the aquarium trade. Mexico, Indonesia, Singapore, Fiji, Sri Lanka, Philippines and Vanuatu are the main exporters, accounting for close to 17% of the global trade (Wabnitz et al. 2003). The most commonly collected seastar in the aquarium trade is *Linckia laevigata,* which is taken mainly from the shallow waters of the tropical Indo-Pacific (Shimek 2004). According to the Global Marine Aquarium Database (GMAD), this species accounts for 3% of the total global trade in marine invertebrates. Almost all *L. laevigata* are taken from the wild, with few resulting from captive breeding (Wabnitz et al. 2003). Calado (2006) identified 11 echinoderm species in Portuguese waters as potential target species for the marine aquarium trade (Table 3).

Lack of legislation on the capture and trade of ornamental species in European waters, associated with the high market prices that marine ornamental species can attain and the growing restrictions on tropical marine ornamental collection and trade (Wood 2001), may lead to unsustainable use of these new and valuable resources (Table 3), further impairing the conservation of marine habitats (Calado 2006).

The fishery for the seastar *Oreaster reticulatus* has resulted in its decline in Canadian shallow-water populations (Sloan 1985); nevertheless illegal harvesting of *O. reticulatus* has started in Panama, and seastars are sold as souvenirs to tourists and for the aquarium trade at some localities such as Isla Grande, Portobello and San Blas (Guzmán & Guevara 2002). Certain countries in the Caribbean, for example Mexico, Jamaica, Trinidad, Venezuela and others, allow the extraction of *O. reticulatus* without apparent restrictions, which could increase short-term demand and commerce in other areas once the populations in these countries diminish (Guzmán & Guevara 2002).

Little is known of the true extent of the global use of echinoderms as souvenirs, although dried seastar candleholders, toy cars sporting sea urchins as wheels, and sand dollar necklace pendants are seen frequently in souvenir shops (Guzmán & Guevara 2002). The limited information available

Table 3 Echinoderms from Portuguese waters of potential for the ornament industry

Class	Species	Common name
Crinoidea	*Antedon bifida*	Atlantic feather star
Echinoidea	*Arbaciella elegans*	
	Brissus unicolor	Groove burrowing urchin
	Centrostephanus longispinus[a]	Banded urchin
	Cidaris cidaris	Pencil spine urchin
	Diadema antillarum	Lime urchin
	Echinocardium cordatum	Sea potato
	Spatangus purpureus	Heart urchin
Asteroidea	*Echinaster sepositus*	
	Ophidiaster ophidianus[a]	Red seastar
Ophiuroidea	*Ophioderma longicauda*	Snake brittle star

[a] Species with strict protection under the Barcelona Convention.

Adapted from Calado 2006.

comes from the results of a survey of the Mexican echinoderm trade (people involved in various aspects of the echinoderm trade along Mexico's Pacific and Caribbean coasts were interviewed (www.sheddnet.org, www.projectseahorse.org). Currently, in Mexico, an estimated 62 fisheries, each collecting an average of 12,000 seastars annually, collect seastars for the souvenir industry; at least 200 retail stores in major tourist centres sell seastars or sea urchins individually or as part of other shell crafts.

Use of echinoderms in biotechnology

Pharmaceutical companies are constantly screening marine organisms for biochemical compounds for potential use in medicine (e.g., cures for cancers), traditional healing (e.g., fertility enhancers) and for industrial applications (e.g., bioadhesives). Various biologically active substances have been isolated from echinoderm species. Kuznetsova et al. (1982) demonstrated that triterpene glycoside, isolated from 19 holothurian species of the Pacific tropical zone, exhibited cytotoxic activity against yeast and tumour cells. Haug et al. (2002) isolated antibacterial activities from extracts of several tissues from the sea urchin *Strongylocentrotus droebachiensis*, the sea cucumber *Cucumaria frondosa* and the seastar *Asterias rubens*. Palagiano et al. (1996) isolated up to 20 steroid glycosides (that caused growth inhibition in bacteria and fungi) from the starfish *Henricia downeyae*. The detected antibacterial activity indicates that echinoderms may serve as a useful source when searching for novel antibiotics (Petzelt 2005).

It has been shown that novel polysaccharides present on echinoderm surfaces seem able to stimulate early host defence and microbial clearance, but not the later phases of inflammatory tissue injury associated with sepsis. These are the most promising alternative or integrative treatments for pneumonia currently under development (Cazzola et al. 2004, Zito et al. 2005).

Lectins are proteins that possess binding sites for specific mono- and oligosaccharides (Kelly 2005). In marine invertebrates, lectins act as humoral factors in the defence mechanism, resulting in activation of phagocytes (Petzelt 2005). After binding to the specific carbohydrate chains on the erythrocyte surface, these lectins damage the cell membrane, leading to cell lyses (Petzelt 2005). Several unique lectins are found in echinoderms (Petzelt 2005). A lectin with biological activities such as mitogenic and chemotactic characteristics was described in the venom of the pedicellariae of the sea urchin *Toxopneustes pileolus* (Nakagawa & Kimura 1982). Another lectin, which exhibited cytotoxicity against mouse cancer cells and human lung cancer cells, was isolated from brown sea cucumbers (Gana & Merca 2002). These studies provide evidence that the unique lectins from echinoderms have huge potential against several tumour activities.

Echinoderms are deuterostomes and therefore phylogenetically more closely related to chordates than to other marine invertebrate phyla. This close phylogenetic relationship is confirmed by the identification of echinoderm proteins with high levels of homology to vertebrate proteins expressed in particular syndromes or tumour cells. A sea urchin gene showing very strong sequence and structural homology with the gene coding for dystrophin, which is defective in Duchenne muscular dystrophy, has been identified (Zito et al. 2005). The partial characterisation of this gene helped in the construction of an evolutionary tree connecting the vertebrate dystrophin gene family with related genes in invertebrates (Wang et al. 1998, Zito et al. 2005).

Sulphated polysaccharides abound in vertebrate tissues, and some invertebrate species, and are a rich source of sulphated glycosaminoglycans (GAGs) (mucopolysaccharides) with novel structures (Kelly 2005). Tapon-Bretaudiere et al. (2002) found that fucosylated chondroitin sulphates (FucCS) from a sea cucumber promoted the proliferation of blood vessels and had a concomitant capacity to prevent venous and arterial thrombosis in mammals. Mourao et al. (1996), Mourao & Pereira (1999) and Li et al. (2000) described novel FucCS from sea cucumbers that possess anticoagulant activity *in vivo*, and Li et al. (2000) suggested that echinoderm FucCS may be a potential alternative to heparin for blocking metastasis and inflammatory reactions without the undesirable side effects of anticoagulant heparin. Based on its potency, better therapeutic index, fewer undesirable side effects, natural occurrence, high abundance, and ease of purification, intact FucCS could be used as a therapeutic agent in the treatment of cancer (Borsig et al. 2007). Also, products containing sea cucumber FucCS are now available through natural product outlets. Traditional Chinese medicine commonly uses sea cucumber in treating weakness, impotence, debility of the aged, constipation due to intestinal dryness, frequent urination, and joint problems. Western medicine is using sea cucumber to treat rheumatoid arthritis, osteoarthritis, ankylosing spondylitis and connective tissue disorders. Australia has approved the use of sea cucumber as an over-the-counter treatment for arthritis and the Japanese have a patent using sea cucumber chondroitin sulfate for HIV therapy (Natural Products Web site, 2008, http://www.psoriasis.com/seacucumber.html).

Echinoderms may become useful even in bionics (Petzelt 2005). Recently, Aizenberg et al. (2001) discovered that the brittle star *Ophiocoma wendtii* possessed single calcite crystals arranged to function as lenses. These lenses focus light on to nerve bundles that run behind them and that presumably receive the signal to be further processed. In total, thousands of lenses form a compound eye that covers the upper surface of the animal, resulting in a function similar to a digital camera that builds up the picture pixel by pixel (Aizenberg et al. 2001). At present, engineers in the photonic industry are trying to imitate the perfect calcite lenses and their use in signal reception (Petzelt 2005).

The marine bioprospecting industry is not regulated and, although at an early stage of development, the huge potential of the Echinodermata to provide bioactive products highlights the need for urgent action to regulate this kind of activity.

Use of echinoderms as experimental model systems

Echinoderm embryos and larvae have been used as experimental model systems in several lines of research for more than a century. Echinoderms produce enormous quantities of eggs, which are fertilised externally in seawater and develop as simple, optically clear, free-living, virtually identical embryos, readily visible under a light microscope (Zito et al. 2005). Echinoderm embryos can be grown in culture and their development can be conveniently manipulated at the cellular and molecular levels to provide a reliable and regular resource of material for biochemical or molecular biology analyses. Research on echinoderm embryos has led to significant advances in the areas of developmental biology, cell biology and immunology. For example, echinoderm larvae were central to classical studies that resulted in fundamental biological concepts including Hans Driesch's demonstration of nuclear equivalence in development, Theodor Boveri's characterization of the chromosomal basis of inheritance, and Elie Metchnikoff's exploration of cellular immunity (Amemiya et al. 2005).

Evolutionary biologists have used echinoderms to test theories of life-history evolution (Raffaelli 2006). Congenic pairs of sea urchin species, one exhibiting direct and the other indirect development, have been used to investigate the developmental basis for changes in life-history patterns (Amemiya et al. 2005). Evolution and development are both manifestations of the heritable genomic regulatory programmes that determine how the morphological characters of each species are built (Hinman et al. 2003). Regulatory control systems include large numbers of genes encoding DNA-sequence-specific transcription factors, as well as downstream genes, among the most important of which encode components of intercellular signalling systems (Hinman et al. 2003). The study of gene regulatory networks aims to map and understand the transcriptional circuitry of developmental programmes and the biology of the sea urchin embryo offers natural advantages for a regulatory network of development (Davidson et al. 2002). Not many regulatory steps separate the initial zygotic gene expressions that first distinguish a given patch of embryonic cells from the activation of terminal differentiation genes in the progeny of these cells (Davidson 2001). Furthermore, the sea urchin embryo gives rise only to a very simply constructed larva that consists of single-cell-thick structures and only 10 to 12 cell types (Davidson et al. 1998), rather than to a morphologically complex juvenile version of the adult body plan, as in the development of insects and vertebrates (Davidson et al. 2002).

Echinoderms are well known for their striking regenerative capacity; asteroids and crinoids can rapidly and completely regenerate arms following self-induced or traumatic amputation (Clark 1968, Wilkie 2001, Carnevali 2006). These echinoderm groups in particular, therefore, have provided a valuable experimental model to investigate the regenerative process from the macroscopic to the molecular level (Carnevali & Bonasoro 2001, Carnevali 2005) and for the identification of the genes involved in the process of neural regeneration (Thorndyke et al. 2001, Kelly 2005). Echinoderm regeneration also provides a convenient model for examining the effects of persistent micropollutants on the developmental physiology (cell proliferation, morphogenesis, differentiation, tissue renewal) of marine animals (Kelly 2005). Regenerative medicine may benefit significantly from the extensive study of echinoderm models in parallel with traditional mammal models, in the reasonable hope that what echinoderms can do so easily may eventually become easy also for other animals, humans included (Lagasse et al. 2001, Carnevali 2006).

Echinoderms as bioindicators of environmental quality

Few echinoderm species survive in environments that are affected by high levels of anthropogenic activities (Sugni et al. 2007) but the long-term effects of low chronic chemical contamination on echinoderms are no less dangerous and are certainly more insidious (Carnevali et al. 2001). Echinoderms are benthic animals and are therefore particularly susceptible to the presence of micropollutants stored in marine sediments. Uptake of these pollutants occurs either across external epithelia or by the uptake from food. Many echinoderm species are second- or third-level predators and are particularly susceptible to biomagnification processes (Carnevali et al. 2001, Sugni et al. 2007). For example, Fowler & Teyssié (1997) reported high assimilation and subsequent strong retention of certain activation products of radionuclides (e.g., ^{65}Zn, ^{60}Co, ^{m110}Ag) for seastars, giving potential for biomagnification.

In contrast to vertebrates, invertebrates defend themselves against offending microorganisms by means of non-specific, innate immune mechanisms (Hultmark 1994, Medzhitov et al. 1997, Medzhitov & Janeway 1998, Cooper 2003) such as phagocytosis, nodule formation and humoral-based reactions (Beck 1998). The efficiency of this primitive immune system is witnessed by the fact that 95% of existing animals are invertebrates. This immune system relies on both cellular and humoral components. The immune cells are involved in phagocytosis, encapsulation, hydrolytic enzyme secretion and the respiratory burst (Chia & Xing 1996). The last is a mechanism by which a phagocytic cell drastically increases its oxygen consumption on encounter with foreign material (Coteur et al. 2005). All these oxidants are collectively called reactive oxygen species (ROS). From the study of complex field contaminations, it appears that contaminants released in the environment, such as metals, modulate starfish amoebocyte ROS production. This impact potentially represents a threat to the sustainability of natural populations of echinoderms and thereby to the stability of benthic ecosystems (Coteur et al. 2005).

Echinoderms are prime candidates for model toxicological test organisms for the marine ecosystem for many reasons, including their ubiquitous distribution, their benthic and relatively sedentary lifestyle, their susceptibility to the presence of micropollutants stored in marine sediments, and their sensitivity to many types of contaminants (Hermelin et al. 1981, Delmas & Régis 1984, Bowmer et al. 1986, Zito et al. 2005). Many echinoderms undergo asexual reproduction (fission) or lose parts of their bodies by defensive autotomy. Subsequent regenerative processes are characterised by enhanced cell proliferation, morphogenesis, differentiation and tissue renewal. During these cellular processes, some persistent and ubiquitous pollutants can exert their effects as endocrine disrupters (EDCs) (Colborn et al. 1993, Gray et al. 1996). The regeneration response of the crinoid *Antedon mediterranea* is especially sensitive to endocrine disrupters such as polychlorinated biphenyls (PCBs), and exposure to these chemicals induces significant variations in the timing and mode of arm regeneration (Carnevali et al. 2001, Kelly 2005).

There is considerable published evidence suggesting that vertebrate-type steroids can be synthesised by echinoderms (Schoenmakers 1979, 1980, Schoenmakers & Voogt 1980, Voogt et al. 1990, 1991, Köhler et al. 2007), and that reproduction, growth and development are regulated and mediated by a combination of neuroendocrine mechanisms and local growth regulators closely analogous to those seen in the normal developmental processes of vertebrates (den Besten et al. 1989, Anderson et al. 1994). In some echinoderm classes, there is limited but significant published evidence of the disruptive effects of contaminants on steroid metabolism and steroid levels and on detoxification mechanisms, such as the cytochrome P450-dependent mono-oxygenase (MO) enzyme system (den Besten et al. 1989, 1990, 1991, Schweitzer et al. 1997, den Besten 1998). Higher enzyme levels or activities are evidence of a molecular response to toxicant exposure. In this system, cytochrome P4501A plays a central role in the metabolism of a variety of xenobiotics (such as PCBs or polyaromatic hydrocarbons [PAHs]) and has been found to be a very sensitive biomarker in the asteroid *Asterias rubens* (Everaarts et al. 1994). Therefore, echinoderms can be considered key organisms in both basic and applied research in this field and can be usefully employed for developing new successful experimental approaches and strategies (Carnevali 2005). Sea urchin gametes, embryos and larvae can be used for fast, low-cost and reliable screening and testing of toxic substances and for detailed studies of their mechanism of action (Zito et al. 2005).

Current conservation measures

Current controls of the management of echinoderm fisheries include closed seasons during times of spawning; gear restrictions; designation of no-take, marine-protected areas; daily catch limits; minimum legal size; prohibition of night fishing for nocturnal species; and restrictions on the use of scuba for harvesting (Williams 2002, Food and Agriculture Organization 2004, Toral-Granda 2006). Unfortunately, the level of compliance of these conservation controls is thought to be poor (Andrew et al. 2002). Rotational fishing has also been suggested as an appropriate harvest strategy for fisheries that occur on sessile and sedentary species, primarily because it allows higher spawning stock abundance than does an annual harvest strategy (Humble 2005). Nevertheless, the duration of the period between harvests is very difficult to determine because it is extremely sensitive to the assumed mortality, growth and recruitment rates. During the no-harvesting time, severe depletion may still occur due to environmental variability (Humble 2005). In echinoderm fisheries, the general trend is of depletion of different areas within the fishery. For example in Chile, the strong production trends are based on the continued expansion of the fishery into new areas in the south, leading to a sustained ‘fishing-down’ phase. However, once all areas have been developed, there will be no more opportunity for fishing down and it is likely that production will drop significantly (Andrew et al. 2002). At this time, it is difficult to determine whether the declines simply represent the fish down of accumulated biomass. Nevertheless, the magnitude of the observed declines suggests that many of those not assessed have been overfished and are in decline. The strong and persistent spatial structure in stocks paired with large-scale or ineffective management and excessive effort from mobile fleets all contribute to declining fisheries and therefore world production (Andrew et al. 2002).

Of the recent emerging global conservation policies, only the Habitats Directive (HD) (Joint Nature Conservation Committee 1992), which aims to ensure biodiversity through the conservation of natural habitats and wild fauna and flora in the European territory of the Member States, is directly applicable to echinoderm species. In the HD, the asteroids *Asterina pancerii* and *Ophidiaster ophidianus* and the echinoids *Centrostephanus longispinus* and *Paracentrotus lividus* are given ‘strictly protected status'. Also, the Red List of Threatened Species (International Union for Conservation of Nature [IUCN] 2007), established by the IUCN, states that the echinoid *Echinus esculentus* is at "lower risk near threatened". Although this is the only echinoderm species mentioned in the Red List, it does not mean that other echinoderm species are not endangered; rather it reflects the significant lack of knowledge on the state of other echinoderm populations.

As pointed out by Bruckner et al. (2003), current trade information provides strong support for the inclusion of several echinoderm species (the sea urchin and sea cucumbers from Tables 1 and 2) in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) because they meet the CITES criteria for inclusion of species in Appendix II (CITES 1973, 2007). The United States submitted a discussion document (CoP 12 Doc. 45) to the CITES' Secretariat requesting the inclusion of harvested sea cucumbers to be discussed by the Conference of Parties in Chile (November 2002). Several issues have to be addressed before sea cucumbers species can be included in Appendix II of CITES. These include (1) a significant investment in establishing a better understanding of the taxonomy because there are many undescribed species that are common in shallow water, (2) a clear need to improve the ability to distinguish taxa in the form in which they are traded (it is very difficult to determine the species from the dried processed product, which is the dominant component of the international trade in sea cucumbers) and (3) an urgent need to establish basic biological information on which to base management strategies. Such information is difficult to obtain, even from countries with established regulated fisheries, such as Australia, Canada, New Zealand and the United States where available data refer only to selected high-value species and catch data may be incompletely reported (Bruckner et al. 2003).

Future needs

One way to reduce the commercial exploitation of wild echinoderm stocks is to develop laboratory culture methods to produce individuals for commercial ends and this is being done to supply the food market (Kelly et al. 1998). For example, sea urchin culture has been practised on a large scale in Japan for many decades, and effective methods for the culture and reseeding of species in these waters have been long established (Kelly 2005). Nevertheless, outside Japan, sea urchin cultivation is a fairly recent practice, less than 10 yr old. Sea cucumber cultivation originated in Japan in the 1930s and juveniles of the temperate species *Stichopus japonicus* were first produced in 1950 (Battaglene 1999). Methods for mass cultivation of the tropical *Holothuria scabra* are now well established and practised in India, Australia, Indonesia, the Maldives and the Solomon Islands (Battaglene 1999). In Japan, the grow-out systems are applied, meaning that hatchery-reared juveniles are mainly released to managed areas of seafloor (Hagen 1996; Sakai et al. 2004). The release of large numbers of captive-bred animals into the wild will undoubtedly affect the genetic composition of those populations (Kelly 2005). Similarly, where cultured sea urchins are caged on the seafloor or in suspended culture, their gametes will be shed to the surrounding seawater. Therefore, consideration should be given to (1) the desire to genetically manipulate brood stock for better growth characteristics of their progeny, the 'blue revolution' (the application of biotechnology to aquaculture, Greer & Harvey 2004) and (2) the preservation of genetic diversity in sea urchin populations (Robinson 2004, Kelly 2005), which gives rise to very important ethical issues. The loss of a genetically unique wild stock can have far-ranging repercussions.

The compilation of life-history characteristics, species distribution and demographic data would help understand the severity of the exploitation of echinoderm species. Unfortunately, various parameters such as recruitment, growth and mortality are available for only selected, high-value species, and catch data may be incompletely reported, complicating the ability of scientific authorities to make management decisions. It is necessary to improve the collection of data to quantify the extent of harvesting echinoderms and to document the location and catch data by species. It is also necessary to develop a global database of echinoderm species to summarise information on biology, ecology, threats, monitoring and conservation. As suggested by Bruckner et al. (2003), significant investment is needed to clarify echinoderm taxonomy, specifically identification of live and dried sea cucumbers in trade; this will enable the inclusion of echinoderm species in Appendix II of CITES. Beyond increasing the number of echinoderm species to be protected, it is important to improve the conservation management of already protected species.

Echinoderm fisheries management requires an ecosystem approach by which there is improved information sharing among government agencies, non-governmental organizations and academia and a dialogue between all users, including the industry and communities dependent on echinoderm resources. The development and integration of some of the suggested measures and the consideration of the different spatial scales (local, regional and global) will permit the sustainable use of echinoderm species as resources.

Conclusions

The biological features of echinoderms that make them susceptible to overexploitation include a complex reproductive cycle (some with late maturity), density-dependent reproduction, complex larval stages and sporadic rates of recruitment. In addition, most echinoderm species have a specific habitat preference and are slow moving, which restricts their distribution and makes them vulnerable to local extinction. Many echinoderm fisheries have no management system or restrictions in place.

Despite the long history of echinoderm collection for human consumption, the ecological implication of their removal from coastal marine ecosystems is not understood. Nevertheless, it is known that some echinoderm species are important in determining habitat structure for other species and can represent a substantial portion of the ecosystem biomass. For example, the sea urchin *Paracentrotus lividus* is a key species that controls the dynamics of seaweeds and seagrasses (Kempf 1962, Verlaque 1987, Sala & Zabala 1996).

Even when echinoderms are not targeted species, they are exposed to a significant amount of damage as a by-catch in commercial fisheries. Echinoderms are popular not only as a delicacy but also in the aquarium trade and as souvenirs. The growing restrictions on tropical marine ornamental collection and trade indicate that there is an increasing risk of subtropical echinoderm resources being heavily harvested. Lack of legislation, in subtropical areas, regulating the capture of a high number of potential species can be a major problem threatening the sustainable use of these marine resources.

Echinoderms are also a target of biotechnology prospecting and various biologically active substances have been isolated from echinoderm species. The target species for this activity are not specific and there is little financial benefit to local communities. There is a need to regulate bioprospecting to ensure a sustainable future.

Existing conservation mechanisms must be integrated and applied consistently on a global scale. Echinoderm fisheries management requires an ecosystem approach by which there is improved information sharing among government agencies, non-governmental organizations and academia, and a dialogue between all users, including the industry and communities dependent on echinoderm resources. The development and integration of some of the suggested measures and the consideration of the different spatial scales (local, regional and global) will permit the sustainable use of echinoderm species as resources. There is a clear need to improve our biological knowledge about the target species to ensure that the diversity of this wonderful group of marine animals is maintained.

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ANCHOVY AND SARDINE IN THE ADRIATIC SEA — AN ECOLOGICAL REVIEW

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Abstract Sardine (*Sardina pilchardus*, Walbaum, 1792) and anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) are two commercially important coastal pelagic species. The important ecological role of these two species in Mediterranean ecosystems has been recently highlighted and in the Adriatic in particular, anchovy and sardine have been found to play an essential role through the capture of energy from the lower trophic levels, making it available to the higher trophic levels. Furthermore, they are of major importance for Adriatic fisheries, accounting, together, for approximately 41% of total Adriatic marine catches and constituting extremely important shared fisheries resources. The ecological and fisheries importance of these two species, which essentially coexist in a relatively small area, prompted the authors to carry out a critical review of the information regarding their ecology. For each species information available on reproduction and migrations, feeding and predation, schooling and behaviour, growth and mortality, and genetic variability was collected and critically evaluated in an ecosystem functioning and fisheries context. The aim of the review is to try to understand the ecological differences and similarities allowing the coexistence of the two species as well as to identify the extent and geographic distribution of information as an aid to future research efforts.

Introduction

European pilchard or, more commonly, sardine (*Sardina pilchardus*, Walbaum, 1792) and European anchovy or, more commonly, anchovy (*Engraulis encrasicolus*, Linnaeus, 1758) are two commercially important coastal pelagic species. Sardine is distributed across the north-eastern Atlantic, from Iceland to Senegal, and the Mediterranean, including the Adriatic Sea (Whitehead 1985). Anchovy is distributed across the eastern Atlantic (from Norway to South Africa—perhaps reaching Durban) and all of the Mediterranean, Black and Azov Seas, with stray individuals in the Suez Canal and Gulf of Suez (Whitehead et al. 1988).

The important ecological role of anchovy and sardine in Mediterranean ecosystems has been recently highlighted through the use of mass-balance ecosystem models (Ecopath with Ecosim; Christensen & Walters 2004, Coll et al. 2006, 2007). The study by Coll et al. (2007) showed how the northern and central Adriatic ecosystem is dominated by the pelagic compartment, with particular reference to the plankton and small pelagic fishes (mainly anchovy and sardine). The importance of pelagic fishes within the ecosystem was supported by the wide impact of anchovy and sardine on higher and lower trophic levels, possibly related to bottom-up (control of predators) and wasp-waist (control of both predators and prey) control situations (Coll et al. 2007). Positive impacts of anchovy and sardine were reported on demersal predators (hake *Merluccius merluccius* and conger eel *Conger conger*) whilst negative impacts were highlighted on other small pelagic species (Coll et al. 2007). Thus, these two species have an essential role within the ecosystem through the capture of energy from the lower trophic levels (i.e., the plankton), making it available to the higher trophic levels (Coll et al. 2007). Very similar findings were reported for the Catalan Sea (Coll et al. 2006). Furthermore, it was found that in the Catalan Sea the amounts of nitrogen excreted by anchovy were equal to almost 2% of the total phytoplankton demand in the entire water column during periods of stratification (Tudela & Palomera 1999). This 'anchovy-mediated nitrogen pump', as the authors called it, may gain further importance in the context of the diel vertical migrations typical of anchovy, which may cause a net production increase of over 5% in the top 10 m of the water column (Tudela & Palomera 1999). This fundamental role is emphasised in shallow waters such as the northern Adriatic because the food chain is shorter and energy is trapped within the system (Bombace 1991). The findings of Bulgakova (1996) support this: In the Black Sea, anchovy consumes 8000 tonnes (t) of plankton during the summer season, corresponding to 20% of the daily plankton production in the entire basin. The crucial role of pelagic species in regulating energy flow within the ecosystem was described for upwelling systems by Cury et al. (2000). Top-down control (of prey) was detected in South Africa, Ghana, Japan and the Black Sea whilst bottom-up control (of predators) has been described in the Benguela, Guinea and Humboldt Currents. Thus small pelagic fishes constitute intermediate trophic level wasp-waist populations and because of their position within the ecosystem, the effects of overfishing, causing reductions in the abundance, composition and distribution of these species, may cause drastic changes in the state of the system overall (Cury et al. 2000).

Exploitation and fishery

Sardine and anchovy are of major importance for Adriatic fisheries, irrespective of the country. Together these two species account for approximately 41% of total Adriatic marine catches (averaged over the period 1970–2005, Fishstat+, FAO 2007). The eastern Adriatic fishery targets mainly sardine but the proportions of the two species caught by the Italian fleet has fluctuated in time. Figure 1 summarises the official General Fisheries Commission for the Mediterranean (GFCM) catch time series for sardine and anchovy in the Adriatic Sea between 1970 and 2005. Total catch of sardine (Figure 1A) increased steadily between 1970 and 1981 when a maximum was recorded at 88,518 t. Overall, this period was followed by a rather sharp decrease between 1982 and 1995. A successive increase was recorded between 1995 and 1998, followed by a decrease thereon, with the minimum value being reached in 2005 (20,372 t). The eastern Adriatic fishery (the Yugoslavian Federal Republic initially and then Croatia, Montenegro and Slovenia together) experienced a sudden decline between 1990 and 1995, followed by a slow increase. Italian catches, on the other hand, fluctuated between 1990 and 1998 but since then have decreased dramatically.

Total catches of anchovy (Figure 1B) are characterised by an increase between 1970 and 1974 when they amounted to 42,912 t in all countries. This increase was followed by a marked decrease that reached a relative minimum in 1977 and then rose sharply between 1978 and 1979 when an absolute maximum in fisheries production was obtained at 62,492 t (Figure 1B). After that anchovy catches collapsed, reaching their historical minimum of 7055 t in 1987 (Figure 1B). This minimum was followed by 6 yr of stable low catches whose recovery started in 1996. In 2005 overall anchovy catch was reported at 49,301 t (Figure 1B).

Western Adriatic Sea (Italy)

The Italian fleet has, throughout the years, fished approximately equally for sardine (average 1970–2005: 16% of Italian Adriatic catch) and anchovy (average 1970–2005: 19% of Italian Adriatic catch), with a slight prevalence of anchovy (Fishstat+, FAO). The catch of both species comprises an average of 35% of total Italian Adriatic catch (Fishstat+, FAO) and 28% of the total Adriatic

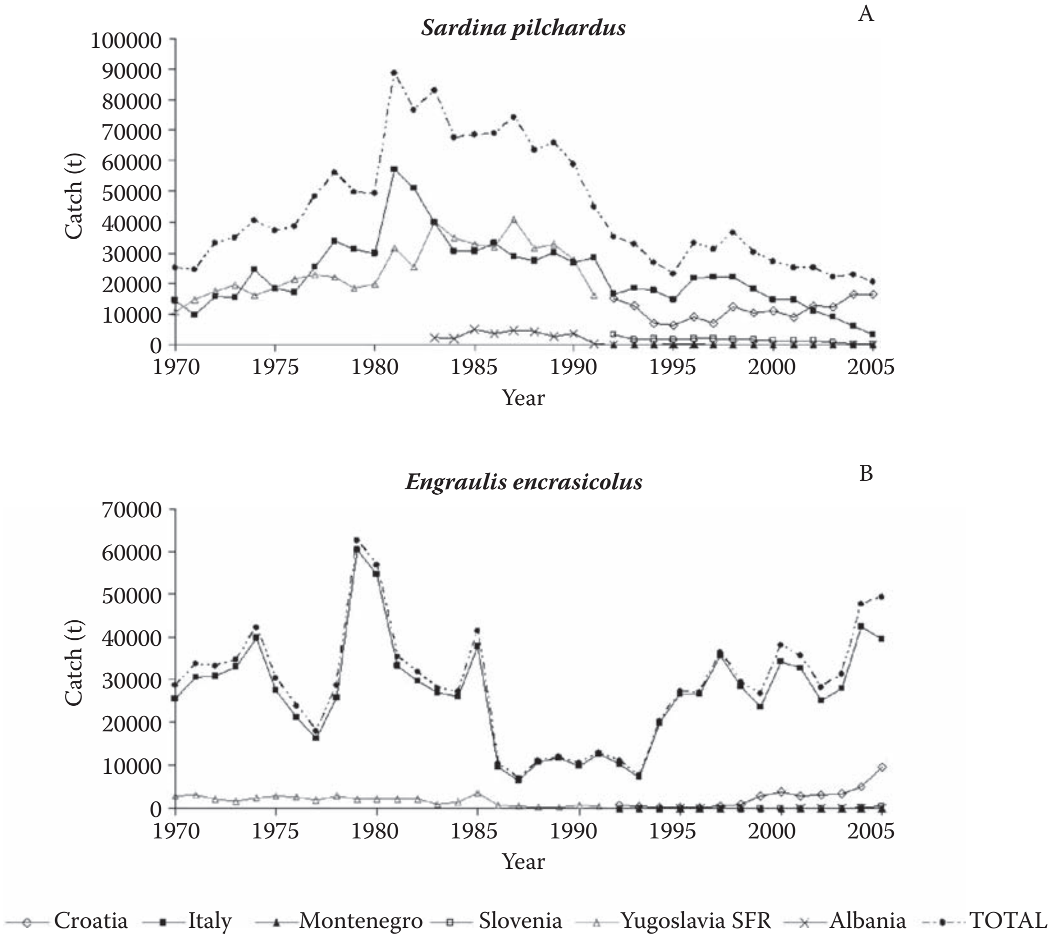

Figure 1 Official General Fisheries Commission for the Mediterranean (GFCM) catch time series for (A) sardine and (B) anchovy in the Adriatic Sea between 1970 and 2005, illustrating total catch and catch divided by country: Italy (1970–2005), Yugoslavia SFR (1970–1991), Croatia, Montenegro, Slovenia (1992–2005) and Albania (1983–2005). (Derived from FAO-Fishstat+ data.)

marine catch (excluding brackish waters); in 1979 the two species constituted 51% of the total Italian Adriatic catch and 43% of the total Adriatic marine catch. Sardine catches prevailed between 1986, when the anchovy fishery collapsed, and 1993; since then, anchovy has dominated catches, reaching 35% of the total Italian Adriatic catches alone in 2005 (Fishstat+, FAO). In 1998 the Italian anchovy fishery was valued 35 million euros (Falco et al. 2007).

Figure 2 illustrates the main Adriatic fishing harbours for small pelagic fishes. In Italy, the pelagic fleet is distributed mainly from Trieste in the north to Bari in the south, with most catches coming from the northern and central Adriatic between Trieste and Vieste. Trieste, Chioggia, Porto Garibaldi, Cesenatico, Cattolica, Ancona, San Benedetto del Tronto and Vieste can be considered the main ports, along with a number of minor ones, namely Grado, Marano Lagunare, Caorle, Goro, Rimini, Fano and Giulianova (Cingolani et al. 1996, 2003a,b, Santojanni et al. 2001).

The Italian fishery for small pelagic fishes was historically composed primarily of 'lampara' vessels (purse seiners operating in darkness aided by the use of lights). In 1959 midwater pelagic pair trawlers ('volante') were introduced and since have progressively increased, now dominating the fleet. The Italian Adriatic fleet is thus at present composed of approximately 50 pairs of volante

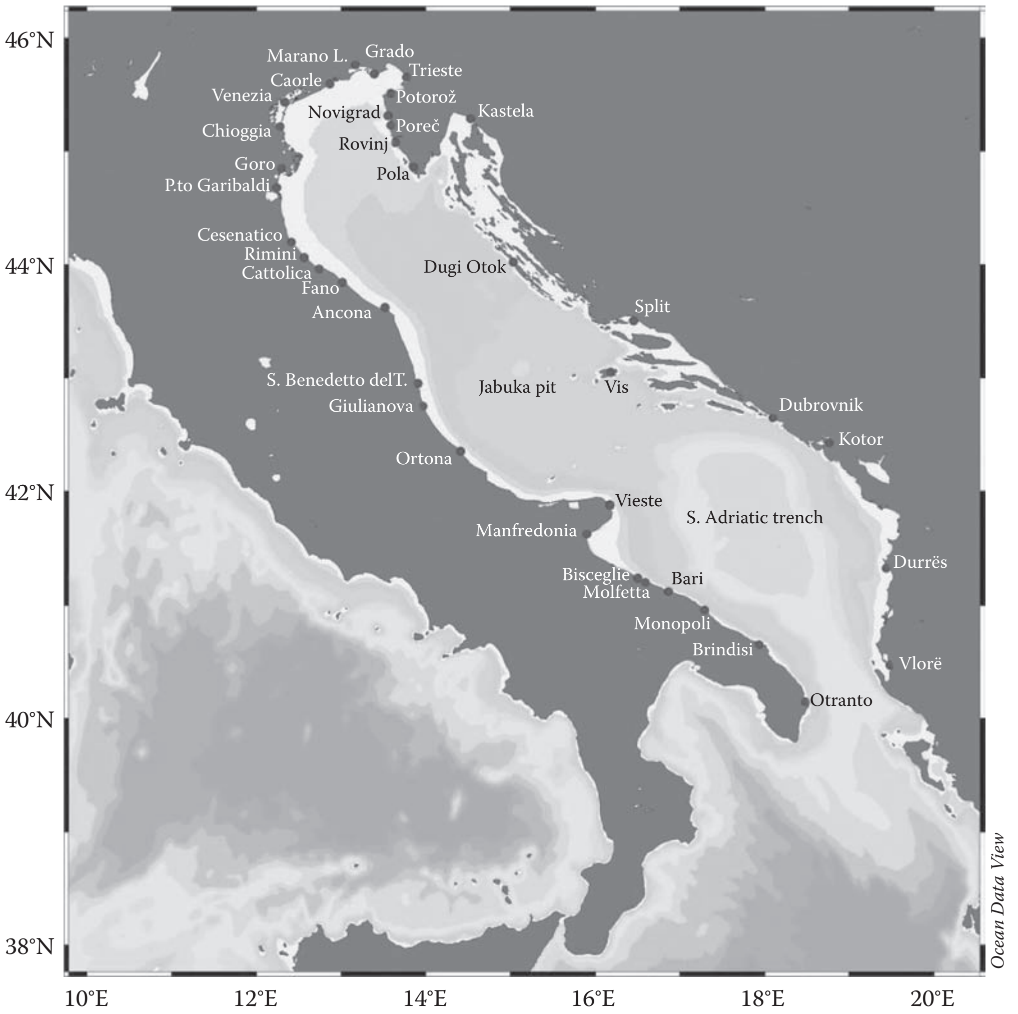

Figure 2 The main fishing and sampling harbours for small pelagic fishes in the Adriatic Sea.

and 40 lampara (Falco et al. 2007). Volante are used in the northern and central Adriatic Sea, where they fish during the day when sardine and anchovy schools are close to the bottom. Most lampara vessels operate south of Ancona, fishing on calm nights (with the exception of full-moon nights) when they rely on the fact that small pelagics are nearer the surface, aggregating them with the use of lights (Cingolani et al. 1996, Falco et al. 2007). There are approximately 25 lampara vessels south of Ancona, although during the lampara season (between April/May and November) this may increase when purse seiners from the southern Adriatic and Sicily move northwards to target anchovy and sardine (Cingolani et al. 2001, Falco et al. 2007). In addition, a fleet of small *lampara* operates in the Gulf of Trieste (Falco et al. 2007).

Eastern Adriatic

In contrast to the western Adriatic, eastern Adriatic small pelagic fisheries have concentrated mainly on sardine (Mužinić 1954, Tičina & Giovanardi 1997, Tičina & Kačić 1997, Tičina et al. 1999, Grbec et al. 2002, Cingolani et al. 2003a). Sardine comprised an average of 65% of total Yugoslavian catches

(1970–1991), 55% of Croatian catches (1992–2005), 14% of Montenegrin catches (1992–2005) and 81% of Slovene catches (1992–2005) (Fishstat+, FAO).

The Croatian fleet is distributed between Umag in the north and Dubrovnik in the south, and the main fishing grounds are between Istria and the mid-Dalmatian islands (Figure 2) (Škrivanić & Zavodnik 1973, Tičina et al. 2000, Cingolani et al. 2003a,b).

Traditionally, the eastern Adriatic small pelagic fleet has been primarily composed of coastal purse seiners that used lamps to attract and aggregate the fish at the surface (Tičina et al. 1999). A rapid increase in the number of purse seines and an expansion of the fishing grounds further off shore occurred in the period between 1945 and 1960 (Grbec et al. 2002). The first pelagic trawlers were introduced in 1978, which, since then, have concentrated in the north (Istria and Kvarner) (Grbec et al. 2002) and like Italian pair trawlers, fish during the day all year round (Tičina & Giovanardi 1997, Tičina & Kačić 1997). In the central eastern Adriatic, on the other hand, small pelagic fishes (mainly sardine) are still fished at night with purse seines between April and October (Mužinić 1954, Tičina & Giovanardi 1997, Tičina & Kačić 1997, Tičina et al. 1999). As in Croatia, purse seines were the predominant fishing gear used in Slovenia up to 1978, when pelagic trawlers gradually started taking over, causing the disappearance of purse seines by 1991 (Marčeta 2001). The gaining of independence in 1991 caused a drastic reduction in the fishing grounds available to Slovenia, and as a consequence, at present there are only two commercial midwater pelagic trawlers operating (Marčeta 2001). The Albanian fishery for sardine started in 1951 in the Gulf of Valona, when catch was reported to be 226 t, and has developed considerably since (Kapedani 2001). Between 1980 and 1990 the fleet expanded both in terms of fishing grounds (they started fishing further offshore) and in terms of fishing gear, with the introduction of midwater pelagic trawlers (Kapedani 2001). From the 1990s onwards, 90% of the national fishing fleet switched to bottom trawling and in 2001 the pelagic fleet was reported to be a mere 10% of the entire Albanian fleet (Kapedani 2001).

The information available in the literature regarding the recruitment of young sardine and anchovy to the fishery are varied and allow the general conclusion that both species become available and accessible to the fishery at whatever age/size the fishermen are allowed (or decide) to catch them. The major body of evidence is constituted by the Italian, bianchetto, (fry) fishery, which, in the Adriatic, is mainly concentrated on the Apulian coast between Manfredonia and Bari (Figure 2). In Italy, the term bianchetto is used to describe juveniles of clupeid fishes, mainly sardine but also anchovy and sprat, *Sprattus sprattus* (Marano et al. 1981). Despite being prohibited for many years, the fishery for bianchetto has a long tradition in the western Adriatic, where its product is sold at high prices on the national and local markets (Marano et al. 1981). Since 1977, for reasons linked mainly to the high availability of juveniles during certain periods of the year, this fishery has been allowed in restricted periods (any 2 months between January and April), following a strict legislation regarding authorised vessels and gear and for sardine only, the fishery for anchovy bianchetto being prohibited (Marano et al. 1981, Romanelli et al. 2002). In Manfredonia bottom trawls with very fine cod-end meshes (5-mm stretch) are used to catch bianchetto during the day (Ungaro et al. 1994). In Bari, Bisceglie and Monopoli bianchetto is fished with bottom trawls but also, to a lesser extent, during the night by means of purse seines with light attraction. In the 1980s the average total catch of sardine bianchetto in the Gulf of Manfredonia was approximately 20 t day^{-1} (total number of vessels: 200) (Rizzoli 1982, 1983) but in 1991 it was reported to be on average 6 t day^{-1} (total no. of vessels: 203) (Ungaro et al. 1994). This decrease incentivised research into the consequences of targeting juvenile sardine. It was found, in both the Gulf of Manfredonia and Bari, that the catch of bianchetto vessels between the end of January and April was almost exclusively (≈90%) composed of young sardine, whereas anchovy dominate in previous months before migrating offshore (Marano et al. 1981, Rizzoli 1983, Ungaro et al. 1994). Similar results are reported for other regions in Italy, namely Calabria and Liguria (Piccinetti et al. 1997, Romanelli et al. 2002).

No data regarding the exploitation of sardine and anchovy larvae and post-larvae are available for the eastern Adriatic Sea, but, by law, sardine below 10 cm and anchovy below 9 cm cannot be caught in Croatia. Kačić et al. (1985, 1987) reported a massive occurrence of sardine juveniles in the eastern Adriatic bays (Novigrad and Karin bays) in 1983 and that year the first catches of juveniles occurred in April at a mean length of 81 mm.

Regarding the fishery for adults, according to Cingolani et al. (1998), the size at first recruitment of sardine to the adult commercial fishery oscillates between 12 and 13.5 cm depending on the year and the area considered. For anchovy, this size is reported to be between 9 and 10 cm, the period of peak recruitment being between October and February (Cingolani et al. 1996). Recruitment indices have been calculated for Adriatic anchovy in the period 1975–2006 and have highlighted how recruitment was estimated to be much higher in the 1970s compared with the mid- to late 1980s (Cingolani et al. 1996). Furthermore, the recruitment indices estimated for 1986 and 1987 (the years of the anchovy collapse) were very low, possibly implying that the collapse was likely due to a failure in recruitment in those years (Cingolani et al. 1996, 2003b, Santojanni et al. 2003), the size of recruitment being of extreme importance in determining stock abundance in short-lived species such as anchovy.

Aims of the review

The ecological and fisheries importance of these two species, which essentially coexist in a relatively small area, prompted the authors to carry out a critical review of the information available regarding their ecology. For each species information available on reproduction and migrations, feeding and predation, schooling and behaviour, growth and mortality, and genetic variability were collected and critically evaluated in an ecosystem functioning and fisheries context. The aim of the exercise was to try to understand the ecological differences and similarities allowing the coexistence of the two species as well as of identifying the extent and geographic distribution of information as an aid to future research efforts.

Sardine, *Sardina pilchardus*

Reproduction and migrations

Like most clupeoids, sardine is a serial batch spawner exhibiting indeterminate annual fecundity (Ganias et al. 2007). Thus, females, whose oocytes do not mature simultaneously, produce multiple batches of eggs over a protracted spawning period (Blaxter & Hunter 1982, Ganias et al. 2003). Table 1 summarises data available in the literature regarding the extent of the spawning season, spawning peak, temperature and salinity ranges for the Adriatic Sea. In the Adriatic Sea spawning takes place mainly in winter, generally between October and May, although eggs have been reported as early as September (Vučetić 1971) and as late as June (Teskeredžić 1978). Within this time period, there are peaks of spawning, generally one or two (winter and spring), whose timing greatly depends on the area and a series of environmental factors (Table 1). The timing and location of spawning appear to be driven by a number of interacting biotic and abiotic factors, most important of which are temperature, salinity and food availability (Regner et al. 1987). Spawning, in the Adriatic Sea, has been reported to take place between 9 and 20°C at salinities ranging from 35.2 to 38.8 psu, with spawning peaks occurring between 11 and 16°C (Table 1). It has been reported that sardine spawns at depths between 30 and 150 m (Škrivanić & Zavodnik 1973), although more typically between 60 and 120 m (Kačić 1980, Vučetić 1975, Sinovčić 2001). It is in search of favourable environmental conditions that sardine adults migrate from and towards spawning areas and their tolerance to variations in temperature and salinity changes according to their condition (Mužinić 1973). The available scientific literature regarding the spawning areas of sardine in the Adriatic Sea

Table 1 Periods and optimal hydrographic conditions for sardine and anchovy spawning in the Adriatic Sea

Species	Area	Spawning season	Spawning peak	Temperature range (temperatures at peak spawning) (°C)	Salinity (psu)	Reference
Sardine	Split	Oct–May	Jan–Feb	10.2–20.2 (10.2–12.4)	35.2–37.0	Gamulin 1940
	Central Adriatic	Winter				Mužinić 1954
	Northern and central Adriatic	Oct–May				Gamulin & Karlovac 1956
	Central Adriatic	Oct–Apr	Dec–Feb	(13–16)	37–38	Gamulin & Karlovac 1957
	Vlora bay, Seman-Viase bay, Sazan Island (Albania)	Nov–Feb	Dec & Feb	12–20	37.5–38.5	Rakaj 1962
	Central Adriatic	Nov–Apr		11.9–19.4	37.1–38.8	Karlovac 1969a
	Central Adriatic	Oct–May	Mar	13.1–18.0	38–38.5	Karlovac 1969b
	Central Adriatic	Sept–May				Vučetić 1971
	Central Adriatic	Oct–April	Jan			Vučetić 1975
	Kvarner, Susak and Dugi Otok	Nov–June	Nov & Apr	11.6–11.7	38.1–38.2	Teskeredžić 1978
	Northern and central Adriatic (Trieste-Gargano)			8.4–14.7 (12.1–13.9)	37.6–38.8	Regner et al. 1987
	Southern Adriatic (Gargano-Otranto)	Oct–May	Oct & Dec			Casavola et al. 1998
	Northern and central Adriatic (Trieste-Gargano)			9–15 (11–15)		Regner et al. 1988
	Albania (2003)	Sept–Apr				Kolitari 2006
	Albania (2004)	Oct–Apr				Kolitari 2006
	Albania (2005)	Oct–Apr				Kolitari 2006
Anchovy	Northern Adriatic	Summer				Syrski 1876
	Northern Adriatic	Summer				Graeffe 1888
	Northern Adriatic	Apr–Oct				Steuer 1910
	Northern Adriatic	June–Sept				Stiasny 1910
	Central Adriatic (mid-Dalmatian islands)	Apr–Aug	May, July, Aug			Gamulin 1940
	Mljet Island	May–Sept		13–27		Vučetić 1957
	Northern and central Adriatic	Apr–Oct	May, Aug–Sept			Varagnolo 1964a
	Dugi Otok Island	May–Sept	June			Vučetić 1964
	Istria	May–Sept				Zavodnik 1969

(continued on next page)

Table 1 (continued) Periods and optimal hydrographic conditions for sardine and anchovy spawning in the Adriatic Sea

Species	Area	Spawning season	Spawning peak	Temperature range (temperatures at peak spawning) (°C)	Salinity (psu)	Reference
	Northern Adriatic	Apr–Oct	June–July	11.6–27.5 (22)	9.1–38.5	Zavodnik 1970
	Northern Adriatic	May–Sept	July–Aug			Štirn 1969, 1970
	Central Adriatic (mid-Dalmatian Islands)	May–Sept	May–June			Vučetić 1971
	Central Adriatic (mid-Dalmatian Islands)	Mar–Nov	June–July	13.2–23.7 (18.3–22.1)	33.86–38.69	Regner 1972
	Gulf of Trieste	Apr–Oct	July			Specchi & Furlan 1974
	Central Adriatic	Late spring and summer	Aug			Sinovčić 1978
	Gulf of Trieste	Apr–Oct	May–June, Aug			Di Marcotullio & Catolla Eulambio Di Marcotullio 1983
	Northern and central Adriatic	Apr–Oct	June–Sept			Regner et al. 1985
	South-western Adriatic	Apr–Oct				Casavola et al. 1987
	Gulf of Trieste	Apr–Oct	Aug	12–28 (21–28)		Orlandi et al. 1994
	Fano	Apr–Oct	July	12–26 (25–26)		Orlandi et al., 1994
	South-western Adriatic	May–Sept	Aug			Casavola et al. 1996a
	South-western Adriatic	Apr–Oct	July–Sept			Marano et al. 1998
	Miramare (Trieste)	May–Sept	July	>17 (21–28)		Specchi et al. 1998
	Inshore coastal waters (Kastela bay)	Apr–Oct	Aug			Sinovčić 2000b
	Open waters (Vis & Bisevo Islands)	March–Oct	July			Sinovčić 2000b
	Albania (2003)	Apr–Oct				Kolitari 2006
	Albania (2004)	May–Oct				Kolitari 2006
	Albania (2005)	May–Oct				Kolitari 2006

reports a series of contrasting results. Although the presence of eggs has been observed in all continental shelf waters of the Adriatic Sea (Gamulin & Hure 1955, 1983), there is general consensus on the existence of a number of areas where spawning is more intense. Previous to 1979, no studies encompassed the Adriatic Sea in its entire width but were concentrated in small localised areas mainly off the eastern coast. Rakaj (1962) described the main spawning grounds of sardine off the Albanian coast, locating them between Vlora Bay and Sazan Island. Gamulin (1948) described a spawning area around the mid-Dalmatian Islands, Gamulin & Karlovac (1956) reported an important spawning ground in the open sea off the same islands, whilst Hure (1961) described spawning around Palagruža Island. Other authors came to the conclusion that Istrian waters did not support a significant enough number of eggs to be considered important. Štirn & Kubik (1974), in describing sardine migrations along the northern and central Adriatic, pointed to three main spawning areas, one in the northern part located off Dugi Otok island, the other two in the central Adriatic around the exterior of the mid-Dalmatian Islands and offshore around Palagruža island. Since 1978, an important cooperation between the Institute for Oceanography and Fishery of Split and the Laboratorio di Biologia Marina e Pesca of Fano allowed egg and larval surveys to be carried out regularly across the entire northern and central Adriatic from the Gulf of Trieste to the line connecting the Gargano promontory and Kotor. This collaboration lasted until 1996, and in 1984 was also extended to the south-western Adriatic with the participation of Laboratorio Provinciale di Biologia Marina di Bari. The results of these investigations revealed the existence of two main spawning grounds in the Adriatic Sea (Piccinetti et al. 1980, 1981, Regner et al. 1981, 1987): the northern Adriatic off the Dugi Otok Island and the southern Adriatic around the exterior of the mid-Dalmatian Islands and extending offshore to Palagruža. In some years, coinciding with very intense spawning, these two areas may be joined and the southern spawning area may also extend along the Italian coast down to Otranto (Piccinetti et al. 1981, Gamulin & Hure 1983, Casavola et al. 1985).

The deep Jabuka (Pomo) pit, where no sardine eggs have ever been recorded, separates these two areas (Regner et al. 1987) and may also represent a physical barrier to migrations (Škrivanić & Zavodnik 1973). Similarly no sardine eggs have ever been found in the southern Adriatic trench, which constitutes a second physical barrier enclosing the Adriatic Sea to the south (Škrivanić & Zavodnik 1973, Gamulin & Hure 1983).

Although dictated by similar factors (temperature, salinity and food availability), migration patterns of adult sardine, as well as of larvae and post-larvae, are different between the two spawning grounds. In the northern area migration is longitudinal. Thus, in winter (starting as early as September) the adult population migrates southwards from the Gulfs of Trieste and Venice and the Istrian coast towards Dugi Otok (and to a lesser extent the Kvarner region) for spawning (Škrivanić & Zavodnik 1973, Štirn & Kubic 1974, Tičina et al. 2000). At the onset of sexual maturation, adults search for a favourable environment for eggs and larvae and move away from the northern Adriatic waters, which, despite being extremely productive, are also hydrographically unstable and more subject to environmental variability owing to their shallow nature (Štirn & Kubic 1974, Regner et al. 1988, Tičina et al. 2000). At the end of spawning, in spring (as early as March), the spawners follow the reverse route and migrate northwards towards the productive northern Adriatic waters in search of food (Štirn & Kubic 1974, Regner et al. 1988, Tičina et al. 2000). Varagnolo (1964a) found sardine eggs in Chioggia and the Venice lagoon between mid-May and early June. The literature regarding the reproduction of this species made this author suppose that the unusual presence of eggs in that area and season was most probably due to the migration of late spawners from the eastern Adriatic waters (Varagnolo 1964a).

Migration to and from the central Adriatic spawning grounds is, on the other hand, transverse (Mužinić 1973, Škrivanić & Zavodnik 1973, Regner et al. 1988). In general, in the central Adriatic, the large adult sardine are found offshore whilst the smaller ones are more concentrated inshore (Mužinić 1954, 1973). The presence of larger individuals inshore in certain times of the year thus appears to be explained by migrations to and from the open sea. During the last stages of sexual maturation, in late autumn/winter, adult sardines migrate offshore towards the deeper, colder waters of the outer Dalmatian Islands and Palagruža, fleeing from the temperature gradients and low salinities found inshore (Mužinić 1973). Data from catches and horizontal egg distribution indicate that this movement is gradual (Gamulin & Karlovac 1956). The inverse happens in early spring when adults, larvae and post-larvae turn towards the inshore waters (Mužinić 1973). It has been found that this migration is rapid, with individuals covering on average 11.9 km day^{-1} (Mužinić 1950). In spring, therefore, adults and juveniles are found inshore along the eastern coast and in the channels where they are fished rather intensively between April and October (Mužinić 1954, Vučetić 1955, Županović 1955, Mužinić 1973, Škrivanić & Zavodnik 1973). Kačić et al. (1985, 1987) described in detail the migration of post-larvae and juveniles into the channels and bays along the north-eastern Adriatic coast (Istria, Velebit channel, Gulf of Rijeka, Novigrad Bay and Karin Bay) in the mid-1980s when quantities were so high they could be fished from shore. At this time, sardines are recruited to the fishery, the first consistent catches of juveniles being variable from year to year (February–June). Overall, juveniles caught early in the fishing season (April) were around 8 cm and grew rapidly and consistently, the mean size of catch at the end of May being around 12.5 cm. Length-frequency distributions highlighted the fact that there was a progressive occurrence of new young, evidence of continuous spawning (Kačić et al. 1985, 1987, Sinovčić 2000a). The overall age structure of the juveniles present in this area between April and October was composed of the 0+ (83%) and 1+ (17%) age classes (Sinovčić 2000a). Fishermen reported that this cohort resided within the Bays of Novigrad and Karin for at least 1 yr, meaning that the cohort either did not spawn or spawned within the bays and thus did not contribute to the following year's spawning offshore (Kačić et al. 1985, 1987). Tagging experiments have shown that spring migrations are not complete and a second round of inshore migrations may occur in late summer (Mužinić 1973).

To explain such migratory patterns, the issue of tolerance to temperature and salinity variations comes into play. The reasons for the two inshore migrations appear to be different. The first, in spring, is related to feeding after an intense spawning period and this assumption is supported by the fact that the fat content in tissues at the onset of migration is very low and its increase once inshore is rapid (Krvarić & Mužinić 1950). The second inshore migration, in late summer-early autumn, coincides with the initial phases of sexual maturation. The fact that the fat contents in tissues are high at this stage excludes feeding as an explanation (Mužinić 1973). In support of this, whereas in spring the optimum feeding conditions appear to be inshore, with zooplankton concentrating at the surface, in August and September the best feeding opportunities, in terms of zooplankton concentrations, are found offshore (Hure 1964, Mužinić 1969). In August–September the deeper offshore waters are characterised by sharp temperature and salinity gradients whereas the coastal waters are more homogeneous; the movement of adults inshore in this period may indicate a decrease in tolerance to variations in the physical properties of the water masses during the initial phases of sexual maturation (Mužinić 1973). A decrease in tolerance is also associated with the final stages of gonad maturation, when sardine migrate offshore to the spawning grounds in search of homogeneous hydrographic conditions, high salinities and optimum temperature ranges (Mužinić 1973, Skrivanic & Zavodnik 1973, Županović 1985, Regner et al. 1987, 1988, Tičina et al. 2000). The opposite appears to be true in spring during the feeding migration when sardine appear to be less sensitive to hydrographic variability (Tičina et al. 2000). Information regarding the movement and spawning of sardine in the central western Adriatic Sea is scarce. Considering the possibility that a transverse migration from the coast to offshore takes place in the central western Adriatic, as it does in the eastern part, it must be pointed out that a study of the optimal allocation of sampling effort for age and length of small pelagic fishes from commercial fisheries in the western Adriatic Sea (Anonymous 1995) found no relationship between the size of sardine and depth.

Overall, sardine is adapted to the dynamics of the environment and appears to choose intermediate areas, avoiding extremes (Škrivanić & Zavodnik 1973). Some authors, though, have pointed out that temperature and salinity alone are not sufficient to explain the location of spawning grounds (Regner et al. 1987, 1988).

Buljan (1964) estimated the productivity of the Adriatic Sea on the basis of its hydrographic properties and divided the entire basin into four primary production zones:

1. Zone A: The open waters from the line connecting Ancona and Dugi Otok Island southwards, covering 57% of the Adriatic surface area and being the least productive of all
2. Zone B: The shallow north Adriatic and the Italian coastal waters down to the Gargano promontory, covering 23% of the entire Adriatic area and being characterised by high productivity
3. Zone C: The shallow waters of the channels within the Croatian bays and islands, covering 18% of the Adriatic and being of medium productivity
4. Zone D: The lagoons and enclosed bays along both the western and eastern coasts covering only 1–2% of the surface area and being highly productive

The temperatures in Zones B and C are probably too low (<10°C; Buljan & Zore-Armanda 1974, Artegiani et al. 1997a) during the maximum spawning season (December to March) and salinity in Zone D, which is mainly in correspondence with river outlets, is probably too low in winter (Regner et al. 1987). So, despite food being of major importance for post-larval development and survival, all sardine spawning grounds mentioned are located within the least productive Zone A. In winter, the Adriatic is characterised by north-south increasing temperature and salinity gradients (Russo & Artegiani 1996). Chlorophyll *a* and phytoplankton, which are correlated, show the inverse pattern, decreasing from north to south. This decreasing trend in primary production shows discontinuities in frontal and upwelling zones (i.e., in zones where water masses of different origins and properties meet) (Regner et al. 1987) and it is in these frontal zones that sardine spawn most intensively (Regner et al. 1987, 1988). The importance of upwelling areas for the reproduction of clupeoid fish is extremely well documented in the literature, such as the Peruvian anchoveta (*Engraulis ringens*) off Peru and the South African and Namibian pilchard (*Sardinops agax*) in the Benguela (Cury & Roy 1989, Cole & McGlade 1998). Regner et al. (1987), in a survey of the entire Adriatic in 1982, showed that in that year the upwelling zones were located in two areas, one on the line connecting Ancona and Dugi Otok Island and the other, further south, on the line connecting the Italian coast between Ortona and Vieste, and the mid-Dalmatian islands. These belts were characterised by colder, more dense waters of deep origin reaching the surface. At the boundaries of these upwelling belts were zones where the upwelling broke up (characterised by intense mixing) and these corresponded to the two deep trenches in the Adriatic: the Jabuka pit and the southern Adriatic trench south of Palagruža. Sardine spawning areas, located at depths ranging from 10 to 20 m, coincided with the boundaries of these frontal zones produced by the upwelling and in both cases (northern and central areas) they were divided into two distinct zones, one on each side of the front (Regner et al. 1987). Phytoplankton distribution was the same and was concentrated at a depth of 10–20 m. Overall it appears that, within their tolerance limits to temperature and salinity, sardine choose the areas that have the most favourable trophic conditions for spawning (Regner et al. 1987). The highest numbers of sardine larvae occur in the same areas as the eggs with progressive spatial shifts away from the spawning ground with increasing age: towards north-west in the northern spawning area and southwards in the southern spawning area, reflecting the circulation in these areas (Zore-Armanda 1968, Regner et al. 1987).

The two upwelling zones described by Regner et al. (1987) are coincident with two gyre systems formed around Palagruža sill and between Ancona and Dugi Otok Island (Zore-Armanda 1968, Buljan & Zore-Armanda 1974, Russo & Artegiani 1996, Artegiani et al. 1997a,b). Here the cold and less-saline waters from the northern Adriatic (of ‘Alpic’ origin; Škrivanić & Zavodnik, 1973) meet the warmer, more saline waters of the intermediate layer coming from the Mediterranean (MLIW, Modified Levantine Intermediate Waters), causing the upwelling conditions that result in equilibrium zones and favouring the formation of sardine spawning grounds (Škrivanić & Zavodnik 1973). It is known that processes of concentration (stability of the water column, convergence and front formation) and retention of eggs and larvae are necessary if reproduction is to be successful in the long term (Bakun 1986, Riveiro et al. 2004), and the formation of these two gyres, with consequent upwelling, obtains exactly this.

Several studies have observed that in years when these 'ingressions' of saline intermediate waters of Mediterranean origin are of significant proportions, in spring/summer the coastal waters of the eastern Adriatic have lower surface temperatures and higher salinity. These conditions favour primary productivity in the euphotic zone and result in significantly increased sardine catches along the eastern Adriatic coast (Županović & Zore-Armanda 1963, Škrivanić & Zavodnik 1973, Županović 1985, Grbec et al. 2002).

The temporal and spatial distribution of these gyres (and upwelling areas) fluctuates from year to year but overall there appears to be a temporal sequence dictating the progressive location of spawning as the spawning season progresses. Initially spawning mainly occurs at the boundary between Buljan's (1964) Zones A and B along the Italian coast between Ancona and the Gargano. When the temperature falls below 10°C, the main spawning area shifts towards the open central and southern Adriatic, finishing off closer to the eastern coast (Regner et al. 1988).

Figure 3 illustrates an attempt at summarising the migratory patterns of sardine.

Temperature and salinity are the principal factors affecting spawning and egg and larval survival but within the broadest optimum ranges, food availability then becomes of utmost importance. Hjort (1914) put forward the theory that in very fecund fish species there is a period, termed the critical period, during which mortality is very high. He postulated that the critical period coincided with the phase following the absorption of the yolk sac, that is, the transition between larval and post-larval phase, when the individual has to start feeding exogenously. This has been found to be true for several pelagic fish species, such as the South American pilchard *Sardinops sagax* (Ahlstrom 1954), although other authors found the critical period to be that during which the larva actually depends on the vitellus (e.g., in Pacific jack mackerel *Trachurus symmetricus*) (Farris 1961). Karlovac (1967) reported consistent drops in numbers of sardine during the transition from the larval to the post-larval stage (around 6 mm), suggesting that the critical period of sardine is at the end of the vitellus absorption stage and implying that food availability plays a decisive role in the long-term success of a cohort. However, before reaching the post-larval stage, eggs and larvae have to survive. If 'parental effects' exist in sardine, they are probably manifest through the variation of egg quality (and subsequent larval quality) throughout the spawning season to anticipate the heterogeneous biotic and abiotic conditions consequent of such a long spawning season and enhance survival of post-larvae in food-limited conditions (Riveiro et al. 2000). Factors that have been reported to affect egg and larval quality include egg size (Blaxter & Hempel 1963); size, condition and age of adult females (Karlovac 1967, Kristjansson & Vollestad 1996); and biochemical composition of the egg (Craik & Harvey 1987, Pickova et al. 1997, Chicharo et al. 1998, Chicharo et al. 2003). Riveiro et al. (2004) described the variations in egg quality in a study of sardine eggs caught off the Iberian Peninsula (Spain) and found that egg size decreased with increasing temperature and that embryonic development time decreased with increasing temperature. Consequently, eggs spawned earlier are exposed to predation for longer periods, but this longer exposure to predation is counterbalanced by the fact that eggs spawned earlier have a higher protein content that speeds development (Riveiro et al. 2000, 2004). If the organic content of larvae depends on the quality of the eggs, then larvae hatched in low temperatures would have a greater probability of survival once the vitellus has been absorbed. Food limitation is obviously one of the most important factors affecting larval survival (Cushing 1975), but the results of these studies reiterate the fact that the overall success of

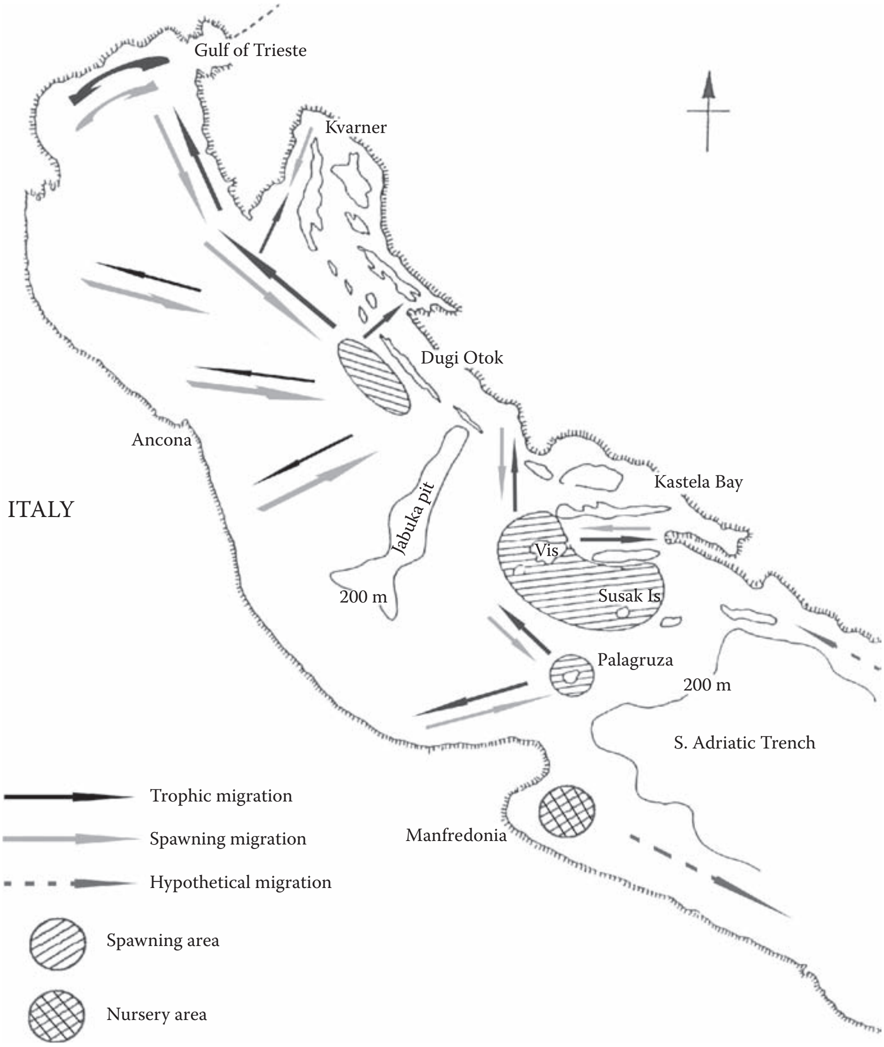

Figure 3 The migrations of sardine in the Adriatic Sea.

a year-class appears to be strongly dependent on temperature and its variation during the spawning season (Riveiro et al. 2004). Gamulin & Hure (1955), in a major contribution to the study of the duration of egg development in sardine from the central Adriatic Sea, related duration to temperature. They found that spawning and fertilisation occur at the same time of the day depending on the month: between 1800 and 2200 in December and between 1900 and 2400 in March. The difference between timing as the spawning season progresses is probably due to the lengthening of daylight hours (Gamulin & Hure 1955). Total duration of development of the egg to hatching was found to be strongly dependent on temperature: Average duration at 18°C was 46 h, whereas at 13°C it was 88 h. Considering the fact that winter temperatures in the northern Adriatic are lower, the time taken for egg development to be completed could be up to 4.5 days (Gamulin & Hure 1955).

The age and length at first sexual maturation have direct repercussions on the reproductive potential of a fecund species because they define the duration of the reproductive cycle, thus affecting population growth (Sinovčić et al. 2003). In general, sardine are sexually mature for the first time at the end of their first year of life, but this again depends on temperature and food availability

Table 2 Length at first maturity of sardine and anchovy in the Adriatic Sea

Species	Area	Sex	Method	Lm (cm)	Lm$_{50}$ (cm)	Smallest mature (cm)	Reference
Sardine		All	MAC	13–14		<12	Mužinić 1954
	Krka River estuary (Croatia)	All	MAC	7–12	8	7.1	Sinovčić et al. 2003
	Krka River estuary (Croatia)	All	MAC	7–11.5	7.9	7.1	Sinovčić et al. in press
	Albania	All	MAC			12	Kolitari 2006
Anchovy	Dalmatian Islands (Croatia)	M	MAC			10.3	Mužinić 1956
	Dalmatian Islands (Croatia)	F	MAC			10.9	Mužinić 1956
	Northern Adriatic (Italy)	All	MAC	8–9			Varagnolo 1967
	Central Adriatic (Croatia)	M	MAC			8.6	Sinovčić 1978
	Central Adriatic (Croatia)	F	MAC			9.7	Sinovčić 1978
	Northern & central Adriatic (Italy)	M	MIC	7.5			Rampa 2005
	Northern & central Adriatic (Italy)	F	MIC	8.6			Rampa 2005
	South-western Adriatic (Italy)	All	MAC	9			Marano et al. 1998
	Novigrad Sea (Croatia)	All	MAC		9	8	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	M	MAC		7.9	6.7	Sinovčić & Zorica 2006
	Novigrad Sea (Croatia)	M	MAC		8.5	7.1	Sinovčić & Zorica 2006
	Novigrad Sea (Croatia)	All	MAC		8.2	6.7	Sinovčić & Zorica 2006
	Albania	All	MAC			10	Kolitari 2006

Lm = length at first maturity; Lm$_{50}$ = length at which 50% are mature; MAC = macroscopic analysis; MIC = microscopic analysis; M = male; F = female.

(Sinovčić et al. in press). Mužinić (1954) reported that first sexual maturity generally occurs between 13 and 14 cm, although some individuals have been observed to be mature at sizes smaller than 12 cm (Table 2). On the other hand, more detailed studies carried out in the nursery area of the Krka River estuary (Croatia) revealed that the smallest sizes at first sexual maturity were between 7 and 12 cm; the smallest female was 7.1 cm, the smallest male 7.3 cm long, 50% of individuals were sexually mature at 8 cm and the entire sample at 11.5 cm (Table 2) (Sinovčić et al. 2003, in press). These data were all derived from macroscopically determined maturity stages. The transition from immature to mature can be described by a sigmoid curve (Sinovčić et al. 2003, in press). The smaller individuals, at their first spawning, spawn later in the spawning season compared with larger individuals, thus having, in their first spawning year, a shorter spawning period and lower fecundity (Mužinić 1954, Sinovčić 1983a, Abad & Giraldez 1993). The size and age at first maturity of *Sardina pilchardus* are dependent on a number of factors, including latitude (the length at which 50% are mature (L$_{50}$) decreasing from north to south; Silva et al. 2006) and are, possibly, regulated by density-dependent effects (Parrish & Mallicoate 1995).

Information regarding the reproductive cycle, particularly the presence of a resting stage, is controversial because sardine is a batch spawner and the extent of the spawning season, as well as the spawning peak, vary from year to year and according to area. The months of June, July and August are a resting phase when the gonad weight is at its minimum; the months of September, October, and to some extent November, correspond to the prematuration phase, adults being fully active in winter, with variations from year to year (Mužinić 1954). The presence of a resting phase in July and August is also reported for the Aegean Sea but in the Ionian Sea it appears to be longer, lasting from June to September (Somarakis et al. 2006). Mužinić (1954) also observed that the maturity stages of larger individuals were more advanced in the prematuration phase and similar observations were made for males compared with females. The sex ratio of sardine populations also varies with time of the year (and maturation stage) as well as with area. Mužinić (1954) further reported that the overall sex ratio of individuals caught with purse seines (i.e., at night at or near the surface) to be female skewed (52.5% females). Sex ratio may vary with depth, the two sexes occupying different levels of the water column, and thus the method used to catch the individuals may yield different sex ratio values. In fact, during the same period, the sex ratio of individuals caught with bottom trawls (during the day in proximity of the bottom) was strongly in favour of males (63.7% males). Several years later the same author reported an equal sex ratio with the exception of the maturation and spawning periods (Mužinić 1979). Casavola et al. (1998) found that the sex ratio in the south-western Adriatic Sea in November was slightly in favour of females. Sinovčić et al. (2003, in press), in the Krka River estuary, found an overall sex ratio in favour of females, with the exception of three size classes: 9.0 and 9.5 cm (dominated by males) and 12.0 cm (equal proportions). Kolitari (2006) reported sex ratios in favour of males for Albanian waters in 2003–2005. Generally in fishes, variations in sex ratio according to size have been explained in terms of different mortality and growth rates of the two sexes (Turner et al. 1983).

Sardine, as other pelagic species, are highly fecund, but overall fecundity depends on the duration of the spawning period and on whether the right environmental conditions to ensure continuous gametogenesis are present (Sinovčić et al. in press). Information regarding fecundity is extremely important to the definition and estimation of the spawning fraction of a stock (spawning stock) and thus of the entire population. Regner et al. (1981) calculated mean relative fecundity for the entire northern and central Adriatic Sea to be 929.90 eggs g^{-1} (SE = 23.46 eggs g^{-1}); Sinovčić (1983a,b) found relative fecundity to be equal to 944.4 eggs g^{-1} (SE = 48.48 eggs g^{-1}). These values are all reasonably consistent and, overall, associated with small standard errors, implying that relative fecundity is constant. Sinovčić (1983a,b), on sardine from the central Adriatic, reported absolute fecundity to range between 11,337 and 12,667 oocytes per female at the peak of the spawning season, and relative fecundity as 359.07–1488.46 oocytes g^{-1} (specimens: 14.9–20.8 cm; 21.37–72.32 g). The relationships between absolute fecundity F and total length L, weight W and age A were calculated from these data as follows:

$$\text{Length:} \quad F = 0.0398\, L^{4.7812} \quad (R^2 = 0.956,\ p < .01) \tag{1}$$

This equation indicates a significant positive relationship between length and fecundity, which increases approximately five times with respect to length.

$$\text{Weight:} \quad F = 606.6569\, W^{1.1239} \quad (R^2 = 0.992,\ p < .01) \tag{2}$$

$$\text{Age:} \quad F = 7237.785\, A^{1.015} \quad (R^2 = 0.982,\ p < .01) \tag{3}$$

These two equations indicate a significant positive relationship between weight and age, and fecundity, which increases approximately linearly with respect to both.

Fecundity was found to vary within each length, weight and age category; variability, overall, being lower in smaller, younger individuals (Sinovčić 1983a,b).

The biggest problem with the quantification of fecundity as described (i.e., using the method of total relative fecundity) is related to the fact that sardine, as anchovy and other small pelagic fishes, is an indeterminate serial batch spawner and the number of batches spawned over the entire spawning season may be many (for northern anchovy *Engraulis mordax,* it was found to be over 20; Hunter & Goldberg 1980). In the Adriatic Sea, the number of consecutive batches produced by sardine has been reported to be up to 15 during one spawning season (Sinovčić 1986, 1991, Casavola et al. 1996a, Marano et al. 1998). Batch fecundity (eggs spawned in a single batch and the number of batches spawned per year) thus needs to be taken into account if a realistic estimate of the eggs produced by each female during the year is to be made; otherwise there is a risk of underestimating fecundity and overestimating the stock (Regner 1990).

Casavola et al. (1998) estimated the batch fecundity for sardine in the south-western Adriatic based on November samples and reported 8462 eggs batch^{-1} (adjusted to females weighing 20 g), which is within the range of values reported for other areas (7198 eggs batch^{-1} in the Aegean Sea, Ganias et al. 2007; 7646 eggs batch^{-1} in Portugal, Cunha et al. 1992; 10,149 eggs batch^{-1} in the northern Atlantic coast of Spain, Garcia et al. 1992). It is important to bear in mind that in some sardine populations (e.g., the Iberian sardine) batch fecundity has been reported to vary seasonally (Zwolinski et al. 2001) and could be different if taken at peak spawning period rather than at some other time (Ganias et al. 2007).

Feeding and predation

Feeding

Information on the feeding ecology of sardine in the Adriatic is very scarce. The main contribution is a study by Vučetić (1955) in the central Adriatic. The data are limited to the fishing season (April–October) and a few winter samples. Overall it emerged that, during the fishing season, the greatest intensity of sardine feeding occurred at dusk, between 1600 and 1800. Stomach fullness then progressively decreased during the night. This observation explains why sardine caught before midnight were not considered valuable by the processing industry; full stomachs with digestion in progress are difficult to process because the stomach walls decompose more easily (Vučetić 1955). The fullest stomachs in adult individuals caught in winter, on the other hand, were found earlier in the day, implying that at this time of the year, because of the reduced light intensity, sardine also feed during the day. The importance of light for adult sardine feeding is confirmed by the fact that the best catches, of sardine with the fullest stomachs, were made near the surface on nights with a full moon, which agrees with what is known of the vertical migrations of zooplankton.

An analysis of stomach contents in relation to sardine size revealed that adults tend to feed at dusk. Juveniles feed during the day as well (Ercegovic 1940), as do herring (Jespersen 1928). In contrast, Rosoanarivo et al. (1991) in a study on post-larval feeding in the north-western Mediterranean, found that feeding intensity of sardine post-larvae increased dramatically at dusk, coinciding with a significant drop in light intensity. Similar results are reported for sardine larvae in the Cantabrian Sea (Fernández & Gonzalez-Quirós 2006). Larval sardine off the north coast of Spain also feed during the day with peaks at dusk and soon after dawn (Conway et al. 1994).

Information on prey species composition for the Adriatic sardine is virtually non-existent. Karlovac (1967) reported that sardine post-larvae in the central Adriatic Sea feed primarily on zooplankton (the copepods *Oithona* and *Calanus*, as well as on copepod nauplii), but also on phytoplankton (Peridinidae). The omnivory of sardine is well documented from other areas (Cunha et al. 2005). Adult sardine feed on both zooplankton (mainly adults and juvenile copepods) and phytoplankton, although some authors support the thesis that phytoplankton dominates in stomach contents (Cépède 1907, Oliver 1951, Oliver & Navarro 1952) but others have found the opposite (Varela et al. 1990, Bode et al. 2003, Cunha et al. 2005). Larval sardine, in contrast, feed primarily on zooplankton (Conway et al. 1994, Dulčić 1999, Fernández & Gonzalez-Quirós 2006) and copepod developmental stages were the most common (78–89% of stomachs) food organisms found in the stomach contents of larval sardine (4–24 mm total length) from the eastern central Adriatic, the percentage of copepodite stages increasing with increasing larval size (Dulčić 1999). It is evident from recent studies that sardine adopts different feeding strategies according to food availability (Bode et al. 2004, Garrido et al. 2007). In pelagic species, feeding behaviour appears to depend on plankton species composition and concentration, and prey size (van der Lingen 1994, Cunha et al. 2005) and they may, or not, switch between filter-feeding and particulate feeding (Lazzaro 1987, Bode et al. 2004). Laboratory investigations by Garrido et al. (2007) on sardine in the laboratory revealed that feeding mode depends exclusively on prey size and not concentration. They found filter-feeding occurred in the presence of single phytoplankton cells or zooplankton smaller than 780 µm and individuals were observed to school tightly with open mouths at constant swimming speeds, exhibiting no visual selection of prey (Garrido et al. 2007). In contrast, particulate feeding occurred when prey were larger than 780 µm, during which individuals were dispersed, swimming speeds were high and visual detection and attack of prey were observed (Garrido et al. 2007). The same authors also observed that in the presence of both small and large prey, even at high densities, sardine particulate fed and visually selected specific prey (mainly fish eggs), rather than the largest prey (Garrido et al. 2007). Bode et al. (2003) found that the tendency for filter-feeding increased with size. The ability of sardine to use small prey items such as single phytoplankton cells may be one of the factors that allows this species to live and exploit oligotrophic ecosystems, a fact that may be of particular relevance in the open waters of the Adriatic Sea.

Predation

Very few data are available on predation of sardine larvae in the Adriatic Sea and are limited to the observations that a significant amount of sardine larvae are eaten by *Scomber scombrus* post-larvae, whilst the chaethognath *Sagitta* spp. and the copepod *Candacia* feed on both sardine larvae and post-larvae (Karlovac 1967). Fry fishermen operating in the Gulf of Manfredonia (south-western Adriatic) report silver scabbardfish *Lepidopus caudatus* as one of the main predators of anchovy and sardine larval stages in this area. Predators of adult sardine are primarily hake (*Merluccius merluccius*), mackerel (*Scomber scombrus*), tunnids (e.g., *Thunnus thynnus*) and other large pelagic fish species, marine birds and dolphins (Coll et al. 2007).

Schooling and behaviour

Garrido et al. (2007) have shown that schooling behaviour of sardine changes according to feeding strategy. In general, it is reported that larvae are rather dispersed and start aggregating in schools at the late post-larval stage when they move to the nursery grounds and are recruited to the fishery (Kačić et al. 1985, Sinovčić 2000a). The characterisation of schooling behaviour is particularly important in commercial fish species such as sardine because aggregation enhances their catchability. There is a correlation between schooling behaviour and illumination conditions; in total or near darkness schools have been found to be dispersed, overall activity being slow, whereas in light, and as a consequence of sudden illumination, individuals aggregate and drop to the bottom (Mužinić 1964, Azzali et al. 1983). This is a common feature of most small pelagic fish schools (Blaxter & Holliday 1969, Muiño et al. 2003a). Azzali (1980), Azzali et al. (1983) and Baltëza (1985) described the geometry of sardine school as being, on average, 5–10 m wide and 3–20 m high (the majority being up to 8 m high), with the centre of gravity of the majority of schools being around 20 m deep, although this depends on the time of day; similar results were reported by Muiño et al. (2003b) for the Spanish Atlantic. Considering the influence of light intensity, the average density of schools was found to be significantly different between night and day, with a mean of seven individuals m^{-3} during the day and three individuals m^{-3} during the night (Azzali 1980). High interannual variability has been reported for school size and occurrence and appears to be dependent not on area and species composition but on age and size (Iglesias et al. 2003, Muiño et al. 2003b). Nevertheless, overall school morphology is fairly constant (Muiño et al. 2003a). The number of schools present does not appear to depend on fish density (Iglesias et al. 2003, Muiño et al. 2003b) but there is a relationship between the spatial structure of sardine schools and area topography because more heterogeneous aggregations are found in enclosed basins (Giannoulaki et al. 2006).

Growth and mortality

Sardine can grow up to a maximum of approximately 21 cm and 86 g, which corresponds to an age of 8 yr (Sinovčić 2000a). Table 3 summarises the length-weight relationships reported by a number of studies on juveniles and adults and Table 4 gives the von Bertalanffy growth parameters. Initially, age was determined through the use of scales; later this methodology was superseded by otolith (sagittae) microstructure analysis. Age determination of sardine can be successfully carried out on a yearly basis for adults. Larval growth and age can be determined on a daily basis through the quantification of daily growth increments (Ré 1983, Alemany & Alvarez 1994). Larval growth parameters for Adriatic sardine are summarised in Table 5 and their instantaneous mortality rates in Table 6.

Genetic variability

Considering the aforementioned separation between the two spawning grounds and the fact that the Jabuka pit may constitute a physical separation of the two stocks, possibly interfering with migration, the literature regarding the likely existence of two geographically separate subpopulations is worthy of mention. Based on somatic (and other) differences, sardine is considered a polymorphic species (Alegría Hernández et al. 1985). Although genetic studies have described *Sardina pilchardus* population structure as rather homogeneous (Spanakis et al. 1989, Magoulas et al. 2006), some authors reported that it is divided into two separate subspecies, the Atlantic subspecies *Sardina pilchardus pilchardus* and the Mediterranean subspecies *Sardina pilchardus sardina* (Alegría Hernández et al. 1985, Atarhouch et al. 2007) and further distinction has been made for the Adriatic population (Mužinić 1954, Alegría Hernández 1983, Alegría Hernández et al. 1985, Sinovčić & Alegría Hernández 1996, Sinovčić 2000a, Tičina et al. 2000). Based on a series of morphometric, meristic, serological and ecological characteristics, it was considered that the Adriatic population is divided into a northern Adriatic subpopulation and a central Adriatic subpopulation. The characters taken into consideration were the length structure of the population, relative head length, vertebral number, number of gill rakers, the rate of increase of ceratohypobranchial gill rakers, length-weight relationships, condition factor, serological characteristics, spawning grounds, exploitation areas, and migrations. Although there is some evidence of differences (e.g., decrease in variability of relative head length and vertebral number from north to south, decrease in the rate of increase of ceratohypobranchial gill rakers from north to south), most inferences appear to be circumstantial. In fact, the lack of genetic heterogeneity in the Adriatic stock has been demonstrated through allozymic and mitochondrial DNA (mtDNA) surveys (Carvalho et al. 1994) and through sequence variation analysis of a 307-bp cytochrome *b* gene (Tinti et al. 2002a,b). Investigations carried out by Tinti et al. (2002a) confirmed the morphometric and meristic differences described previously for the two Adriatic areas, but the results of the genetic analyses imply that they are mainly due to the different trophic and environmental conditions found in the northern and central Adriatic, which may cause differences in growth rates.

Anchovy, *Engraulis encrasicolus*

Reproduction and migrations

Sardine, like anchovy, is a serial batch spawner that exhibits indeterminate annual fecundity and produces multiple batches of eggs over a protracted spawning period (Blaxter & Hunter 1982). Table 1 summarises data available in the literature regarding the extent of the spawning season, spawning peak, temperature and salinity ranges for the Adriatic Sea. In contrast to sardine, anchovy spawning takes place in the warmer months, generally between April and October, although eggs have been reported as early as February (Zavodnik 1970) and as late as November (Regner 1972).

Table 3 Length–weight relationships of sardine and anchovy in the Adriatic Sea

Species	Area	Time of year	Sex	Size range (cm)	a	b	Reference
Sardine	Central Adriatic (Croatia)					2.914	Mužinić 1980
	NE Adriatic					2.851	Alegria Hernández 1983
	Central Adriatic (Croatia)					2.757	Alegria Hernández 1983
	Central Adriatic (Croatia)				0.00561	3.033	Sinovčić 1983a,b
	SE Adriatic (Albania)	Nov–Mar	All		0.0000171	2.871	Baltëza & Kapidani 1986
	SE Adriatic (Albania)	Nov–Mar	M		0.00001182	2.8662	Baltëza & Kapidani 1986
	SE Adriatic (Albania)	Nov–Mar	F		0.00001156	2.8765	Baltëza & Kapidani 1986
	Novigrad Bay (NE Adriatic)	Apr	All	4.5–13	0.000007765	2.972	Kačić et al. 1987
	Novigrad Bay (NE Adriatic)	May	All	4.5–13	0.000003406	3.122	Kačić et al. 1987
	Novigrad Bay (NE Adriatic)	June	All	4.5–13	0.00000533	3.036	Kačić et al. 1987
	Karin Bay (NE Adriatic)	Apr	All	4.5–13	0.000003697	3.112	Kačić et al. 1987
	Karin Bay (NE Adriatic)	June	All	4.5–13	0.000000837	3.468	Kačić et al. 1987
	Central Adriatic (Croatia)	Sept–Mar			0.0033	3.2764	Sinovčić 1991
	Novigrad Bay (NE Adriatic)	June			0.0066	3.0116	Sinovčić 2000a
	Karin Bay (NE Adriatic)	June			0.0033	3.2638	Sinovčić 2001b
	Krka River estuary (Croatia)	Dec	All	<12	0.0027	3.3532	Sinovčić et al. 2003
	Eastern Adriatic (all)	Sept	All	7.5–18.5	0.0028	3.381	Tičina et al. 2006
	Eastern Adriatic (all)	Sept	All	6–18	0.003	3.321	Tičina et al. 2006
	Krka River estuary (Croatia)	Oct–Feb	All	<12.5	0.007	2.9587	Sinovčić et al. in press
	Krka River estuary (Croatia)	Oct–Feb	M	<12.5	0.053	3.0746	Sinovčić et al. in press
	Krka River estuary (Croatia)	Oct–Feb	F	<12.5	0.034	3.657	Sinovčić et al. in press
	Krka River estuary (Croatia)	Oct–Feb	U	<12.5	0.0063	3.10143	Sinovčić et al. in press
Anchovy	Kastela Bay (Croatia)	Mar–Dec	M	10.0–16.9	0.0099	2.947	Sinovčić 1978
	Kastela Bay (Croatia)	Mar–Dec	F	10.0–16.9	0.0095	2.959	Sinovčić 1978
	Kastela Bay (Croatia)	Mar–Dec	M+F	10.0–16.9	0.0096	2.958	Sinovčić 1978
	Vis & Bisevo Islands (Croatia)	Mar–Dec	M	12.8–18.7	0.015	2.826	Sinovčić 1978
	Vis & Bisevo Islands (Croatia)	Mar–Dec	F	12.8–18.7	0.0244	2.645	Sinovčić 1978
	Vis & Bisevo Islands (Croatia)	Mar–Dec	M+F	12.8–18.7	0.0205	2.709	Sinovčić 1978
	Southern Adriatic (Italy)				0.00532	3.529	Casavola et al. 1981

(continued on next page)

Table 3 (continued) Length–weight relationships of sardine and anchovy in the Adriatic Sea

Species	Area	Time of year	Sex	Size range (cm)	a	b	Reference
	Novigrad Sea (Croatia)	Aug 1989	All	4.4–12.5	0.0021	3.42	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Sept 1989	All	4.4–12.5	0.0037	3.13	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Oct 1989	All	4.4–12.5	0.0047	3.03	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Dec 1989	All	4.4–12.5	0.006	2.95	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Feb 1990	All	4.4–12.5	0.0033	3.2	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Mar 1990	All	4.4–12.5	0.0031	3.24	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	May 1990	All	4.4–12.5	0.0039	3.17	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	July 1990	All	4.4–12.5	0.0037	3.2	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Aug 1990	All	4.4–12.5	0.0036	3.2	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Oct 1990	All	4.4–12.5	0.005	3.09	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Mar 1991	All	4.4–12.5	0.005	3.01	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Apr 1991	All	4.4–12.5	0.0042	3.15	Sinovčić 1998, 1999
	Novigrad Sea (Croatia)	Aug 1989–Apr 1991	All	4.4–12.5	0.0038	3.19	Sinovčić 1998, 1999
	Kastela Bay (Croatia)	1974–1979	All	8.0–18.5	0.004	3.1195	Sinovčić 2000b
	Dalmatian region (Croatia)	1974–1979	All	8.0–18.6	0.0123	3	Sinovčić 2000b
	Novigrad Sea (Croatia)	1987– 991	All	3.9–14.3	0.0038	3.1939	Sinovčić 2000b
	Kastela Bay (Croatia)	1987–1991	All	4.4–18.5	0.004	3.1195	Sinovčić 2000b
	Vis & Bisevo Islands (Croatia)	1987–1991	All	4.4–18.6	0.0205	2.7078	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	M 1+yr	10.2–12.8	0.0045	3.15	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	M 2+yr	11.3–15.1	0.0124	2.747	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	M 3+yr	13.1–16.8	0.03	2.404	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	F 1+yr	11.0–14.1	0.0106	2.8	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	F 2+yr	12.0–15.4	0.0243	2.47	Sinovčić 2000b
	Central Adriatic (Croatia)	1987–1991	F 3+yr	14.0–16.1	0.0198	2.56	Sinovčić 2000b

Central Adriatic (Croatia)	1987–1991	All 0+yr	3.9–11.0	0.0049	3.01	Sinovčić 2000b
Central Adriatic (Croatia)	1987–1991	All 1+yr	10.2–14.1	0.0082	2.904	Sinovčić 2000b
Central Adriatic (Croatia)	1987–1991	All 2+yr	11.3–15.4	0.0174	2.611	Sinovčić 2000b
Central Adriatic (Croatia)	1987–1991	All 3+yr	13.1–16.8	0.0303	2.4	Sinovčić 2000b
Central Adriatic (Croatia)	1987–1991	All	7.5–16.8	0.0152	2.731	Sinovčić 2000b
Northern & central Adriatic (Croatia)	2003	All		0.0025	3.341	Tičina et al. 2006
Novigrad Sea (Croatia)	1993	M	7–14	0.0037	3.196	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	1993	F	7.9–14.5	0.0034	3.229	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	1993	All	4.5–14.5	0.0035	3.211	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Jan 1993	All	6.0–9.5	0.0053	2.96	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Feb 1993	All	4.5–7.0	0.0176	2.345	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Mar 1993	All	7.0–12.0	0.004	3.167	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Apr 1993	All	8.5–12.0	0.0047	3.099	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	May 1993	All	7.5–14.5	0.0035	3.215	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	June 1993	All	9.0–14.0	0.0045	3.114	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	July 1993	All	9.0–13.0	0.0058	3.013	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Aug 1993	All	5.5–13.5	0.0053	3.049	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Sept 1993	All	7.5–11.5	0.0042	3.109	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Oct 1993	All	7.0–11.0	0.0053	3.045	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Nov 1993	All	8.5–11.5	0.0039	3.135	Sinovčić & Zorica 2006
Novigrad Sea (Croatia)	Dec 1993	All	7.5–10.5	0.0091	2.791	Sinovčić & Zorica 2006
Northern Adriatic (Italy)	Oct 2002	All	1.0–13	0.0000001	3.854	Borme 2006
Northern Adriatic (Italy)	May 2003	All	6.5–13	0.000003	3.178	Borme 2006
Eastern Adriatic (Montenegro)	2005	All	5–18	0.006	3.0304	Regner et al. 2006

M = male; F = female; U = undetermined; a = intercept; b = slope.

Table 4 Von Bertalanffy growth parameters for sardine and anchovy in the Adriatic sea

Species	Year	Sex	L_∞ (cm)	K (yr^{-1})	t_0 (yr)	Reference
Sardine			20.5	0.46	−0.5	Sinovčić 1983b, 1986
	1975		19.07	0.37	−3.05	Levi et al. 1985
	1976		18.84	0.38	−3.08	Levi et al. 1985
	1977		19.53	0.29	−3.84	Levi et al. 1985
	1978		19.68	0.29	−3.75	Levi et al. 1985
	1979		19.17	0.32	−3.75	Levi et al. 1985
Anchovy	1979	M	18.6	0.58	−0.6	Sinovčić 1988, 2000b
	1979	F	19.3	0.56	−0.7	Sinovčić 1988, 2000b
	1979	All	19.4	0.57	−0.5	Sinovčić 1988, 2000b
	1989–1991	All	13.2	0.82	−0.5	Sinovčić 1998, 1999
	2005	All	18.9	0.46	−1.247	Regner et al. 2006

Based on the von Bertalanffy growth model: $l_t = L_\infty[1 - e^{-K(t - t_0)}]$ where l_t = mean length at age t, L_∞ = mean asymptotic length, K = growth coefficient, t_0 = age at zero length. M = male; F = female.

Table 5 Growth parameters of larval sardine and anchovy calculated using two different methods

Method	Species	Reference	T (°C)	*a*	*b*	*c*	*r*
Gompertz	Sardine (larvae)	Dulčić 1995	13.1	29.58856	1.967218	0.08410072	0.982
	Sardine (larvae)	Regner et al. 1987	14	5.17	0.3898	0.4199	−0.999
	Sardine (post-larvae)	Regner et al. 1987	16	47	2.1985	0.0169	−0.999
	Anchovy	Regner & Dulčić 1990		27.315	2.0517	0.0892	0.98
	Anchovy	Dulčić 1997		36.87	2.609	0.077	0.99
Method	**Species**	**Reference**	**T (°C)**	L_0	A_0	α	r^2
Laird-Gompertz	Sardine (larvae)	Dulčić 1995	13.1	4.138228	0.1654595	0.08411218	0.982
	Anchovy	Regner & Dulčić 1990		3.51	0.1829	0.0891	0.98
	Anchovy	Dulčić 1997		2.71	0.203	0.0077	0.99
	Anchovy	McFadzen & Franceschini 1997		3.67	0.2226	0.1921	0.99

Gompertz method: $l_t = a \exp(-be^{-ct})$ where l_t = length at time t, *a* = asymptotic length, *b* and *c* = constants. Laird-Gompertz method: $l_t = L_0 \exp[(A_0/\alpha)(1 - e^{-\alpha t})]$ where l_t = length at time t, L_0 = predicted length of larvae at deposition of first ring, A_0 = specific growth rate at L_0, α = constant describing progressive reduction in growth rate with length.

Within this time period, there are peaks of spawning, generally one or two, May–June (Vučetić 1971) and August–September (Regner, 1972), whose timing greatly depends on the area and on a series of interacting biotic and abiotic factors (Table 1). Overall, the reproductive cycle of anchovy can be described as follows (Di Marcotullio & Catolla Eluambio Di Marcotullio 1983, Sinovčić 2000b, Sinovčić & Zorica 2006). Between November and February individuals are in a resting, sexually inactive stage with unripe gonads. In February and March gonads start ripening but the majority are still inactive; between March and August the percentage of ripe males and females increases progressively, reaching a maximum between June and August depending on the area. In September and October the percentage of ripe individuals decreases and eventually most individuals have spent or unripe gonads. Gonad analysis has also highlighted the contemporary presence of

Table 6 Mortality of larval and post-larval sardine in the Adriatic Sea

Year	Area	Life stage	m	Reference
1978/79	Adriatic	Larvae	0.544	Regner et al. 1983
1979/80 (Dec–Jan)	Adriatic	Larvae	0.743	
1979/80 (Feb)	Adriatic	Larvae	0.339	
1980/81	Adriatic	Larvae	0.559	
1981/82 (Dec)	Adriatic	Larvae	0.994	
1981/82 (Mar–Apr)	Adriatic	Larvae	0.382	
	Entire Adriatic	Eggs & larvae	0.5565	Regner et al. 1987
	Northern spawning centre	Eggs & larvae	0.6545	
	Southern spawning centre	Eggs & larvae	0.5878	
	Entire Adriatic	Post-larvae	0.0973	
	Northern spawning centre	Post-larvae	0.0571	
	Southern spawning centre	Post-larvae	0.0559	

Calculated from the equation $N_t = N_0 e^{-mt}$ where N_t = number at time t, N_0 = number at time 0, and m = coefficient of instantaneous mortality.

oocytes at various stages of development, as well as void spaces, within the same female, indicative of serial batch spawning (Di Marcotullio & Catolla Eluambio Di Marcotullio 1983, Sinovčić & Zorica 2006). This cycle is reflected by the monthly trend in the gonadosomatic index (GSI) and gonad weight, whilst the opposite is true for condition and mesenteric fat (Sinovčić 1978, 2000b, Sinovčić & Zorica 2006).

The presence of anchovy eggs in the Adriatic has been reported at temperatures between 11.6 and 28°C, and at salinities ranging from 9.1 to 38.7 psu (Table 1). Spawning peaks occur at the higher temperatures in the range, between 18 and 28°C (Table 1) whereas egg density is inversely proportional to salinity (Zavodnik 1970). Regner (1972) also found water density to be important, with maximum numbers of eggs occurring between 26.6 and 27.4 σt in open waters and between 24.13 and 24.81 σt in coastal areas. During the spawning season eggs are distributed throughout the entire Adriatic within the 200-m depth zone and eggs are absent from the deeper Jabuka pit and southern Adriatic trench (Gamulin & Hure 1983, Regner 1985, Casavola et al. 1987). The main spawning activity takes place in the coastal waters of the western Adriatic between the Gulf of Trieste and the Gargano peninsula (Casavola et al. 1985, Regner 1996, Pinardi et al. 2005) and the largest number of eggs occurs in the Gulf of Trieste and off the river Po delta (Piccinetti et al. 1980, Coombs et al. 1997, Specchi et al. 1998, Piccinetti 2001). Other spawning areas have been located in open waters between Susak Island and the Jabuka pit and around Palagruža Island, as well as in the eastern Adriatic (e.g., Vis and Biševo Islands) but here the intensity of spawning is substantially lower (Regner 1972, Piccinetti et al. 1979, Gamulin & Hure 1983, Regner 1996, Sinovčić 1978, 2000b). Maximum egg production occurs earlier in open waters than in coastal areas (Vučetić 1971, Regner 1972, Piccinetti et al. 1979, Sinovčić 2000b). In addition, eggs from the open sea are larger than those in coastal areas (Regner 1972). These last two factors are most likely linked to the migrations occurring within the anchovy population before, during and after the spawning season. Anchovy adults migrate from the deeper overwintering waters to shallower coastal areas for spawning (Sinovčić 2000b) and similar migrations have been reported for the Black Sea (Majarova & Chugunova 1954, Demir 1963). Once spawning is completed and temperatures fall, adults return offshore, whilst juveniles generally remain closer to the coast until January, or until the following year when first maturity is attained (Sinovčić 2000b, Marano 2001). Several authors have found that anchovy length is closely correlated with depth and individuals smaller than 15.5 cm are rarely found at depths greater than 100 m (Piccinetti 1971, Mužinić 1972, Sinovčić 1978). Offshore winter migration of the younger portion of the population is therefore only partial and depends on the area considered. Thus, only the larger individuals (releasing larger eggs) are found offshore in spring, when spawning commences whereas, at this time, the individuals found inshore are young at their first spawning and release smaller eggs (Regner 1972). The presence of two spawning peaks as reported by several authors (Varagnolo 1964a, Di Marcotullio & Catolla Eluambio Di Marcotullio 1983) may also be explained in terms of this partial migration. Larger adults migrate inshore early in spring for spawning but the younger individuals, at their first spawning, arrive inshore later in the season and spawn later (Di Marcotullio & Catolla Eluambio Di Marcotullio 1983, Millan 1999).

Several studies have been carried out on the spatial relocation of the spawning centres during the spawning season (Regner 1985). Štirn (1969) reported this shift to occur against prevailing currents but the major body of evidence is in favour of the opposite theory. Vučetić (1964) supported the idea that areas of maximum spawning intensity in the eastern Adriatic were displaced from the offshore waters off Dugi Otok island towards the coastal Istrian waters as the spawning season progressed and similar findings were reported by Kačić (1980). Varagnolo (1965) hypothesised that the maximum spawning activity in the Gulf of Venice moved coastwards and anticlockwise along the coast. Piccinetti (1970), based on fisheries production data, hypothesised the following movements of adult (>1 yr) anchovy in the northern and central Adriatic Sea. In winter adults are found in waters deeper than 50 m from off Senigallia down to the Jabuka pit. In March, at the onset of spawning, they move north-eastwards and inshore towards Istria, reaching it at the end of March. The coastal anticlockwise migration continues from Istria towards the Gulfs of Trieste and Venice, which are reached in April. Here the fish stay until July–August and September, respectively, and then move round to the mouth of the river Po between August and October. A smaller portion of fish, instead of moving from the open waters towards Croatia in March, shifts towards the Italian coast and slowly moves northwards, converging with the other group off the Po River delta. Between October and November adults migrate east or south-east from the area round the Po River to deeper waters, closing the circle. Juveniles, as mentioned, reside in coastal waters for longer periods of time. This theory appears to partially explain the spatial movements of anchovy throughout the year, corroborating previously mentioned findings and the fact that large numbers of young are found in the bays of the eastern Adriatic coast (Sinovčić 1978, 1998, 1999, 2000b, Sinovčić & Zorica 2006). Nevertheless, it does not take into account the area south of the line connecting Pescara and Dugi Otok and thus the conspicuous numbers of eggs found along the entire western Adriatic coast down to the Gargano promontory and, to a lesser extent, further south to Brindisi (Casavola et al. 1985, 1987, Regner 1996, Marano 2001). Gamulin & Hure (1983) offered a wider perspective of the movements of anchovy during the spawning season through data collected during a series of egg surveys carried out in the entire Adriatic in the mid 1970s. Early in the spawning season, in April and May, most eggs were concentrated offshore in two main areas: between Pesaro and Pula, and Ancona and Dugi Otok Island in the north and between Vieste and the mid-Dalmatian Islands further south. Isolated areas of high egg density were found off Bari and off Dubrovnik. In July very high concentrations of eggs were still to be found in the same areas, but the highest by far were to be found further north towards the Po River delta and the Gulfs of Trieste and Venice, which had been virtually devoid of eggs in April–May. Later, in September–October, high egg densities were found solely off the Po River estuary. Gamulin & Hure (1983) reported low spawning intensity for both the Kvarner region and the inner mid-Dalmatian Islands. Considering all available information, it appears that adult anchovy do shift their spawning centres throughout the spawning season in a manner very similar to that described by Piccinetti (1970), but the north-eastwards migration towards Istria starting from March seems to be equally balanced by a westwards migration towards the Italian coasts. There is one area that has been described as harbouring conspicuous numbers of anchovy larvae, post-larvae and juveniles, but relatively low egg densities. This is the Gulf of Manfredonia in the south-western Adriatic, where there is a massive presence of anchovy post-larvae and juveniles between October and January but the number of eggs found across the years has been low in comparison (Casavola et al. 1985, 1987, Marano et al. 1998). This area has thus been described as being solely a nursery area fostering young that were spawned elsewhere and

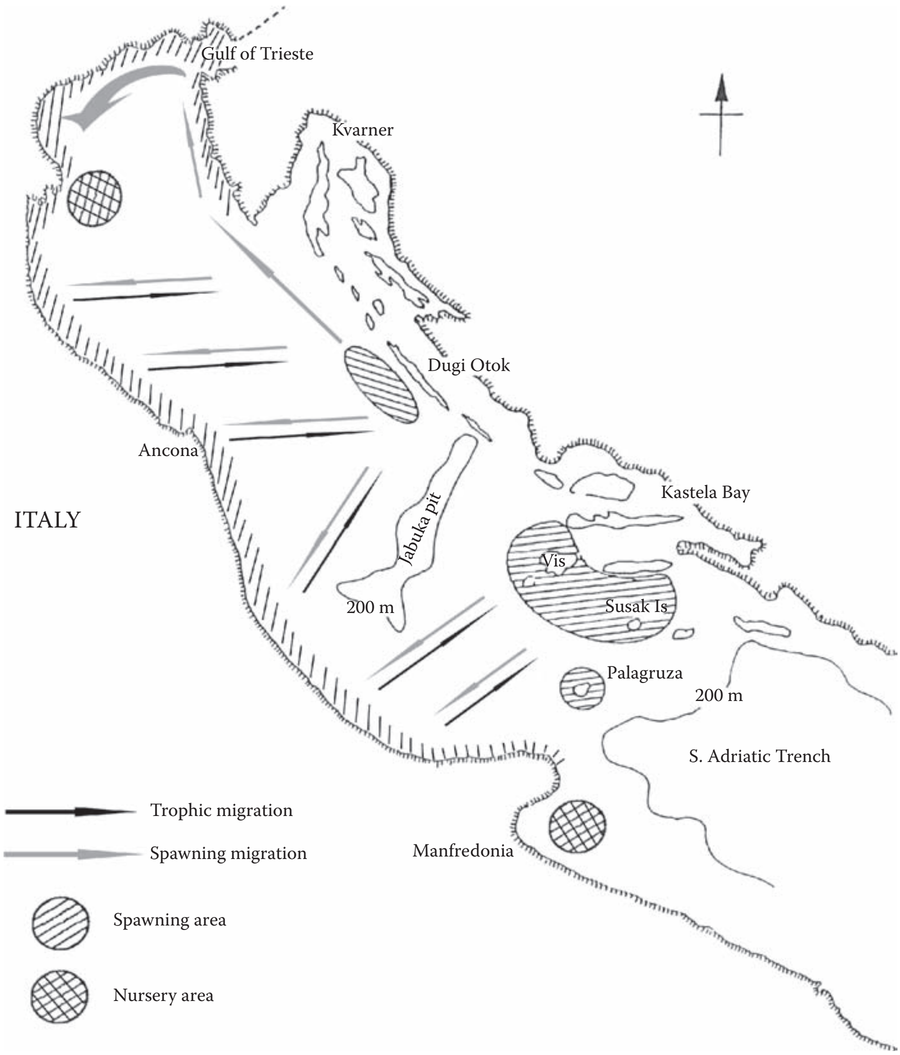

Figure 4 The migrations of anchovy in the Adriatic Sea.

congregated in the Gulf of Manfredonia in a second instance (Marano et al. 1998). A preliminary analysis of the Adriatic current system indicates that these larvae originate from the coastal, shallow depths north of the Gargano peninsula (A. Russo personal communication, April 2008). To a lesser extent, the Novigrad Sea in the eastern central Adriatic is similar (Sinovčić 1998, 1999, Sinovčić & Zorica 2006) but with the difference that in these areas the presence of larvae is consistent with the current system described and the consequent drift of eggs from spawning grounds. Figure 4 summarises the migratory patterns of anchovy.

It is believed that the onset and duration of spawning are heavily influenced by temperature (Palomera 1992, Motos et al. 1996) but considering the wide range of optimal temperatures (and salinities) reported (Table 1) and the fact that increases in egg production occur within these ranges, it is food availability that appears to govern the spawning dynamics of anchovy in both spatial and temporal terms, temperature and salinity being a proxy of hydrographic conditions favouring enhanced production (Regner 1985). Štirn (1969), in a study on the area off the Po River estuary, highlighted the importance of the trophic chain constituted by the diatom *Nitzschia*, the cladoceran

Penilia and anchovy. More specifically, a significant positive correlation was found between anchovy eggs and *Penilia* and between this cladoceran and temperature, confirming the indirect influence of temperature on anchovy reproduction (Štirn 1969). It is well known that food availability has a major influence on fish population dynamics, both directly (through starvation, intra- and interspecific competition and effects on metabolism and fecundity) and indirectly (through increased susceptibility to variations in abiotic factors, disease, predation on poorly fed individuals and variations in growth) (Nikolskii 1969). Thus, the shift in spawning centres throughout the spawning season reported may be one in search of optimal trophic conditions for spawning and egg, larval and post-larval survival (Varagnolo 1964b, 1965). Vučetić (1971, 1975) found that variations in egg densities in the central Adriatic were closely correlated with variations in zooplankton and increases in egg numbers coincided with enhanced ingressions of nutrient-rich Mediterranean water that are known to enhance productivity in the eastern Adriatic. Regner (1974) also found that variations in total egg numbers coincided with variations in mean annual primary productivity in the central eastern Adriatic Sea, albeit in an indirect manner, through variations in zooplankton as reported by Specchi et al. (1998) for the Gulf of Trieste. The egg and larval surveys carried out by Gamulin & Hure (1983) confirmed this effect and showed how egg density distributions in the entire Adriatic Sea were closely correlated with the distribution of zooplankton, particularly copepods (the main food of anchovy), coinciding with Zone B described by Buljan (1964). Among others, Palomera (1992) for the north-western Mediterranean and Motos et al. (1996) for the Bay of Biscay showed that anchovy take advantage of a combination of stable weather conditions and nutrient enrichment phenomena, which, in these areas, occur prevalently in relation to the transitional zones associated with riverine freshwater inputs during the summer months.

Similar findings have been found for the Adriatic Sea, with particular reference to the Po River. As mentioned, one of the areas of major spawning intensity of anchovy in the Adriatic Sea is off the mouth of the river Po. The river Po influences the hydrography of the northern Adriatic Sea considerably through its freshwater (which in summer enhances vertical stratification) and nutrient inputs (Artegiani et al 1997a). Coombs et al. (2003) in a study on anchovy spawning and larval distribution at the Po River plume described this region as being favourable to larval survival because of the additional water column stability associated with the low salinity of the river outflow, but the relationship between enhanced stability and larval survival could not be proved. Coombs et al. (1997) found that the highest abundance of eggs was found close to the front created by the river Po plume; this abundance was reported to decrease offshore and was correlated with a decreasing inshore-offshore gradient in chlorophyll *a*. Similar findings were reported several years later by Borme (2006) for a frontal zone created by the Po River freshwater run-off off Pesaro in autumn. In this case the temperature was homogeneous along the water column, allowing anchovy to aggregate in areas of high food concentration (the inshore, freshwater, side of the front). The same author found a radically different situation in the spring of the successive year. At that time, a strong thermocline was present and zooplankton was very abundant and homogeneously distributed in the water column; in this case temperature not food was the factor driving distribution and anchovy was found to be more abundant in the warmer surface layer (Borme 2006). Palomera (1992) suggested, for the north-western Mediterranean, that anchovy adapt the duration of the reproductive period on the basis of the maximum freshwater outputs of the Ebro and Rhône Rivers, thus giving eggs and larvae the maximum chance of survival. Santojanni et al. (2006a) obtained very interesting results regarding the interaction between anchovy recruitment (defined as the 0+ age class), Adriatic currents and the Po River run-off. These authors found significant positive correlations between anchovy recruitment and autumn south-south-east and east-south-east winds, as well as with autumn Po River discharge in the previous year. River run-off was thus found to play an important role in autumn instead of spring as reported for other areas (Lloret et al. 2004). These two factors were hypothesised as indirectly enhancing anchovy recruitment through the modification of the Western Adriatic Coastal Current (WACC) (Santojanni et al. 2006a), which is responsible for maintaining nutrient-rich coastal freshwaters separate from the more saline offshore waters (Pinardi et al. 2005). Increased intensity of south-south-east and east-south-east winds and increased Po discharge in autumn may have been responsible for pushing this boundary further offshore, increasing the area of high food availability favourable for anchovy development (Santojanni et al. 2006a). The WACC most likely plays a major role in the transport of larvae and post-larvae from spawning to nursery areas, as evidenced by the fact that although anchovy eggs are released both inshore and offshore late post-larvae and early juveniles are found solely along the Italian coast between September and January (Pinardi et al. 2005).

Vučetić (1957) reported spawning around Mljet island (eastern Adriatic) to take place between 1900 and 2100 whilst Varagnolo (1964b) observed spawning between 1800 and 2000 off Chioggia. Embryonic development time varied according to temperature: 96 h at 16.5°C, 40 h at 20–21°C, and 24 h at 27–28°C (Vučetić 1957, Varagnolo 1964b). Laboratory studies by Regner (1985) showed that there is an inversely proportional relationship between total egg development time and temperature that was best described by an inverse logistic equation (Regner 1985, 1996):

$$D = 1/C\ [1+e^{a+bT}]$$

where D is development time (h), C = asymptote, T = temperature (°C), and a and b are constants. For anchovy this relationship is (Regner 1985, 1996)

$$D = 1/1.012896\ [1 + e^{4.914322-(0.257451\ T)}]$$

Larval development time, from hatching to yolk sac resorption, occurs earlier at higher temperatures and is best described by a power function (Regner 1996):

$$D = C\ T^{-b}$$

where D is development time (days), C = constant, T = temperature (°C) and b = constant and for anchovy is (Regner 1996)

$$D = 270065.2774\ T^{-3.8079}$$

Mouth opening and eye pigmentation occur at 3.50 mm but yolk sac resorption is slightly later at 3.54 mm (Regner 1985). Similarly, also on the basis of laboratory studies, egg survival was found to be inversely proportional to temperature. At 17.14°C survival was estimated at 19.8%, whilst at 24.1°C it was estimated at 67% (Regner 1985).

D'Ancona (1931) described anchovy larvae and post-larvae from the Gulf of Naples and reported the switch from one to the other at about 4–5 mm length, by which time individuals had resorbed the yolk sac and developed a mouth opening as well as pigmented silver eyes. Duka (1963) and Regner (1972) reported this switch to occur earlier, at 3.1–3.5 mm and at 2.8–3.9 mm, respectively, and the switch size of 3.67 mm reported by McFadzen & Franceschini (1997) falls within these ranges.

As for sardine, Regner (1974) found the critical period (Hjort 1914) for anchovy development to be at the end of yolk sac resorption in coincidence with the switch to exogenous independent feeding, with survival rates being around 0.5–1% depending on food availability. Laboratory experiments carried out by the same author in later years supported his earlier findings, that is, a sudden increase in mortality, due to starvation, within 1–2 days of resorption and this depended on temperature (6% survival at 21.3°C and 14% survival at 21.8°C; Regner 1985). Contrasting results were found by Regner (1985) on wild larvae. The presence of a critical period was not confirmed and in contrast, larval mortality was reduced after the transition from yolk sac to active feeding.

Eggs are distributed in the surface layer generally within 10 m deep (Vučetić 1957, Gamulin 1964, Regner 1972, Coombs et al. 1997) with the highest concentrations occurring within 1 m of the surface (Varagnolo 1965, Coombs et al. 1997). Ghirardelli (1967) and Specchi (1968) in the Gulf of Trieste found the highest egg concentrations between 7 and 27 cm from the surface. The distribution of eggs was found to be non-random, probably contagious (Regner et al. 1985). Larvae generally have a similar vertical distribution to eggs although the maxima are found deeper, at around 6–8 m from the surface (Coombs et al. 1997, 2003). The first signs of diel migrations have been reported to commence at 8–10 mm total length off the Po River, with maximum abundances at 6–8 m depth during the night and at 16–18 m depth during the day (Coombs et al. 1997). Off the Po River estuary, larvae and post-larvae were found to be further offshore compared with the eggs and this observation was consistent with the easterly drift caused by the plume (Coombs et al. 2003). Temperature, salinity and density ranges for larvae and post-larvae were found to be very similar to those found for eggs, with maximum densities occurring at 13.15–23.85°C, 34.91–38.9 psu, and 24.5–27.8 σt (Regner 1972, 1985), implying, again, that larval and post-larval distribution in the water column is mainly related to the distribution of food particles. An inshore-offshore drift of post-larvae was found throughout the spawning period (Regner 1985).

As for sardine, the age and length at first maturation have direct effects on the reproductive potential of the species because they define the duration of the reproductive cycle and ultimately affect overall population growth (Sinovčić et al. 2003). Overall, anchovy attains first sexual maturity at the end of the first year of life (Sinovčić 1988, 2000b, Marano 2001, Sinovčić & Zorica 2006). The lengths at first maturity are summarised in Table 2. Mužinić (1956) found the smallest mature male to be 13.3 cm and the smallest female to be 13.7 cm in the Dalmatian Island area, the smallest mature male found by Sinovčić (1978) in Kastela Bay (central eastern Adriatic) was 8.6 cm and the smallest female 9.7 cm, whereas in Novigrad Bay (north-eastern Adriatic Sea) the Lm_{50} (length at which 50% were mature) was 7.9 cm for males (smallest 6.7 cm) and 8.5 for females (Sinovčić & Zorica 2006). The smallest mature anchovy specimen found in Albanian waters was 10 cm (Kolitari 2006). Varagnolo (1967) reported length at first maturity irrespective of sex to be 8–9 cm in the northern Adriatic but Rampa et al. (2005) reported 7.5 cm for males and 8.6 cm for females in the same area, the length at first maturity following a decreasing gradient eastwards. Marano et al. (1998) found an overall length at first maturity of 9 cm for the south-western Adriatic. The transition from immature to mature stages in anchovy occurs over a range of lengths, which can be described by a sigmoid curve (Sinovčić & Zorica 2006), and males mature earlier than females (Sinovčić & Zorica 2006). Sexual development starts earlier in larger fish (Mužinić 1956, Sinovčić 1978) and this size difference explains why eggs at the beginning of the spawning season are larger than those at the end of the spawning season (Mužinić 1956, Regner 1972, Sinovčić 1978).

The sex ratio of the anchovy population in the Adriatic is essentially 1:1. Variations in sex ratio throughout the year are in accordance with the overall physiological/reproductive state; males dominate during the spawning period and females during the inactivity period (Mužinić 1956, Padoan 1963, Sinovčić 2000b).

Fecundity in anchovy is high and, as for sardine, it is not predetermined but depends on the duration of the spawning season and food availability to ensure continuous gametogenesis (Sinovčić & Zorica 2006). Like sardine, anchovy is a serial batch spawner and the number of batches released across the entire spawning period may vary (Regner et al. 1985, Casavola et al. 1996b, Sinovčić & Zorica 2006). The number of batches released by anchovy can be up to 20 in the Adriatic (Marano et al. 1998, Marano 2001). Thus, the same problems described for sardine regarding the quantification of fecundity using the method of total relative fecundity also apply to anchovy and these pitfalls are related to the estimation of stock biomass based on relative fecundity and not batch fecundity. The use of relative fecundity, in fact, appears to inflate biomass estimates considerably, which in a management context may be dangerous. A number of fecundity estimates are mentioned in the literature, some of which take into account serial batch spawning; others do not. Piccinetti et al. (1979) and Regner et al. (1985) reported a relative fecundity for anchovy of 1299 eggs g^{-1} of female, relative fecundity being a relative stable factor, and similar results were found by Varagnolo (1967) some

10 yr earlier. Casavola et al. (1996b), on the south-western Adriatic, reported batch fecundity values for the first time. These authors found that the model best expressing the relationship between batch fecundity (eggs batch^{-1}, F) and the weight of hydrated ovary-free females (W_h^* in g) was a weighted linear one:

$$F = a + bW_h^*$$

which for anchovy was found to be

$$F = 186.7 + 448.4W_h^*$$

Thus, batch fecundity increases linearly with increasing female size. The average batch fecundity was reported to be 7019 eggs batch^{-1} mature female^{-1}, whereas the relative batch fecundity was 437.2 eggs batch^{-1} g^{-1} of female (Casavola et al., 1996b). Casavola (1998) and Marano et al. (1998) for the south-western Adriatic reported a value of batch fecundity equal to 11,866 eggs batch^{-1} mature female^{-1}, which translates into a relative batch fecundity of 638.98 eggs batch^{-1} g^{-1} of spawner. These values are within the range of values reported in the scientific literature for other areas of anchovy distribution (Bay of Biscay: 202–662 eggs batch^{-1} g^{-1} of female, Motos 1996; Catalan Sea: 307–561 eggs·batch^{-1}·g^{-1} of female, García & Palomera 1996; Black Sea: 652.3 eggs batch^{-1} g^{-1} of female, Lisovenko & Adrianov 1996). Obviously the time at which samples are taken greatly affects the values obtained for batch fecundity, especially because fecundity increases as the spawning season progresses (Motos 1996).

Feeding and predation

A number of studies have been carried out on the feeding ecology of post-larval, juvenile and adult anchovy.

Regner (1985) reported that post-larvae from the central eastern Adriatic feed mainly on copepod developmental stages (eggs, nauplii, meta-nauplii and copepodites) and only rarely on phytoplankton. Coombs et al. (1997) and Conway et al. (1998) studied the distribution of eggs and larvae in relation to food availability and their feeding habits at the outflow of the river Po. Their results showed that anchovy larvae contained food in their guts only during the day and food contents depended on the size of the individuals, the maximum size of food items increasing in progressively larger larvae, although small items were still taken. The guts of larvae smaller than 6 mm contained copepod nauplii only, those smaller than 8 mm copepod nauplii and eggs, whereas those bigger than 8 mm had stomach contents very similar to those of adults, containing copepodite stages and small adult copepods such as *Oithona* spp. (Coombs et al. 1997). Ontogenetic differences in feeding were also observed by Borme (2006) in larger individuals: Copepodite stages and calanoid copepods were found to be taken by individuals 1–2 cm in length, whilst above 2 cm diet was very similar to that of adults (essentially copepodites and adult copepods). Conway et al. (1998) found feeding incidence to decrease with increasing larval length up to 10–10.9 mm, to then increase again. The decreased feeding activity of post-larvae was also observed by Borme (2006) between 10 and 29 mm and was ascribed to the fact that at this stage the digestive tract is not yet completely developed. Similar results were reported by Regner (1972) for the eastern Adriatic and by Tudela et al. (2002) for the north-western Mediterranean.

In contrast to Regner (1985), no other studies have reported the presence of phytoplankton in the guts of anchovy larval stages in the Adriatic, leading to the conclusion that they are exclusively zooplanktivorous (Coombs et al. 1997, Conway et al. 1998, Borme 2006). This may be because in the areas investigated by these authors (areas affected by the Po River discharge), zooplankton is rarely limiting. In support of this suggestion Budnichenko et al. (1999) found that in the

Azov Sea microphytoplankton constituted 87% of anchovy stomach contents in the absence of mesozooplankton.

Feeding in the Adriatic occurred mainly during the day (Duka 1963, Regner 1972, Conway et al. 1998) as in other areas (Tudela & Palomera 1995, 1997, Plounevez & Champalbert 1999). Borme (2006), in a study of feeding ecology in two frontal zones of the western Adriatic, confirmed this essentially diurnal feeding pattern and reported two main peaks in feeding activity, one around 1500 and another 1 h after sunset, possibly related to peaks in food availability, although some night-feeding activity was observed. Light thus plays an important role in the feeding activity of anchovy and this is supported by the fact that juveniles and adults appear to catch their prey through visual selection (Borme 2006). In fact, in the western Adriatic, active selection was found to occur for the copepods *Oncaea* spp., *Euterpina acutifrons*, *Temora longicornis* and bivalve and decapod larvae. The dinoflagellate *Noctiluca scintillans,* however, seems to have been actively avoided because it was never found in gut contents despite its very high abundance in the plankton (Borme 2006). Overall, Borme (2006) found the diet of juveniles and adults to be fairly constant within seasons, both in terms of species composition (which tended to reflect seasonal zooplankton composition) and prey dimensions, being essentially dominated by medium-sized copepods. In the northern Adriatic (Po estuary and Gulf of Trieste), the cladoceran *Penilia avirostris* is a very important component of anchovy diet (Štirn 1969, Specchi et al. 1999), to the extent that Štirn (1969) highlighted the importance of the *Nitzschia-Penilia*-anchovy trophic chain. This species was never found by Borme (2006), probably because *Penilia* is very abundant in summer plankton and this author worked only on spring and autumn samples. Occasional cannibalism of adult anchovy on larvae was observed but this may be an artefact of sampling (Borme, 2006).

Conway et al. (1998) found feeding success of larvae to be unaffected by prey concentration, with the latter factor affecting food intake only when below 50 items l^{-1}.

Borme (2006) reported average food evacuation rate to be 0.715 h^{-1}, the average amount of food ingested to be 8.959 g of stomach content dry weight 1000 g^{-1} of somatic wet weight, and the average daily requirement to be 5.9% of its total body weight, equivalent to 36.14–35.74 calories g^{-1} of total wet weight. These values, with the exception of the amount of food ingested, which is higher in this study, are within the ranges reported for anchovy in other areas (Tudela & Palomera 1995, 1997, Plouvenez & Champalbert 2000). Tirelli et al. (2006) studied the energy density (E_D, a measure of fish growth and food consumption) of anchovy in the Adriatic Sea and found it to be between 2667 and 7022 J g^{-1} wet mass overall, a value that is within the range of E_D found for other engraulids. Furthermore, these authors found a linear relationship between E_D and fish size up to 9 cm although a higher variability characterised larger males and females, probably linked to reproductive state (Tirelli et al. 2006). Similarly, differences were found between sampling periods and individuals caught at the end of summer had higher E_D values than those caught in spring (Tirelli et al. 2006).

Although predation is widely advocated as one of the important causes of fish mortality, especially in the larval stages, very few data are available on predation of anchovy in the Adriatic Sea. Sardine guts contain anchovy post-larvae and anchovy eggs (Vučetić 1963) and larvae have frequently been found in the gut contents of the jellyfish *Pelagia noctiluca* (Zavodnik 1991). The massive presence of this jellyfish between 1978 and 1987 led several authors to believe that its predation on anchovy eggs and larval stages may have influenced the collapse in anchovy biomass and catches recorded in 1987 (Avian & Rottini Sandrini 1988, Piccinetti & Piccinetti Manfrin 1991, Orlandi et al. 1994, Regner 1996, Specchi et al. 1998). In support of this thesis, Möller (1984) showed how the jellyfish *Aurelia aurita* affects populations of herring *Clupea harengus* by eating their larvae. Fry fishermen operating in the Gulf of Manfredonia reported silver scabbardfish *Lepidopus caudatus* as one of the main predators of anchovy and sardine late larval stages in this area.

Juvenile and adult anchovy are eaten primarily by hake (*Merluccius merluccius*) (Froglia 1973), mackerel (*Scomber scombrus*), tunnids (in particular by juveniles of *Thunnus thynnus*; Orsi Relini et al. 1999) and other large pelagic fish species, marine birds and dolphins (Coll et al. 2007).

Schooling and behaviour

Anchovy is a schooling species (Borme 2006). Diel vertical migrations are reported to start at around 8–10 mm when larvae live at the surface in schools during the night, shifting to deeper waters during the day (Coombs et al. 1997, Borme 2006). This vertical migration is retained into adult life but schools, when at the surface at night, tend to be more dispersed, with a mean density of 1–2 individuals m^{-3} compared with a mean density of 8 individuals m^{-3} during the day (Azzali 1980) and this has also been reported for other areas (Catalan Sea; Iglesias et al. 2003). Mužinić (1964) interpreted this migration as a reaction to light conditions, corroborated by the fact that one of the two main fisheries for anchovy (and sardine) makes use of artificial light to aggregate individuals at the surface during the night.

Adult anchovy in the Adriatic have been found to disperse in smaller schools offshore during the winter, aggregating into progressively larger groups inshore as the spawning season advances (Štirn & Kubik 1974, Kačić 1980) and similar findings are reported for the Black and Azov Seas (Demir 1963). Acoustic surveys carried out in the entire western Adriatic have revealed that anchovy is found in patches of extremely high densities within areas of low densities, irrespective of total abundance (Azzali 1980, Azzali et al. 2002). This makes the species particularly vulnerable to exploitation and susceptible to overexploitation as catchability and the perceived density appear to remain relatively constant (Auckland & Reid 1998, Petitgas et al. 2001). Petitgas et al. (2001), in a study of the schools of several species, including *Engraulis encrasicolus*, found that more fish do not mean more schools and that the aggregation pattern, at intermediate levels of biomass, was independent of stock abundance. This feature was highlighted in the Adriatic Sea by the fact that in 1985, 2 yr before the collapse of the anchovy stock, the biomass was already showing signs of depletion even though catches reached a peak. Nevertheless, the spatial distribution of these high-density patches changes according to biomass levels because during the collapse of the stock in 1987 an overall coastwards shift of these patches was observed but the opposite occurred once the stock started to recover in 1995 (Azzali et al. 2002).

Compared with sardine, anchovy has been found to aggregate in considerably larger schools both horizontally and vertically and the volume of anchovy schools is, on average, four times greater than that of sardine schools (Azzali 1980, Azzali et al. 2002).

In general it has been found that offshore patches are monospecific, whilst inshore ones are mixed (anchovy and sardine) (Mužinić 1978, Azzali et al. 2002). Giannoulaki et al. (2006), in the south Ionian Sea, found that the largest anchovy aggregations (≈20 $miles^2$) were found in open waters. The same authors reported that in winter, similarly to sardine, the degree of land enclosure influenced the spatial structure of anchovy aggregations, which were found to be more heterogeneous in shallow, enclosed waters; the same topographic characteristics did not have any influence in summer on anchovy (Giannoulaki et al. 2006). Iglesias et al. (2003) found that variability of the schools of pelagic species in the Catalan Sea was not influenced by species composition, but by the age and size of individuals, regardless of the species.

Growth and mortality

Anchovy can grow up to a maximum of approximately 20 cm, which corresponds to a lifespan of 6 yr (Padoan 1963, Sinovčić 1978, 2000b, Mužinić 1972). Table 3 summarises the length-weight relationships reported by a number of studies, some on juveniles, some on adults; and Table 4 the von Bertalanffy growth parameters. Sinovčić (2000b) reported the fastest growth in length and weight to occur in the first 3 yr, asymptotic length being attained in the fourth year (3+). Furthermore, growth was faster in males although they reached lower asymptotic lengths (Table 4). Based on the analysis of age-length keys, anchovy growth is negatively influenced by density at sea. Slower growth was reported for 1978 (the year of maximum estimated biomass at sea) compared with 1986 and 1989 when biomass was at its lowest. In 1995 the data suggest that growth rates slowed again during the period of stock recovery and biomass increase (Santojanni et al. 2003). Age was determined through the use of otolith (sagittae) macrostructure analysis. Age determination of sardine and anchovy can be successfully carried out on a yearly basis for adults. Larval growth and age can be determined on a daily basis through the quantification of daily growth increments (Ré 1983, Alemany & Alvarez 1994). Larval growth parameters for Adriatic anchovy are summarised in Table 5. Regner (1985) reported that larval growth occurred in two stages; an early stage of fast growth followed by a stage of slow growth just before complete resorption of the yolk sac. This two-stage process was explained by the fact that, in the later stages, energy is probably diverted from somatic growth to the anatomical changes associated with independent feeding (i.e., mouth formation and eye pigmentation). Larval and post-larval growth are heavily influenced by temperature, food availability, oxygen and salinity, with temperature the principal factor (Regner 1985, Dulčić 1997). McFadzen & Franceschini (1997) reported growth rates of 0.417–0.540 mm day^{-1} in 4- to 8-mm larvae off the Po River estuary, with a decreasing trend from inshore to offshore. They also reported the lengths at the deposition of the first growth ring on otoliths (3.08–4.10 mm) and these lengths also decreased from inshore to offshore. These differences were hypothesised to be related to food availability, which was most abundant inshore (Coombs et al. 1997), supported by the fact that a significantly higher proportion of larvae were in poor condition offshore, 22% being classified as starving against 6% inshore (McFadzen & Franceschini 1997). Dulčić (1997), for the northern Adriatic, reported growth rates of 0.43 mm day^{-1} for 3-mm larvae and of 1.06 mm day^{-1} for 14.3-mm larvae, at approximately 23°C. Growth rates for late larvae/juveniles between 30 and 60 mm in total length were preliminarily calculated for different seasons and the values obtained ranged from 0.55 to 0.72 mm day^{-1}. Young anchovies reach the size of 60 mm in less than 3 months (Arneri et al. 1998).

Larval mortality can be approximated by the exponential equation (Regner 1985)

$$N_t = N_0 e^{-mt}$$

where N_t = number at time t, N_0 = number at time 0, and m = coefficient of instantaneous mortality.

Regner (1985) reported two periods of increased mortality in the larval stages of anchovy and these corresponded to the time between hatching and the closure of the blastodisc and to the time when the switch between yolk sac feeding and independent feeding occurs. Despite this finding, no evidence of the presence of a critical period (Hjort 1914) was found in the wild (Regner 1985). Piccinetti et al. (1982) found mean daily mortality of post-larvae (3–8 mm) to be approximately 35.1% and similar values were obtained by Dulčić (1995; 40.4%) and Coombs et al. (2003; 43.2–44.7%). In particular, Dulčić (1995) found that the instantaneous mortality rates of eggs and yolk sac larvae and of post-larvae (−0.485 and −0.518, respectively) were considerably higher during a summer of intense phytoplankton blooms in the northern Adriatic compared with those reported for post-larvae (−0.432) in the same area in ‘normal’ years by Piccinetti et al. (1982).

Genetic variability

Numerous studies have been carried out throughout the years regarding the subdivision of *Engraulis encrasicolus* into different races, subspecies or even species. It is obvious that technological innovation and the advent of genetic analysis enabled discriminations previously based on morphological/somatic differences to be substantiated or denied. Fage (1911, 1920) divided European anchovy into two different races (or subspecies), distinguishing between Atlantic anchovy (further subdivided into northern and southern) and Mediterranean anchovy (further subdivided into eastern and western). Alexandrov (1927) distinguished three subspecies within the Mediterranean, namely *E. encrasicolus mediterraneus* (western Mediterranean and Adriatic), *E. encrasicolus ponticus* (western

Black Sea) and *E. encrasicolus maeoticus* (eastern Black Sea and Azov Sea), and these were found to be different from an immunological point of view by Altuchov (1974). Majarova & Chugunova (1954) further subdivided *E. encrasicolus ponticus* into *E. encrasicolus ponticus orientalis* (eastern Black Sea) and *E. encrasicolus ponticus occidentalis* (western Black Sea) based on the following somatic differences: number of vertebrae, dorsal fin rays, branchiospines, migration patterns, feeding and spawning habits, and overwintering areas. Pousanov (1936), on the other hand, combined Black Sea and Mediterranean Sea anchovy into one race, separate from the Azov Sea anchovy. Dulzetto (1947) described *E. encrasicolus russoi* as living exclusively in the salty lakes of Ganzirri and Faro (Messina, Italy). Junquera & Perez-Gandaras (1993), based on morphological differences, discriminated Gulf of Lions anchovy from Atlantic anchovy. Levi et al. (1994) analysed the anchovy stock in the Adriatic Sea on the basis of growth rates from otolith readings and found two distinct stocks: one in the northern Adriatic, between Chioggia and Ancona, characterised by slower growth (individuals of the same age in the north were, overall, smaller than those in the south) and a silver colouration and the other in the central and southern Adriatic, from San Benedetto and Vieste, characterised by faster growth and a black/dark coloration. These observations are in line with those reported by fishermen.

All these hypotheses regarding the presence of different races of European anchovy were based essentially on morphological and somatic differences; later studies, on the other hand, focused on genetic differences that have been widely used for species identification and the detection of intraspecific variation among stocks. Compared with other coastal pelagic species around the world, European anchovy shows a remarkable degree of phylogenetic complexity and genetic population subdivision (Bembo et al. 1995, Magoulas et al. 2006). Spanakis et al. (1989) reported significant genetical differences between anchovy populations in the Ionian and Aegean Seas based both on morphometric and allozyme frequency analyses, leading these authors to consider them as two different stocks. Bembo et al. (1995, 1996a), using mtDNA analysis on anchovy from the eastern Mediterranean, found that Aegean Sea and Adriatic Sea samples could be differentiated from all others. Bembo et al. (1996b) investigated the differences between northern and southern Adriatic Sea anchovy by use of morphometric and allozyme frequency analyses and confirmed the presence of two stocks exactly as described by Levi et al. (1994). Pasteur & Berrebi (1985), in the Gulf of Lions, found allozyme frequency differences between anchovy from the open sea and those from brackish waters. Borsa (2002) and Borsa et al. (2004), in an expanded study exending across the entire Mediterranean Sea and using nuclear DNA markers, confirmed the presence of two habitat-specific species regardless of geography that could also be distinguished morphologically: one from brackish waters (renamed *E. albidus*), the other from open waters (*E. encrasicolus*). The same authors speculated on the existence of a third species from the Aegean Sea and Sicily (Borsa 2002). Magoulas et al. (1996, 2006), on the other hand, on the basis of mtDNA analysis of samples from all over the Mediterranean, described European anchovy as consisting of two distinct clades that probably evolved as separate isolated populations and went through secondary mixing following range expansion. The first, Clade A, originating most probably from the Atlantic off western Africa and successively migrating north to Portugal and into the Mediterranean and Black Sea, whereas the second, Clade B, characterised by its long-lasting presence in the Mediterranean, probably originated from the eastern Mediterranean (Adriatic Sea) (Magoulas et al. 2006). Overall, Magoulas et al. (1996, 2006), using the ratios of the previously mentioned clades as a basis, found the following well-defined subdivisions in Mediterranean anchovy: Aegean Sea, Adriatic Sea and the western Mediterranean Sea (including the Gulf of Lions, the Catalan Sea and the Ionia Sea). Given the low rate of the gene flow between the subpopulations, these three subdivisions have implications for management that should take into account the existence of separate stocks exploited by different countries versus the same stock exploited by different countries (i.e., a shared stock), and this is of particular importance in the context of future research and exploitation of these two species within a small area such as the Adriatic Sea. Nevertheless, the third group could not be fully explained by the two species described by Borsa et al. (2004), *E. albidus* probably representing a locally adapted population from Clade B (Magoulas et al. 2006). Tudela et al. (1999) found no significant genetic differences between anchovy from the north-western Mediterranean but reported significant morphological differences, which they attributed to environmental factors. Finally, Ivanova & Dobrovolov (2006), through the use of muscle protein analysis found no evidence to support the presence of two subspecies of *E. encrasicolus*, one Atlantic and one Mediterranean.

Discussion and conclusions

The ecological and economic importance of sardine and anchovy in the Adriatic Sea means that they have been the object of intense research efforts in the past and this research continues. It is evident that ecological studies have predominated on the eastern side of the Adriatic, resulting in a more thorough knowledge of the ecology of sardine compared with that of anchovy, which is strongly associated with the freshwater river run-off characteristic of the western side. There are thus gaps in knowledge of both species and there is great scope for improvement. The Adriatic anchovy and sardine stocks are probably the largest in the Mediterranean. Their dependence on environmental and climatic factors is strong but not completely understood and their fishery is one of the most important small pelagic fisheries in the whole Mediterranean. This review has allowed, among other things, the identification of major gaps in knowledge, which are summarised next.

The most interesting aspect that has emerged from this review is the fact that sardine and anchovy have two very different reproductive strategies. The two species have mirror-like reproductive strategies, with sardine spawning mainly in winter and anchovy during the warmer months. These differences appear to be driven by a series of factors that include the oceanography of the area and especially salinity and temperature. These factors are likely to be of crucial importance in explaining the coexistence of two species that essentially exploit the same food resources by means of a temporal and spatial division of the habitat and the possible separation of ecological niches. In particular, this separation apparently leads to an absence of spatial and temporal overlap of larvae and post-larvae of the two species thereby excluding competition for resources in the most vulnerable stages of their life cycle. The question then arises of whether this separation is due solely to physical properties of the water masses (i.e., salinity), or there are other interacting factors that play a crucial role. To date there have been no studies that have attempted to explain whether there is a real separation of the ecological niches of anchovy and sardine or whether they partially or completely overlap. The unravelling of such questions requires studies of the feeding ecology of the different life stages of both species. But, despite the great importance of the sardine stock in the Adriatic marine ecosystem (Coll et al., 2007), there is an almost complete lack of data on feeding habits of larvae, late larvae (fry), juveniles and adults, both in qualitative terms (diet) and in quantitative terms (daily rations). For anchovy the situation is slightly better but still there is scope for improvement. Does the high plasticity in feeding habits exhibited by sardine (compared with anchovy, sardine in other seas can thrive on phytoplankton alone if necessary) play a role in this? Genetic studies suggest that the ancestral anchovy was estuarine. So, on a geological timescale, does this mean that anchovy occupied the most favourable environment first and sardine ‘arrived’ later and had to adapt to the remaining available habitat?

Similarly, knowledge of the location of sardine nursery areas is fragmentary, as is knowledge of the contribution of these nurseries to the adult stocks. For example, in Italy, the only known extended nursery area is the Gulf of Manfredonia, in the south-western Adriatic. What is its contribution to the northern and central Adriatic stock? This area also supports a thriving fry fishery (the bianchetto fishery): Where do these post-larvae come from? What, if any, is the impact of this fishery on the adult population? Where do post-larvae migrate from here? In addition, very few data are available regarding the extent and dimensions of the eastern Adriatic sardine nursery areas. Anchovy nursery areas, on the other hand, appear to be mainly located along the western side of the Adriatic. However, the transport mechanism, by which eggs laid in the open sea and near the coast end up as late larvae found mostly along the western coast, is not clear, and the same applies to the eastern coast. The location of nursery areas and the transport mechanisms that govern the arrival and departure of post-larvae to and from these areas are of crucial importance in a multinational fisheries management stock. To bridge these gaps, specific echosurveys should be carried out coupled with the genetic analysis of individuals at different life stages in different areas. These *ad hoc* field investigations, if linked to modern modelling tools, should improve this crucial area of knowledge.

Studies regarding the influence of environmental conditions and fluctuations on the sardine and anchovy populations in the Adriatic Sea are sporadic and fragmentary, offering few conclusive insights. For example, the upwelling areas identified by Regner et al. (1987) as crucial locations for sardine spawning have not received due scientific attention in subsequent years. Now, with the available oceanographic numerical modelling tools, it should be possible to resume this kind of investigation following similar studies of other important small pelagic fisheries (e.g., Bay of Biscay, Benguela current off South Africa), paying particular attention to the interaction between the environment and recruitment success. The same applies to anchovy with respect to the river Po plume in late spring and summer. Information is also missing on the impact on the reproductive potential of the stock of purse seiners, which specifically target large and old spawners, known to produce larger numbers of better, bigger eggs.

These points also raise an important question related to the health and protection of the populations of pelagic fishes in the Adriatic. For the sake of this discussion, the following is a summary of the collapse and recovery of the Adriatic anchovy stock. The anchovy stock collapsed in 1987 and its recovery is only recent. The collapse was hypothesised to be due to two consecutive years of low recruitment (1986 and 1987). Anchovy stock abundance may have been affected by the fishery but, nevertheless, this cannot have been the main reason for the collapse because the decrease in biomass started well before fluctuations in fishing effort and fishing mortality were of any relevance (Santojanni et al. 2003, 2006b). The presence of low levels of spawning individuals does not necessarily imply low recruitment levels in the subsequent year and suggests that the low levels of reproducers in the years prior to the collapse may not be enough to explain the crash in anchovy abundance. Overfishing (or, more precisely, recruitment overfishing) thus may not have been the primary cause of the anchovy decline (Cingolani et al. 1998, Santojanni et al. 2003, 2006b). The absence of a clear relationship between spawning biomass and recruits implies that environmental factors may have played a predominant role in determining recruitment levels (Santojanni et al. 2003). The influence of the environment on anchovy and other species' recruitment has been summarised previously and documented for areas other than the Adriatic (Palomera 1992, Borja et al. 1998, Cole & McGlade 1998, Myers 1998, Daskalov 1999, Mullon et al. 2003, Basilone et al. 2004, 2006). Many hypotheses have been put forward and it is likely that the truth is to be sought in a combination of all of them. Azzali et al. (2002) observed a decrease in sea-surface temperature (SST) of 1–1.5°C between 1984 and 1991 and suggest it was one of the causes of the collapse. Regner (1996) suggested that the biomass of anchovy may have been negatively affected by the presence of abundant phytoplankton blooms between 1986 and 1989. Dulčić (1995), on the other hand, highlighted the presence of increasing quantities of mucilaginous aggregates and marine snow covering increasingly extended areas over the period 1986–1989. This effect was especially noticeable in the main anchovy spawning areas and during the spawning period, with the overall result of reducing the surface area capable of supporting an ideal spawning environment (Dulčić 1995). These blooms and marine snow also increased egg, larval and post-larval mortality rates through entrapment (Dulčić 1995, Regner 1996, Specchi et al. 1998). In addition, it has been suggested that the increased predation of larval stages caused by the high abundance of the predatory jellyfish *Pelagia noctiluca* played an important role in the collapse (Regner 1996, Specchi et al. 1998). On the other hand, a study by Klansjscek & Legović (2007) modelled the anchovy collapse under different scenarios in an attempt to understand whether the stock had been overfished or not. Their results pointed to heavy overfishing in 1985 as the main reason for the collapse, which was merely accelerated by the low recruitment levels reported for 1986 and 1987 (Klansjscek & Legović 2007).

Recently, contemporarily with the recovery of anchovy, sardine has been showing signs of depletion.

The question is, what are the causes? As mentioned for anchovy, the most likely causes of the marked decreases in numbers of these species are the interaction between adverse environmental conditions and the fishery. In this respect, should the aim be that of protecting juveniles and young fish or the older spawners?

Finally, data on growth rates and mortalities at various life stages are very scarce for both species, especially information on predation. This precludes the use of up-to-date population models when assessing the stocks for management purposes.

The authors hope that this review will serve not only as a summary of the scientific information available to date on Adriatic sardine and anchovy but also as a starting point for future, structured, multinational and multidisciplinary research aimed at broadening the scientific knowledge of two species that are extremely important to the Adriatic and Mediterranean economy and, as a result of this, are in danger of being severely depleted. In this context, the Adriatic Sea, as a semi-enclosed basin of small dimensions, could be a valuable tool that can be used to understand the evolution of ecological differences between these two species and that acts essentially as a microcosm, the processes of which may then be applied to larger ecosystems.

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A REVIEW OF UNDERWATER STEREO-IMAGE MEASUREMENT FOR MARINE BIOLOGY AND ECOLOGY APPLICATIONS

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Abstract Over the last 40 years, underwater stereo-image measurement systems have employed stereo-cameras and paired single cameras in a variety of configurations. Both still and movie cameras have been used, based on film, video tube and digital sensors. Whilst measurement configurations of all varieties have been used, the transect has been, and still is, the predominant sampling technique. These basic approaches to photogrammetric geometry and sampling techniques are still in use today; however, the image quality has advanced considerably and the use of fully digital video systems and digital still cameras is now commonplace. The wider use of precalibrated, self-contained stereo-image systems, plus the substantial improvements in image resolution and image fidelity, is enabling new possibilities for accurate and reliable measurement of 3-dimensional lengths, surfaces and volumes. These advances are leading to significant improvements in the effectiveness of the management of marine ecosystems for conservation and the estimation of biomass for aquaculture. This work reviews the status of underwater stereo-image measurement and illustrates applications of stereo-image measurement in marine biology and ecology.

Introduction

Stereo-image techniques have been used for underwater measurement since the 1960s. Initially with still and movie film cameras, and later using television camera systems, the primary underwater applications were repairs on marine equipment, abundance or habitat surveys of the seabed, and archaeological site and shipwreck surveys. Pairs of film cameras were typically used in conjunction with a portable reference frame to provide scale and orientation. Synchronised stereo-cameras were first used in the 1980s and provided the significant advantage of dispensing with the reference frame, instead relying on precalibration and stable camera geometry. This new versatility enabled the length measurement of mobile species such as epibenthic crustaceans and pelagic fish, and for the first time the biomass and population distributions of species could be confidently estimated. The 1990s saw the introduction of portable camcorders to the underwater environment and the first use of digital video (DV) image sequences, extending further the versatility of imaging systems and the efficiency of data acquisition.

A broad diversity of platforms has accompanied the development of underwater stereo-image techniques. In shallow water, systems operated by scuba-divers have been and are still predominant in all but habitat-mapping applications, which have generally adopted towed bodies or sleds to efficiently capture imagery over large areas. In deeper water, remotely operated vehicles (ROVs), drop cameras and manned submersibles are needed to extend the depth range beyond the reach of scuba. In deep water the most common techniques are the use of towed bodies and submersibles. The 1990s saw a surge in applications of single-camera video systems on towed bodies. Low-accuracy quantitative measurements became feasible from single cameras through the use of parallel laser beams to determine the approximate scale of the imagery. More recently, stereo-camera configurations have been adopted for deep-water towed bodies to enhance the accuracy and reliability of the measurements. Despite the advances in technology and equipment, for all of these techniques the sampling schemes continue to be largely based on the transect to capture swathes of imagery across the habitat or area of interest.

Trends in equipment

The first underwater photographs taken from within primitive camera housings date to the 1850s, using glass plates as a medium. Various experiments with camera housings and photography from submersibles followed during the next decades. It was not until the invention of O-ring seals and effective watertight housings in 1930s that still and movie film cameras were used extensively underwater. Based on the first use of a regulator in the early 1940s, Jacques-Yves Cousteau's Aqua Lung was marketed commercially in France in 1946. As underwater housings became more readily available, a surge in activity of divers and cameras followed in the mid- and late 1940s. In 1949 the German company Franke and Heidecke developed the famous Rolleimarin underwater housing for a double-lens reflex Rollei 6-cm format camera, which was later generally displaced by 70-mm single-lens reflex (SLR)-type cameras. In the 1950s the use of scuba became more widespread, several underwater feature movies were released and the first documented uses of underwater television cameras to record the marine environment were published (Barnes 1952).

A major milestone in 1957 was the invention of the first waterproof 35-mm camera that could be used both above and under water, later developed into the Nikonos series of cameras with interchangeable, watertight lenses. Stereo-pairs of Nikonos cameras were used to conduct the first metric seabed mapping applications (Hale & Cook 1962, Pollio 1971) and surveys of shipwrecks using either fixed-base (Hohle 1971) or towed-body systems (Pollio 1972). At the same time in the early 1960s, acrylic glass (also known as perspex or plexiglass) housings were used for the first time to allow a wider range of cameras to be used underwater. Simultaneously, universal wide-angle correcting lenses for fields of view up to 105° (Ivanoff & Cherney 1960) were introduced to compensate for refraction at the glass-water interface, reducing the need for camera calibration.

By the end of the 1960s the optical properties of housings were well documented (McNeil 1969), and there were a significant number of different underwater camera systems available. Many systems used dome or correcting ports to minimise refraction, both 35- and 70-mm format cameras were in use and the housings were either aluminium or stainless steel (Seifert 1972). Single and stereo-pairs of the larger format 70-mm cameras were used widely in the 1970s, primarily in structural monitoring of submarine structures, most notably to support oil and gas exploration in the North Sea (Leatherdale & Turner 1983, Baldwin 1984), but also for archaeological mapping of shipwrecks from submersibles (Bass & Rosencrantz 1977), periodic monitoring of marine communities (Torlegard & Lundalv 1974) and mapping of seabed topography (Pollio 1971, Moore 1976).

From the early 1980s, many marine scientists and biologists began experimenting with film photography and video imagery as a non-destructive tool for sampling organisms and mapping habitats. For example, stereo-photography was used to measure the growth of coral (Done 1981) and to estimate the size of free-swimming sharks (Klimley & Brown 1983). The release of the first portable camcorder by Sony in 1983 provided a more convenient and effective medium for underwater imaging. As a consequence, stereo-video cameras were quickly adopted for a wide range of applications in the marine environment using divers (Boland & Lewbell 1986, Hamner et al. 1987) or ROVs (Vrana & Schwartz 1989), and virtually unchanged systems continue to be used for similar tasks (Cappo et al. 2004, Watson et al. 2005). In recent times there have been rapid technological improvements in video cameras, in particular DV tape, progressive scan sensors and significant reductions in size. These advances have improved the utility, reliability and accuracy of stereo-image systems (Harvey & Shortis 1996, Li et al. 1996, Shortis & Harvey 1998, Harvey et al. 2001a, Chong & Stratford 2002, Abdo et al. 2006, Merritt et al. 2006), adding to the other, often-stated advantages of non-contact measurement, such as predictable precision, digital image enhancement and archival storage.

The most recent innovation has been the advent of the fully digital system in the form of either digital still cameras or direct-to-disk recording. The most obvious advantage of these systems is that there is no additional requirement to digitise, via a frame grabber or digital capture card, the images or video sequences to enable image analysis and automated processing. A collateral benefit is that the fully digital pathway virtually eliminates noise, interference and the unreliability of systems that have an analogue recording or signal transmission component (Shortis et al. 1993). Since the late 1990s digital still cameras have been in use for underwater marine science applications such as seafloor mapping from a towed body (Edwards et al. 2003) and are being applied to more demanding measurement tasks due to the high resolution of the images (Abdo et al. 2006). In the last few years, direct-to-disk recording of video sequences has been adopted to bypass the limitations of traditional broadcast systems. Resolution is limited only by the charge-coupled device (CCD) or complementary metal oxide semiconductor (CMOS) sensor rather than the phased alternate line (PAL) or National Television System Committee (NTSC) broadcast specification. Progressive scan images can be captured, eliminating the motion blur associated with interlaced images, and real-time image compression can be included to reduce the storage requirements. Until recently direct-to-disk recording has been limited to less than 10 frames per second (fps) and relatively short cable lengths of tens of metres. However, 30-fps systems with transmission distances of kilometres are now readily available based on high-speed interfaces such as gigabit Ethernet. A direct-to-disk system has been developed for aquaculture applications (Harvey et al. 2004a) and is under development for a deep-water towed-body system (Shortis et al. 2008).

Stereo-cameras must be synchronised to ensure that there are no systematic errors from motion displacement. The accuracy of the synchronisation becomes increasingly important in applications involving fast movement, such as length measurement of rapidly moving fish. Still cameras can be fired synchronously using a single mechanical or electrical trigger. Movie cameras and camcorders typically use an external event to match the frames from the different cameras. Current systems often use a system of flashing LEDs to both set and monitor the synchronisation to the nearest frame. An example of this is illustrated in a subsequent section (see Figure 4). Direct-to-disk systems are synchronised using a hardware trigger generated by the frame grabbers so that the cameras capture images simultaneously. A further advantage of direct-to-disk systems is that the synchronisation is limited only by the electronics and can be accurate to within microseconds.

Purpose-built underwater image-capture systems

Purpose-built underwater image-capture systems have been available since the introduction of the Rolleimarin housings and Nikonos cameras in the 1950s and 1960s. The technology has developed over the years, marked by spurts of activity such as the 35- and 70-mm stereo systems developed for the offshore oil and gas exploration industry in the 1970s and 1980s. By the early 1990s the technology had moved on to camcorders and video cameras within acrylic housings, providing a cost-effective solution for scientific purposes. The technique was widely utilised and was a significant factor in the substantial increase in research activity during this period. Trends in research activity are discussed further in a subsequent section (see Figure 14 and the section on 'Marine biology and ecology applications').

Commercial and research underwater camera systems that are available at the time of writing represent a wide variety of approaches and intended applications. The technology continues to change rapidly, driven by constant innovations in CCD and CMOS sensors, image-recording systems and embedded software. Nevertheless, a snapshot of these systems conveys a sense of the state of the art.

Single cameras and housings

Single-camera systems are prolific through the combination of camcorders or digital still cameras and purpose-built underwater housings. Many of the large commercial camera suppliers offer waterproof housings for their products, usually manufactured from polycarbonate or acrylic. For example, Canon provides underwater housings for more than 40 digital still cameras (Canon 2008) and Sony offers a waterproof housing that is compatible with more than 20 camcorder models (Sony 2008). These housings are often rated to relatively shallow depths of 5–10 m and are clearly aimed at the amateur diver and tourist markets (Sea&Sea 2008). In contrast, professional-quality polycarbonate and aluminium housings rated to depths of 50 to 100m are available from independent manufacturers (Ikelite 2008, Sealux 2008) and there are companies that offer made-to-order polycarbonate underwater housings for virtually any camera (Wills 2008). Accessories such as lighting kits, optical viewfinders, digital viewfinders, external handles and navigation aids are common. Figure 1 presents a selection of different underwater housings for single cameras.

Waterproof cameras, as opposed to conventional cameras encased in waterproof housings, are also available as a niche product. Whilst 35-mm film cameras are still available, this format is limited to the discontinued line of Nikinos cameras and 'single-use' cameras provided for tourists. Universally based on digital sensors, state-of-the-art waterproof cameras have been developed for the amateur diver and tourist markets. Like low-cost underwater housings, waterproof cameras are typically rated at relatively shallow depths of less than 10 m, and often less than 5m. Table 1 shows a sample of waterproof digital still cameras and digital camcorders. Whilst the primary functionality of the cameras is indicated in the table, it is generally the case that digital still cameras can record in movie mode with the resolution limited to 640 by 480 pixels, whilst digital camcorders can record still images limited only by the resolution of the image sensor.

Cameras and housings rated to depths greater than 100 m are a highly specialised component that are made to order or manufactured in-house by large research organisations. One class of video cameras designed for underwater inspection is typically recommended for use in depths of up to 300 m and uses anodised aluminium camera housings with glass or acrylic ports and optical fibre transmission of the video signal (OceanScan 2008). This type of camera housing is capable

Table 1 A selection of waterproof digital still cameras and camcorders available in 2008

Manufacturer	Model	Format	Sensor type	Lens	Maximum depth	Viewfinder type
Panasonic	SDR-SW20	Compact camcorder	0.7-mp CCD	×10 zoom	5 feet	2.7" LCD
Pentax	W60	Compact digital still	10-mp CCD	×5 zoom	13 feet	2.5" LCD
Olympus	1030SW	Compact digital still	10.1-mp CCD	×3.6 zoom	10m	2.7" LCD
Sanyo	Xacti E1	Compact camcorder	6-mp CCD	×5 zoom	10m	2.5" LCD
Vivitar	6200W	Compact digital still	6-mp CCD	×4 zoom	10m	2" LCD

mp = the sensor resolution in millions of pixels; CCD = charge-coupled device.

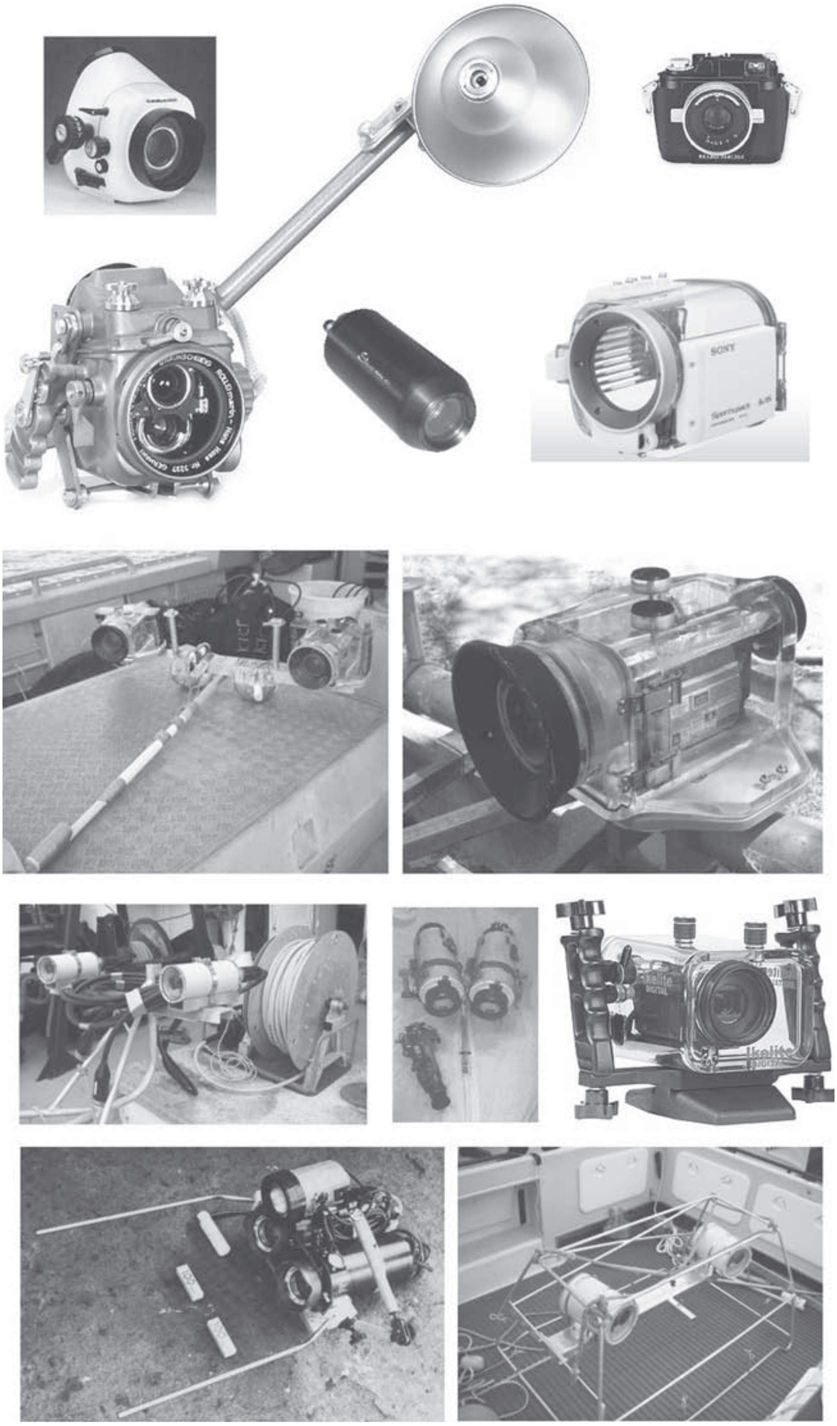


Figure 1 A selection of underwater housings for single cameras and stereo cameras. (Leatherdale & Turner 1983, Shortis et al. 2000, Harvey et al. 2004b, Ikelite, 2008, OceanScan 2008, SeaGIS 2008, Sony 2008, Wills 2008.)

of reaching much greater depths. For example, Shortis et al. (2008) described a deep-water towed-body system capable of deployments to over 1000 m deep. The towed body is equipped with stereo-video cameras, a digital still camera and a laser array projector, all contained within individual aluminium housings with acrylic ports. ROVs and submersibles for exploration or benthic research to depths reaching 5000 m also use similar systems (Davis & Pilskaln 1993, Shepherd & Juniper 1997) with single cameras on pan-tilt devices or stereo configurations of paired single cameras on a fixed base.

Stereo-image systems

All of these different types of single cameras and housings can be combined into pairs to enable 3-dimensional quantitative measurements based on the calibration techniques described in the next section. Remote systems most often opt for configurable single cameras to accommodate changes to instrumentation on general-purpose platforms. For many other applications there are purpose-built stereo-image systems available, designed specifically to be robust and reliable to capture accurate measurements. The common feature of the stereo-camera systems is that the housings are rigidly mounted on a base bar or within a single enclosure to ensure the consistency of the precalibration of the system.

The stereo-camera system most widely used in shallow water for marine ecology and aquaculture is known as the Video Image Capturing and Sizing System (VICASS) Biomass Estimator (AKVAGroup 2008). VICASS is based on precalibrated, broadcast-quality cameras and presents the operator with a user interface that is oriented around the video measurement to produce biomass estimates with accuracies in the range of 2–5% (Petrell et al. 1997, Shieh & Petrell 1998). The estimates are based on species-specific regression analysis of length versus weight (Pienaar & Thomson 1969, Kohler et al. 1995). The biomass estimation is limited to species for which the regression is already known or can be established through validation (Beddow & Ross 1996).

An alternative to self-contained systems such as VICASS are stereo-camera housings that allow the mounting of a variety of video cameras and camcorders (SeaGIS 2008). This type of stereo system is based on a rigid aluminium base bar connecting housings constructed from PVC (polyvinyl chloride) pressure pipe and acrylic ports. The systems can be used in depths of up to 150 m and can be diver operated (Harvey et al. 2005) or used in deeper water as drop cameras (Cappo et al. 2007).

The extensive range of applications within oceanography and marine science does not encourage a consistency in the design and deployment of stereo-image capture systems. Accordingly, the variety of solutions to capturing stereo-images is equally extensive. The few manufacturers of purpose-built systems are not viable on these applications alone and must diversify into other areas, such as marine inspection and security. These factors in combination inevitably lead to ‘one-off’ solutions developed by universities, research institutions, fishery managers and the aquaculture industry. Some recent examples of specific solutions are given in the work of Chong & Stratford (2002), Stokesbury et al. (2004), Abdo et al. (2006), Costa et al. (2006), Merritt et al. (2006) and various articles in Somerton & Gledhill (2005). Figure 1 presents a selection of different underwater housings for stereo-camera systems.

Calibration strategies

Calibration of underwater systems is necessary to achieve accurate and reliable measurements. There are a number of approaches that may be used to obtain system calibration, either as a series of components or as a whole, and may include the refractive effects of the air-glass-water interfaces either explicitly or implicitly. In all cases of calibration, both the interior and exterior orientation of the camera or cameras must be determined. *Interior orientation* is a pseudonym for camera calibration and determines the internal geometric characteristics of the cameras. *Exterior orientation* refers to the position and rotation angles of the cameras relative to each other, also known as *relative orientation*, or with respect to a reference frame or similar fixture.

Correction

Early attempts at system calibrations often relied on fixed-focus correction lenses to produce a near-perfect central perspective (Moore 1976). The use of a correction lens minimised the requirement for camera calibration, other than an estimate of the focal length. Many underwater camera systems have adopted dome, rather than plane, camera ports (McNeil 1969) to eliminate the refraction caused by the interfaces between water, glass and air. If the entrance pupil of the camera lens coincides with the centre of curvature of the dome then there is no deflection of light paths caused by refraction effects. The dome port has the further advantage that there is no degradation of image quality near the edges of the port, as can be the case with plane camera ports due to acute angles of incidence and greater apparent thickness of glass, polycarbonate or acrylic.

The correction lens approach is limited by the quality of the lens manufacture, the alignment of the components and the consistency of the refractive index of the water medium. Similarly, the dome port approach is limited by the quality of the manufacture and alignment of the components. Inevitably this leads to operational constraints and potential systematic errors that degrade the measurement accuracy of the system. Furthermore, dome ports and correction lenses do not completely eliminate the need for camera calibration, as dome ports have no impact on lens distortions of the camera itself and neither solution responds to changes in prevailing conditions. Nevertheless, dome ports and correction lenses have been successfully used to eliminate the majority of the effects of refraction and lens distortions. In applications for which high accuracy is not the primary concern, such as archaeological or habitat mapping, dome ports and correction lenses provide an optimal solution that avoids the requirement for camera calibration.

Modelling

A more flexible and accurate approach is to determine the calibration of the camera or cameras in the prevailing conditions. The derived interior orientation of the camera is based on a set of primary physical parameters describing the principal distance, principal point location, radial and decentring lens distortions, plus secondary parameters such as affinity and orthogonality terms to model deformations of the image or sensor space geometry. The primary physical parameters of the calibration define the location of the lens perspective centre with respect to the image sensor and the lens distortions that represent the departures from a perfect central projection (see Figure 2). Lens distortion characteristics have been well established through extensive testing and validation over several decades (Brown 1966, Ziemann & El-Hakim 1983). Radial lens distortion is rotationally symmetric around the optical axis of the lens and is a consequence of the lens design, which in off-the-shelf cameras always favours image quality over image geometry. Decentring distortion, sometimes known as tangential distortion, is caused by imperfections in the coaxial centring of the lens elements. Radial lens distortion is described by a simple odd-ordered polynomial (Ziemann & El-Hakim 1983) whilst decentring distortion has a more complex mathematical description (Brown 1966). At very close range the formulation applicable to lens distortions becomes more complex, requiring a correction dependent on the location within the depth of field (Fraser & Shortis 1992) if the maximum possible accuracy is required.

Modern CCD and CMOS sensors are not subject to image deformations because of the geometric regularity and stability of the sensor combined with digital transmission of the pixel data (Shortis & Beyer 1996). The secondary parameters describing image deformations (see Figure 3) are associated with photographic film deformation (Robson 1991) or compensation for the effects of the analogue transmission or recording of video images (Shortis et al. 1993). However, Fraser

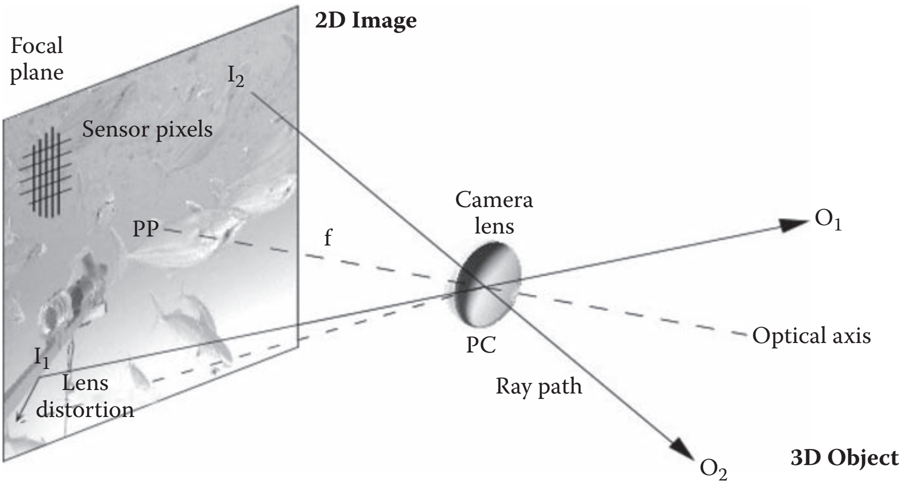


Figure 2 Geometry of interior orientation, also known simply as camera calibration. PP = principal point; f = focal length or principal distance; PC = perspective centre; I = image point locations; O = object point locations.

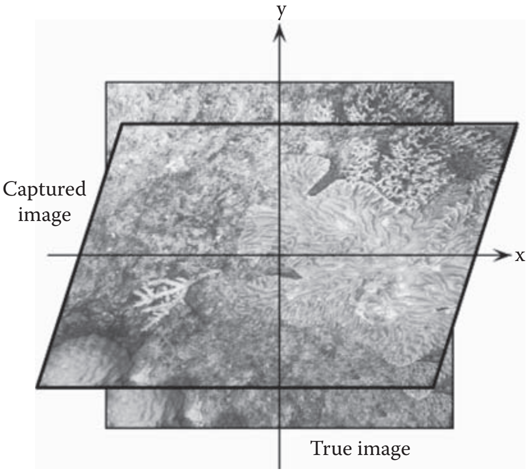
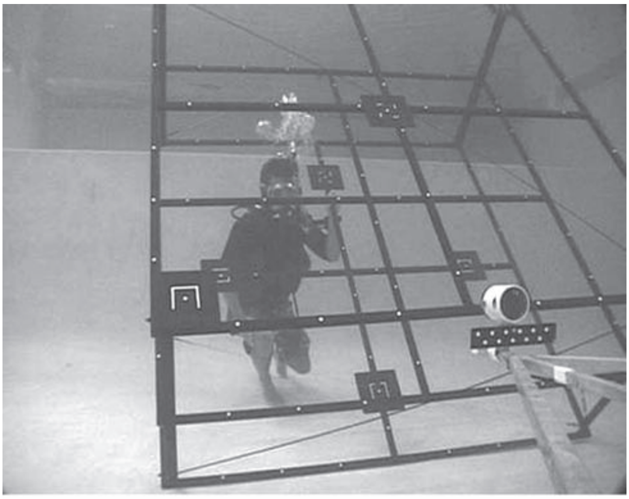


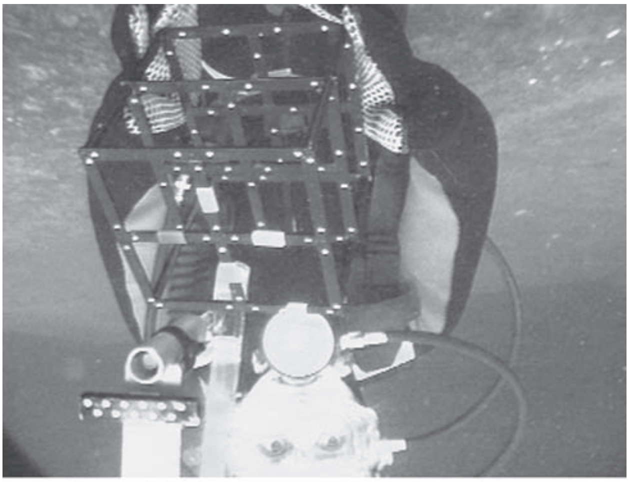
Figure 3 Effects of affinity and orthogonality on image space geometry.

et al. (1995) found that the affinity term in the camera calibration parameter set was strongly correlated with lenses rather than sensors in a calibration test that compared three lenses interchanged between two digital cameras. This suggests that the affine change in scale is associated with an optical effect rather than an image deformation. Whilst this effect may improve the accuracy of the calibration model, affinity and orthogonality terms, as well as the higher-order terms of radial distortion, should always be tested for statistical significance. Insignificant parameters should be excluded from the calibration model to avoid overparameterisation and potentially destabilising effects of parameter correlations (Kenefick et al. 1972).

For stereo- or multicamera systems, the relative orientation of the cameras with respect to each other, or an external reference, must be determined (see Figure 4) to complete the calibration of the system. Initial attempts at system calibrations often relied on a portable control frame that



(A)



(B)

Figure 4 Calibration fixtures (courtesy E.S. Harvey). Note the 180° roll of the lower image (B). Also visible in the foreground of both images are the canisters containing flashing light-emitting diodes (LEDs) to synchronise the left and right cameras and small target plates to check the calibration during deployments. Coded targets are visible at the corners of the large calibration fixture in (A).

positioned the cameras relative to the object to be measured (Newton 1989). The control frame would typically incorporate known locations and scale bars so that the exterior or relative orientations of the stereo-cameras could be predetermined. An even more straightforward solution for a single camera is to use a projective transformation in the plane of the base of the control frame or as defined by structured lighting or laser dots (Davis & Pilskaln 1993), under the assumption that all objects measured are sufficiently close to the plane so that out-of-plane height displacements are insignificant. The technique can also be applied to stereo-cameras by using independent transformations for each camera and then intersections to determine 3-dimensional locations within the measurement volume (Adams 1982). However the weakness of these approaches is that the resultant calibration is specific to a particular geometry and does not generalise to other circumstances. For

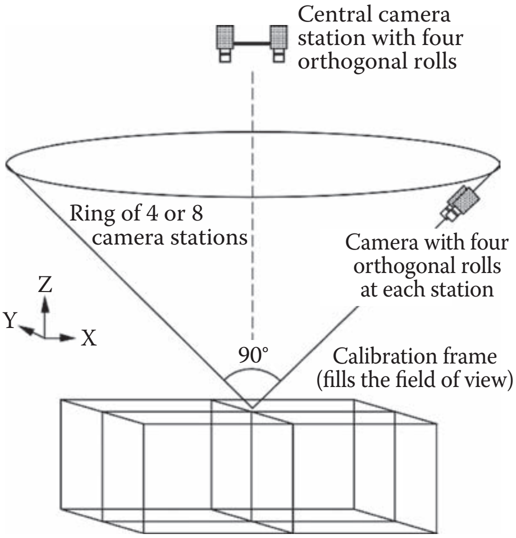


Figure 5 Ideal case of geometry of a self-calibration network.

example, the cameras cannot be used without the control frame and the projective transformation solution will be subject to systematic errors for objects measured outside of the plane used as the datum. Perhaps the most severe limitation is that the imaging system cannot be used independently of artefacts in the field of view, restricting the utility and effectiveness of the system. Nevertheless, these approaches have been used very successfully (Hohle 1971), given the constraints identified.

To achieve the optimum utility and accuracy for underwater camera systems, a rigorous analytical approach is required. Cameras are generally pre- or post-calibrated using a suitable test range (Baldwin 1984) or self-calibration is used in conjunction with a suitable target array (Fryer & Fraser 1986). The standard requirements of a multistation calibration network are required (Granshaw 1980), such as multiple convergent photographs, camera roll at each station and a 3-dimensional target array (see Figure 5). The 3-dimensional target array, usually in the form of a light, easily manoeuvrable calibration fixture, has the size determined by the field of view of the cameras and the likely working distance for the measurements (see Figure 4). Coded targets (see Figure 4) on the fixture can be automatically recognised using image analysis (Shortis et al. 1993), substantially improving the efficiency of the measurement and computation processing. For diver-controlled stereo-video systems and large towed-body systems that are not readily manipulated in the water, it is more effective to tilt and rotate the calibration fixture in the field of view of the cameras (see Figure 6), rather than moving the camera rig, to replicate the convergent multistation network (Harvey & Shortis 1996, Shortis & Harvey 1998). The first rotation set is made with the camera base in the 'normal' horizontal position, and the following rotation sets with the camera base vertical and in other orientations to complete a 0°, 90°, 180° and 270° roll set. An example of a full set of calibration images is shown in Figure 7.

Unlike the test range approach, accurate information for the positions of the targets on the calibration fixture is not required as coordinates of the targets are derived as part of the self-calibration procedure. Hence, it is immaterial if the frame distorts or is disassembled between calibrations, although the frame must retain its structural integrity during a calibration sequence. Scale within the 3-dimensional measurement space is determined by a combined adjustment of the photogrammetric network and distances measured between preidentified targets (El-Hakim & Faig 1981). The known distances between the targets must be accurate and reliable and accordingly are determined between targets on the rigid arms of the frame.

Figure 6 Underwater photography of a calibration fixture. (Courtesy D.A. Abdo.)

The camera calibration model does not need to contain explicit terms for the refractive effects of the glass camera ports and the refractive interfaces as analysis of the effects of the refractive surfaces in the optical path in an ideal camera housing shows that images are displaced radially from the principal point (Li et al. 1996). Whilst the assumptions that the optical components of the housing are symmetrical around the optical axis of the camera and refractive surfaces are in general perpendicular to the optical axis are unlikely to be perfectly fulfilled in practice, it is clear that the primary component of the refractive effect is radial. As a consequence, the approach that has been widely adopted has been to allow the refractive effects of the optical components and refractive interfaces to be absorbed by the conventional, physical camera calibration parameters (Harvey & Shortis 1996, Shortis & Harvey 1998). The principal component is implicitly taken up by the standard, odd-ordered polynomial model for radial distortion, whilst any residual effects from asymmetric components of the housing are partly or wholly absorbed into other parameters of the camera calibration, such as decentring lens distortion or the affinity term. Figure 8 shows the changes in the lens distortion profiles in air and in water for a video camcorder.

Implicit inclusion of the refraction effects requires no assumptions to be made concerning the refractive indices of the air, glass or water media, and modelling of the optical components of the underwater housing is unnecessary. This approach has been used successfully by previous systems (Turner 1993, Schewe et al. 1996), whereas a rigorous approach to optical ray tracing requires assumed values for the refractive indices of the media and either a two-phase calibration approach or knowledge of the shape and position of the refractive surfaces (Kotowski 1988, Li et al. 1997). The refractive index of water is known to change by up to 2% with wavelength, depth, temperature and salinity (McNeil 1969) and the shape of the camera housings and port may change with depth due to changing pressure levels. Hence a procedure that incorporates implicit calibration of the complete system under prevailing conditions and at a particular working range is more accurate and reliable.

Once the interior orientation is known, single-camera systems can be used to acquire measurements when used in conjunction with reference frames or structured lighting systems. For stereo-

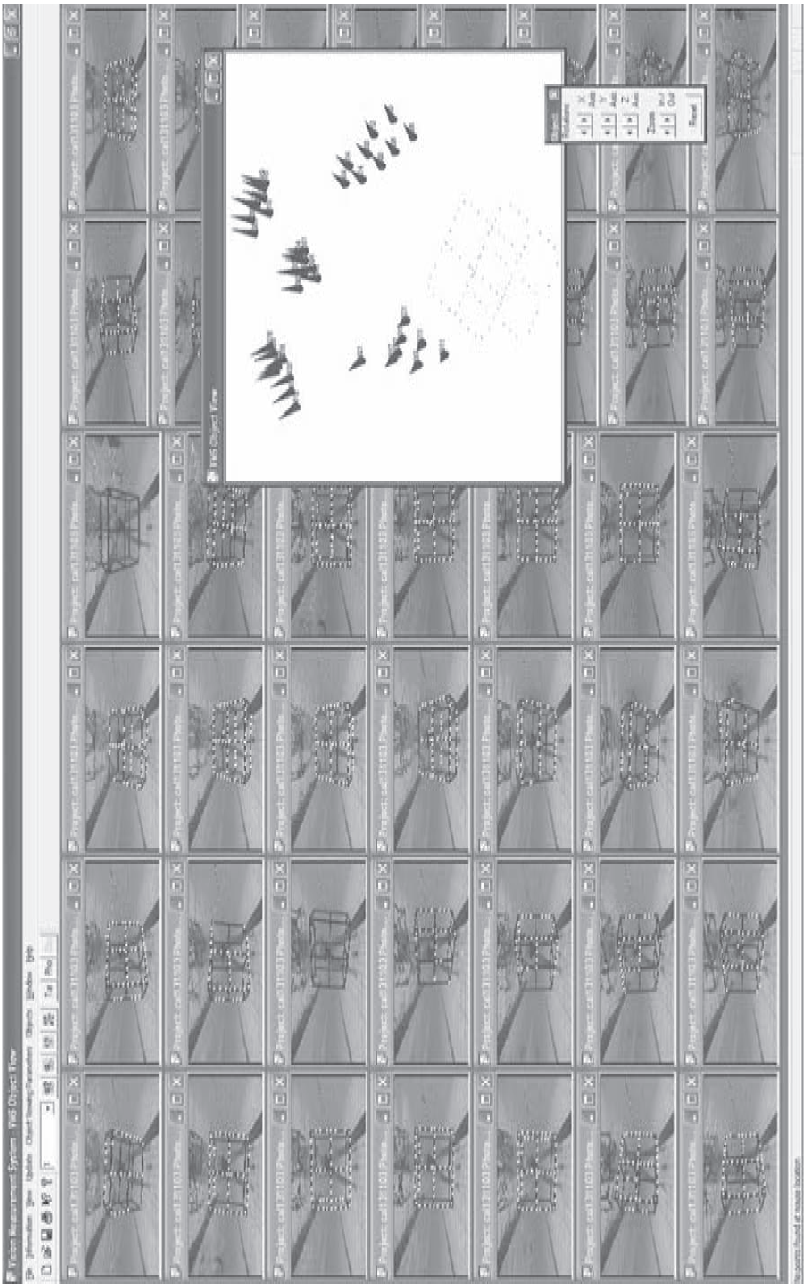


Figure 7 Full set of calibration images from an underwater stereo-image system.

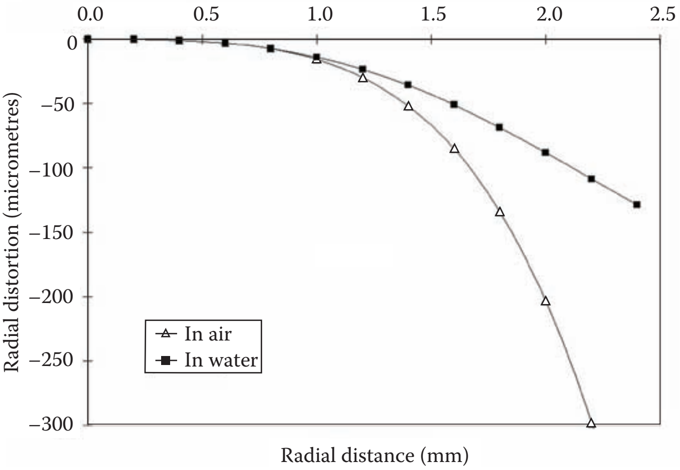


Figure 8 Radial lens distortion profiles from calibrations of a Sony TRV900 video camcorder in air and in water with an acrylic plane port.

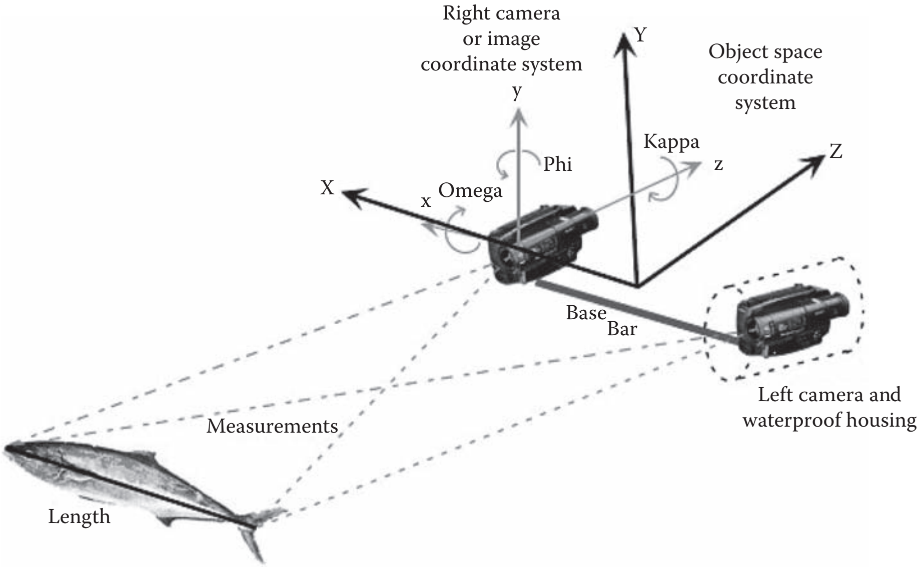


Figure 9 Schematic view of a stereo-image system coordinate system and measurement of a length from 3-dimensional coordinates.

camera systems the relative orientation is required as well as the camera calibration. The data for the pairs of synchronised exposures are initially in the frame of reference of the calibration fixture. To determine a precise relative orientation, each pair is transformed into a local frame of reference for the baseline between the cameras. The local frame of reference is adopted as the centre of the baseline between the camera perspective centres, with the axes aligned with the baseline direction and the mean optical axis pointing direction (see Figure 9). The final parameters for the relative orientation are computed as the average of the values for all pairs in the self-calibration network. Whilst this approach to the computation of the relative orientation is a post-process after the network solution (Harvey & Shortis 1996), an alternative approach is the incorporation of a stereo-pair constraint solution such as that developed by King (1995).

Accuracy and validation

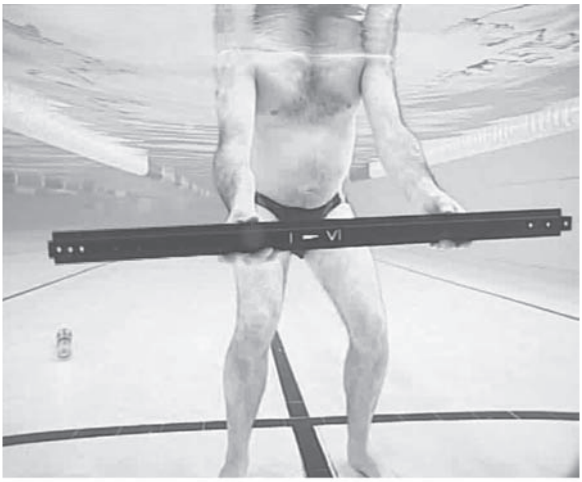
The accuracy and reliability of the calibration of stereo-image systems is dependent on a number of factors. The camera housings must be rigidly connected to a base bar to ensure that the relative orientation is not disturbed. The cameras must be mounted rigidly in the housings to ensure that the total optical path from the water medium to the image sensor is consistent for all measurements, based on a specific calibration. Extensive testing and validation has shown that the calibration is reliable both within and across deployments, based on design considerations such as mounting the cameras in the housings on a rigid connection to the camera port (Shortis et al. 2000). Unlike correction lenses and dome ports, a specific position and alignment are not necessary but the geometric relationship between the camera and the port must be consistent. The direct link between the camera lens and the camera port is especially important for portable camcorders, which have to be regularly removed from the housing to retrieve videotapes and replenish batteries.

Initial validation of stereo-image measurement systems is conducted by introducing a known length, which is measured manually at a variety of distances and orientations within the field of view and expected working range of the system (see Figure 10). In controlled conditions, the root mean square (RMS) error of these validation measurements is typically less than 1 mm over a length of 1 m, equivalent to a length accuracy of 0.1%. This is a best-case scenario in excellent water clarity and using high contrast-targets. Experience with shallow-water measurement of fish silhouettes in more realistic conditions, together with validated measurements of live fish in the field, indicate that length measurements have an operational accuracy of 0.2% to 0.7% (Harvey et al. 2002a, 2003, 2004b). Validations of biomass estimates of southern bluefin tuna and sponges have shown that volume or biomass can be estimated with an accuracy on the order of a few per cent under operational conditions in the field. The southern bluefin tuna validation was based on a comparison between morphometric measurements, such as body length and span, by calliper and stereo-video system, of a sample of 40 fish (Harvey et al. 2003) to produce an accuracy estimate of better than 1% for the total biomass. The volume measurement of sponges was based on evaluation of triangulation meshes on the surface of simulated and live specimens, resulting in errors on the order of a few per cent, and no worse than 10%, for individual sponges (Abdo et al. 2006). Greater variability is to be expected for the sponge measurements because of the uncertainty associated with the unseen substratum surface.

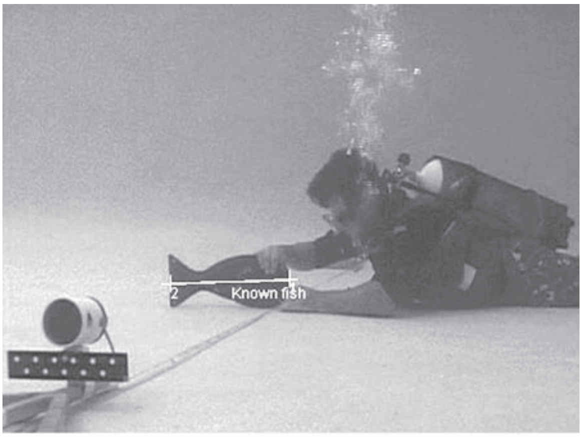
Quantitative measurement

Manual identification of interest points by operators viewing images or video sequences remains the most common form of quantitative measurement. As noted, the use of length-weight or length-age regressions (Pienaar & Thomson 1969, Kohler et al. 1995) is based on operator measurements of body lengths or spans (Harvey et al. 2003). An example of this type of operator measurement, based on mouse clicks in the stereo-images, is shown in Figure 11. Similarly, habitat-mapping applications generally use manual 'scoring' of the video sequences. An operator trained in species recognition will identify flora or fauna of interest by viewing the images or video sequences. In many cases randomisation techniques are adopted, typically through the use of random selection of frames in a video sequence or random dot patterns for which the operator must nominate as a species type (Berkelmans 1992, Leonard & Clark 1993, Carleton & Done 1995).

Because manual measurement and analysis of large volumes of video sequences are time consuming, labour intensive and therefore costly, there is considerable potential benefit in automating measurement processes. For example, Commonwealth Scientific and Industrial Research Organisation (CSIRO) researchers routinely collect more than 100 h of video recordings annually during biodiversity and fishery habitat surveys in the Australian south-eastern fishery region alone (Shortis et al. 2008). Currently, automation techniques employ motion analysis, image segmentation



(A)



(B)

Figure 10 Accuracy validations for underwater stereo-image systems using a length bar (A) and a fish silhouette (B). (Courtesy CSIRO and E.S. Harvey.)

against the background, and colour matching to identify the presence and percentage cover of benthic fauna and differentiate habitat types in video sequences. Automated measurement enables rapid quantification of the cover of complex structures such as the reefs formed by stony corals (see Figure 12), but tuning and validation against manual scoring techniques remains a work in progress. Stereo measurement can then provide the sizes of individual animals or seabed features within selected image pairs to estimate biomass or population distributions (see Figure 13).

The motion analysis techniques have been developed to identify candidates for counting and sizing fish in aquaculture (Harvey et al. 2004a) and detecting objects in sequences recorded by ROVs in deep water (Walther et al. 2004). Motion analysis is first used to identify sections of the image sequences that contain features of interest, effectively eliminating portions of the video that are devoid of features and not of direct interest to habitat mapping or species identification. This processing is effectively an image compression technique that dramatically reduces the amount of video sequences requiring inspection and reduces DV file sizes. The motion detector can be tuned

Object Name: sbt snfl 1

Centroid Coordinates: X 32.8578 Y 344.4087 Z -1683.8337

Object Length: 1230.908 millimetres Precision: 0.699

Residual Parallax (microns): Value: 4.7 Limit: 0

Measured Point to Base Centre: Distance: 1821.3887 Angle: 22.4516

Description:

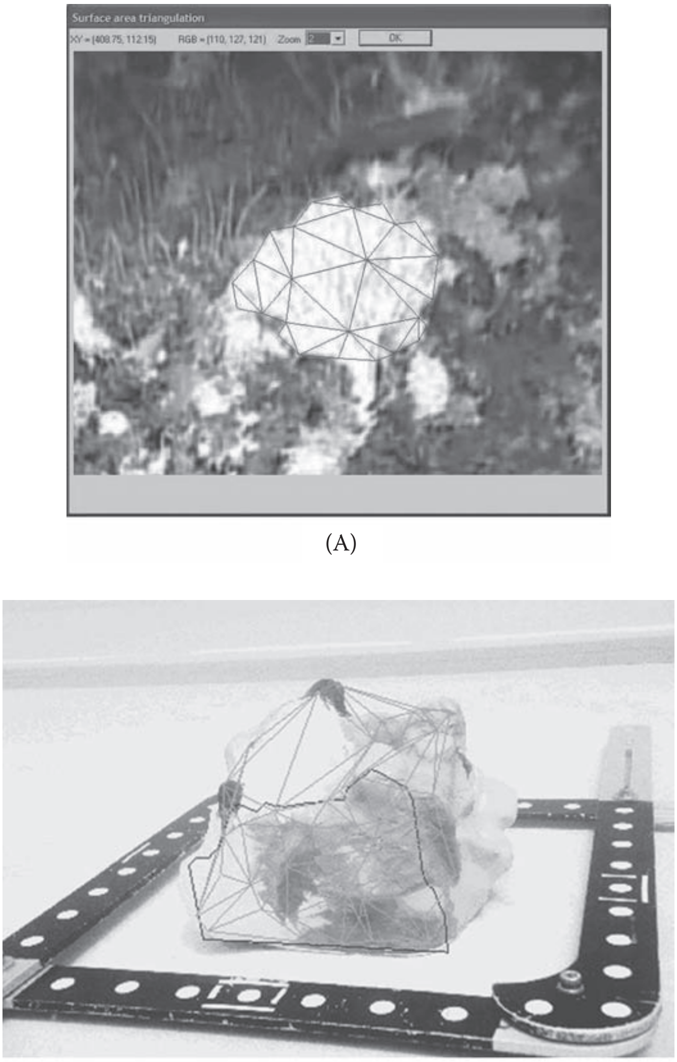
Type: Species

- sbt snfl 1
- sbt snfl 2
- sbt snfl 3
- sbt snfl 4

Figure 11 Body length and span measurements of a southern bluefin tuna (Harvey et al. 2003).

Figure 12 Candidate regions of stony coral detected using a colour signature. (Courtesy of CSIRO and SeaGIS Pty Ltd.)

to detect featureless versus feature-rich regions or specific marine fauna or flora such as stony corals (Shortis et al. 2008) or simply identify objects that require classification (Walther et al. 2004). Edge detection techniques can then be applied to determine the silhouette of the fish or other species to delineate shape and thereby extract metrics such as body length, span or area (Tillett et al. 2000).



XY = (408.75, 112.15) RGB = (110, 127, 121) Zoom 2

(A)

(B)

Figure 13 Triangulation meshes used to determine (A) surface area and (B) enclosed volume. (Courtesy of CSIRO and SeaGIS Pty Ltd., Abdo et al. 2006.)

It is also possible to use stereo-image matching to determine volumes and surface areas of complex structures such as animals or physical features (Abdo et al. 2006). This process is semi-automatic with the region of interest in one of the images defined initially by motion analysis processing. Operator selection of key points followed by epipolar searching and image matching (Gruen & Baltsavias 1988) are then used to provide additional 3-dimensional locations within the boundary on the left and right images. The 3-dimensional data points are used to define the surface based on a Delaunay triangulation, from which surface area and volume can be derived (see Figure 13). An accumulation of such measurements can be used as an estimator of biomass of particular features or species of interest within a transect.

Measurements that directly estimate the volume by generating a detailed reconstruction of the surface of the animal will always provide greater accuracy than a small number of discrete measurements. For example, well-conditioned predator species concentrate food reserves in specific areas of the body (Kohler et al. 1995) and well-conditioned fish often fatten towards the tail. In both cases simple length measurements would fail to detect the change in biomass. Increased automation and sophistication of the measurement techniques will provide increasing levels of accuracy and reliability of estimates of biomass or population distributions.

Trends in techniques

During the last 40 years stereo-image systems have dominated and continue to be the most common choice of configuration for quantitative measurement applications underwater. There are very few instances of other imaging geometries being used for the capture of 3-dimensional information simply because stereo is the minimum configuration required to capture accurate and reliable quantitative data.

As noted, stereo-image systems may be self-contained through fixing the cameras rigidly to a base bar or within a single underwater housing and precalibrating the system (Leatherdale & Turner 1983, Harvey & Shortis 1996). This approach has the advantage that the system can be independent of any external control or physical constraints. The usual mode of operation is that the stereo-image system is manoeuvred by divers or a ROV along a transect or to circular sampling areas to capture imagery. Alternatively, the cameras may be individually calibrated and the stereo system used in conjunction with a control frame that is placed against the object to be measured. The control frame is usually in the form of a quadrapod, also known as a quadrat, which has an area designed to match the field of view of the cameras (Hohle 1971, Fryer 1982). Contemporary systems tend to use simpler designs based on stronger, lightweight materials but the principal is identical (Chong & Stratford 2002).

Despite the dominance of stereo systems, single cameras have been used in a variety of modes of operation. Principal amongst these modes has been the use with control frames and on towed bodies or sleds. Use with control frames is similar to that of stereo-cameras. The fundamental difference is that only 2-dimensional information can be extracted and all objects measured are assumed to be in the same plane as the base of the quadrat (Bohnsack 1979). Use of a single camera on towed bodies or sleds limits the application to qualitative analysis only, such as fish counts or habitat classification (Ebeling et al. 1980a,b). An alternative approach to single-camera imagery from towed bodies is the use of parallel lasers to define the scale of the images. This approach was subsequently extended through the use of additional, crossing laser beams to define a pattern used to determine the orientation and range of the platform relative to the sea bottom (Davis & Pilskaln 1993). The technique allows mapping of features, but like any single-camera approach is limited by scale estimation at a single location (Harvey et al. 2002b) and the assumption that the seafloor is a plane within the field of view or the region of interest.

The coverage of a single pair of stereo-images is limited by visibility restrictions, so a single stereo pair is not feasible for large-area mapping or monitoring projects. The methods adopted for large-area measurement have typically involved strips or mosaics of images, often based on a single camera on a towed body or sled. Extraction of quantitative data requires along-track stereo-pairs of images from the single cameras or selection of frames from video sequences (Moore 1976, Fryer 1982, Edwards et al. 2003). However area mapping has also used transects or mosaics of stereo-images (Bass & Rosencrantz 1977, Shortis et al. 2008), rather than a single camera, to guarantee the stereo coverage of the area of interest.

There are very few examples of the use of true photogrammetric networks of many overlapping images of a single object because this type of approach is not readily adapted to the dynamic and non-uniform underwater environment. Nevertheless, single film cameras have been used to determine cave profiles (Capra 1992), a single video camera has been used to monitor the shape of deployed fishing nets (Schewe et al. 1996) and a network of stereo-images has been used to determine the volume and biomass of sponges (Abdo et al. 2006). In each case a precalibration was conducted to determine the interior orientation of the camera or cameras.

Whilst single cameras, stereo cameras and networks have all been used underwater to capture 3-dimensional information, the clear trend is the continued use of stereo-image systems for measurement tasks ranging from single stereo-pairs for small objects (Shortis et al. 2000) to blocks of images for large-area mapping (Pollio 1971). Stereo-image systems with a fixed configuration are the simplest to use, guarantee stereo coverage and thereby ensure that the capture of 3-dimensional information will be reliable.

Marine biology and ecology applications

The acceptance or rejection of hypotheses in marine biology and ecology usually results from the collection of data using traditional methodologies that are often destructive. Net, grab or trawl techniques remove fauna and flora from the marine ecosystem to gather data on change in individuals or assemblages by measuring wet or dry weights or by volume displacement techniques. The invasive nature of the sampling limits the type and scope of research that can be conducted, especially in monitoring programmes in which repeated sampling is required or when investigating rare species (Hill & Wilkinson 2004, Eleftheriou & McIntyre 2005). Trawl techniques have the further disadvantage that fauna and flora samples are integrated across the length of the trawl, confounding the uncertainly of the sample location. Underwater imaging techniques have the advantage of being non-destructive, geo-located, rapid and repeatable (Harvey & Shortis 1996, Eleftheriou & McIntyre 2005, Shortis et al. 2008), thus allowing the monitoring of individuals and communities without imparting a confounding disturbance on subjects of interest. Underwater imaging techniques can be classified into either acoustic or optical; however, this review is concerned only with optical methodologies such as video or still imagery.

Initially employed in intertidal and laboratory situations, the use of underwater imaging for data collection has increased in the sampling of subtidal habitats and organisms. Underwater imaging techniques have not limited the ability of marine researchers, but rather enhanced and in some cases replaced traditional methodologies (Shortis & Harvey 1998, Harvey et al. 2004b, Abdo et al. 2006). Using underwater imagery researchers may conduct surveys and counts, document and observe individuals and communities, study the behaviour and activity or organisms/populations, identify organisms or features, study geomorphological structures, and even evaluate other methodologies (Eleftheriou & McIntyre 2005). Moreover, depth and air supply constraints associated with conducting research underwater limits the number of samples that can be recorded and collected (Littler 1980, Malatesta et al. 1992), whereas underwater imaging techniques safely and efficiently enhance the ability of the marine researcher to collect data. Ultimately, the application of underwater imagery in marine biology and ecology is dictated by the metric of interest and the size, composition and dispersion of the target, such as individuals, populations or whole communities, being investigated (Maney et al. 1990).

A review of the scientific literature from 1952 to June 2008 found 1768 articles in which underwater imaging techniques were employed in marine research. This is certainly an underestimate because of inaccessible work, such as reports from national committees and government agencies, that are not in the public domain and thereby are not readily available. Nevertheless, the articles published in the scientific journals, conferences and similar media are indicative of the substantive trends in published literature and represent indirectly the level of research and application activity.

From 1983 until 1995 there was a substantial increase in the number of scientific papers published that used underwater imaging techniques to sample the marine environment (Figure 14). This increase in publications, and the implied increase in the use of underwater imaging, coincides with the increasing availability, decreasing cost, increasing reliability and improving resolution of video and still cameras. The number of publications employing underwater imaging techniques decreased after 1995, reaching a plateau after the year 2000. This is possibly due to the common acceptance of

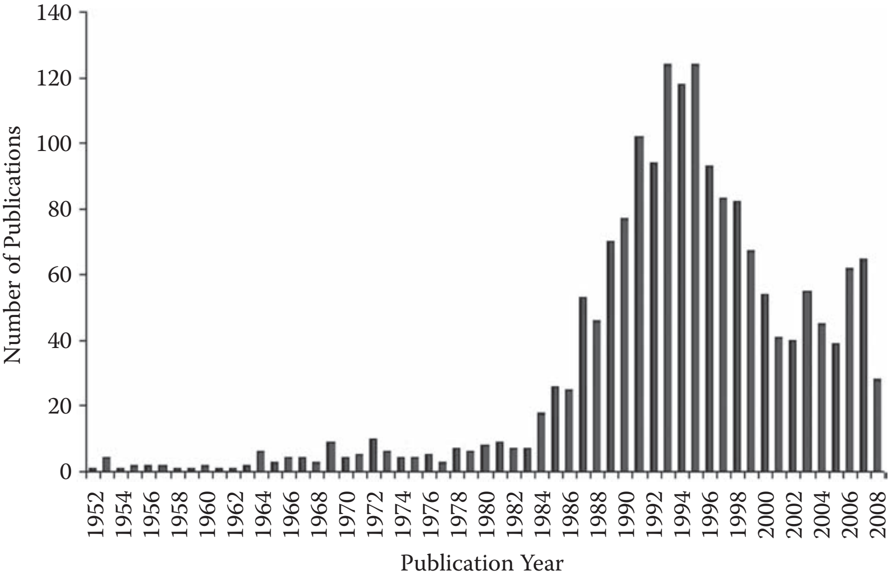


Figure 14 Analysis of the rate of publication of scientific papers on underwater imaging techniques in marine science. Note that citations during 2008 include only January–June.

underwater imaging techniques as a sampling tool as well as lags in appearance of journal articles in bibliographic databases.

The review of the literature indicates that applications of underwater imaging have been predominantly used for monitoring of the behaviour of fish, crustaceans and other invertebrates. Underwater imaging techniques have also been commonly used in research on fisheries and fishing equipment; the abundance and distribution of epibenthic flora and fauna; the abundance, distribution and behaviour of plankton and microflagellates; as well as studies of seafloor properties.

The following sections provide a more detailed review of specific areas of application within marine biology and ecology.

Epibenthic communities and assemblages

Research of epibenthic organisms can involve the measurement of various metrics from counts within quadrats and strip transects, to more complex morphometric measurements of size and biomass, such as simple length measurements, measures of surface area and enclosed volume (Rumohr 1995, Kingsford & Battershill 1998, Eleftheriou & McIntyre 2005).

One of the most common methodologies employed in the study of the epibenthos is the use of either video or still photography to survey the abundance and distribution of epibenthic organisms to gain understanding of the spatial or temporal patterns that occur (Miller & Smith 1984, Service 1987, Bergstedt 1990, Ben Zion et al. 1991, Meier & Porter 1992, Jaap et al. 1994, Vogt et al. 1997, Thrush et al. 1998, Kollmann & Stachowitsch 2001, Houk & Van Woesik 2006, McDonald et al. 2006, Smale et al. 2007). Applications can range from focusing on the abundance of individual organisms (Harriott 1995) to investigating changes in the composition of communities, such as in the study of the dynamics of coral reefs over time (Done 1981, Meier & Porter 1992, Done 1992, Jaap et al. 1994, Kenyon et al. 2006, Goibuu et al. 2008). The use of either video or still imagery can also complement other survey or mapping techniques, such as side-scan sonar, by providing an effective means of extracting ground-truth information for the acquired acoustic dataset (Kronengold et al.

1964, Schwinghamer et al. 1996, Brown et al. 2002, Brown et al. 2004, Foster-Smith et al. 2004, Brown et al. 2005, Birchenough et al. 2006, Rooper & Zimmermann 2007, Grizzle et al. 2008).

Underwater imagery allows for the rapid and continuous survey of the benthos across moderate spatial scales of up to hundreds of metres in transect surveys using video systems (Berkelmans 1992, Michalopoulos et al. 1993, Norris et al. 1997, Ninio et al. 2003, McDonald et al. 2006). Digital still and film cameras provide greater image resolution compared with video, including the recent advances in high-definition video cameras, allowing better identification of organisms and features. The scale of video and film camera surveys ranges from centimetres for quadrats to tens of metres based on mosaics of images (Marks et al. 1995, Yoerger et al. 2000).

Underwater imaging techniques are also readily applicable to behavioural studies of epibenthic fauna, for which the feeding activity, swimming patterns and response to stimuli of the target organism are being investigated (Forward 1989, Forward et al. 1989, Auster et al. 1995, Villanueva et al. 1997, Hudson & Wigham 2003). This can involve both video and still image techniques such as time-lapse series (Smith & Sumpton 1989, Abe & Vannier 1991, Anderson et al. 1991, Gallager et al. 1991, Newell & Gallagher 1991, Huber & Kravitz 1995, Zhou & Shirley 1997, Aizawa 1998, Burrows et al. 1999), with the type of imaging methodology employed determined by the mobility of the epibenthos or the speed of the behaviour. For example, monitoring of a gastropod (Covich & Sanders 1984) is well suited to time-lapse photography whilst the study of barnacle feeding would preferably use video sequences (Trager et al. 1990).

A further application of underwater imagery is to extract or make measurements of the target organisms or features. This allows researchers to study patterns of growth, examine the area of coverage of an organism or its wounds, determine swimming speeds, and obtain various morphometric measurements (Butman et al. 1988, Ben Zion et al. 1991, Tusting & Davis 1993, Oren et al. 1997, Leys & Lauzon 1998, Todd et al. 2001, Duckworth 2003, Handley et al. 2003, Eleftheriou & McIntyre 2005, Beaumont et al. 2007). Single cameras are often used for this application and quantitative measurements require a calibration scale to be incorporated into the image near the organism of interest (Eleftheriou & McIntyre 2005). Such applications can be achieved with either single video or still camera images. However, in both cases, unless the calibration scale is as close as possible to the target organism, significant errors in measurements can occur due to the relative camera orientation and lens distortions, particularly with wide-angle lenses (Harvey & Shortis 1996, Harvey et al. 2002b, Eleftheriou & McIntyre 2005). Further, precise marking of monitoring stations for temporal studies is required to ensure camera misalignment is avoided, limiting the measurement capability of single-camera systems in marine research.

While single camera systems are relatively inexpensive and provide quantitative measurements with low levels of accuracy, the limitations of single-camera platforms can be readily overcome by using stereo-imagery. Stereo-camera systems have enabled many instances of accurate and precise measurements of epibenthic organisms (Bogorov et al. 1970, Lundalv 1976, Rorslett et al. 1978, Swift et al. 1985, Harvey & Shortis 1996, Shortis & Harvey 1998, Chong & Stratford 2002, Negahdaripour & Madjidi 2003, Abdo et al. 2006, 2007, 2008a, Abdo 2007). Stereo-imagery has also been used successfully in many epibenthic-monitoring studies (Done 1981, Cocito et al. 2004, Eleftheriou & McIntyre 2005, Abdo et al. 2008b). Images can be acquired through the use of a single-camera system to capture a sequence or network of images of target organisms that are analysed using advanced software such as MOD3D (Cocito et al. 2003, Valle 2008) or PhotoModeller (Bythell et al. 2001, EosSystems 2008) to produce a 3-dimensional model and enable various morphometric measurements to be made (Bythell et al. 2001, Cocito et al. 2003, 2004). These techniques rely on a scale or reference object in the field of view to ensure that the network of images has an accurate scale and a reliable coordinate system (Abdo et al. 2006).

Stereo-photogrammetry has also been used extensively via the traditional stereo-photography or stereo-video approach using a pair of cameras to capture overlapping images (Done 1981, Harvey

& Shortis 1996, Eleftheriou & McIntyre 2005, Abdo et al. 2006). The captured image pairs are analysed using specialist software such as Vision Measurement System (Shortis & Harvey 1998, Harvey et al. 2003) or PhotoMeasure (Abdo et al. 2006, SeaGIS 2008) to provide stable and robust measurements. The stereo-photography methodology has the advantage over the networks of single images that no reference or scale objects are needed, limiting need for excess equipment underwater, and the robustness of measurement is maintained as movement between successive image captures is minimised (Harvey & Shortis 1996, Shortis & Harvey 1998, Abdo et al. 2006). Stereo-photogrammetry can allow the measurement of surface area and volume data of organisms that are often highly desired metrics in the study of the dynamics of epibenthic organisms and communities (Eleftheriou & McIntyre 2005). Stereo-photogrammetry is particularly suited for studies monitoring temporal changes in epibenthic communities and individuals or when investigating rare species (Done 1981, Harvey & Shortis 1996, Shortis & Harvey 1998, Eleftheriou & McIntyre 2005, Abdo et al. 2006, 2007, 2008b) as data can be obtained without disturbing the target organisms.

Fish communities and assemblages

Accurate and precise, non-destructive data on the length of fishes is difficult to obtain due to the range of habitats occupied by fishes and varying behaviour both within and between species over a range of spatial and temporal scales. Nevertheless, information on the length-frequency or mean length of a fish population is very informative. When linked with even a rudimentary knowledge of the biology of a species, it may allow estimates of recruitment to the adult population, fishing intensity and rates of recovery from fishing (McCormick & Choat 1987). During visual surveys it is common for scuba-divers to count and visually estimate the length of individual fish. However, such estimates suffer from error introduced by the air-water interface in the diver's mask, which causes objects to be magnified in size, appearing closer to the observer than they actually are by a factor of 1.3. Also, researchers using scuba gear have been shown to be inefficient when performance underwater is compared with similar activities in air (Hollien & Rothman 1975).

Visual techniques were first used for quantifying the population densities and community structure of coral reef fishes in 1954 (Brock 1954) and have been subsequently used very effectively for reef fish surveys (Jones & Chase 1975, Bellwood & Alcala 1988, Samoilys 1988, English et al. 1997). The destructive nature of many quantitative methods of coral reef fish assessment has resulted in the widespread adoption and modification of visual census techniques (Odum & Odum 1955, Bardach 1959, Alevizon & Brooks 1975, Brock et al. 1979, Harmelian-Vivien & Bouchon-Navaro 1981, Alevizon et al. 1985, McCormick & Choat 1987, Bellwood & Alcala 1988, Kulbicki 1988, Davis & Anderson 1989, Francour 1994).

Visual census techniques were rapidly adapted to use recordings from underwater movie, television or video cameras to improve the accuracy and reliability (Alevizon & Brooks 1975, Ebeling et al. 1980a,b, Larson & DeMartini 1984, Parker et al. 1994, Gledhill et al. 1996). Video cameras have been used to record transect surveys of reef fishes where the camera is held by scuba-divers (Alevizon & Brooks 1975, Ebeling et al. 1980a,b, Larson & DeMartini 1984, Davis & Anderson 1989, Seaman et al. 1989, Parker et al. 1994, Gledhill et al. 1996) or mounted on manned submersibles (Seaman et al. 1989, Auster et al. 1995, Love et al. 2000, Yoklavich et al. 2000). Counts and identifications of reef fishes made from underwater video recordings have been aided by voice recordings on self-contained audio-tape recorders or directly on to the videotape (Alevizon et al. 1985, Greene & Alevizon 1989, Bortone et al. 1991, Bortone et al. 1994). Reef fishes in deeper water have been surveyed by video cameras mounted on ROVs (Stewart & Auster 1989, Edsall et al. 1993, Adams et al. 1995, Hall et al. 1996) and manned submersibles (Parker & Ross 1986, Shipp et al. 1986, Able & Flescher 1991, Able et al. 1993, Auster et al. 1995, Love et al. 2000, Yoklavich et al. 2000). Video transects are effective for rapidly sampling large, mobile fish in complex environments where the water is reasonably clear. However, they tend to underestimate fish abundance (Davis & Anderson 1989) and the densities of small and cryptic species (Ebeling et al. 1980a).

More recently, remote baited and unbaited video cameras have been effectively deployed with great success (Ellis & DeMartini 1995, Harvey & Shortis 1998, Francour et al. 1999, Willis & Babcock 2000, Willis et al. 2000, Harvey et al. 2002a, 2004b, 2007, Cappo et al. 2004, 2007, Watson et al. 2005, 2007, Langlois et al. 2006, Malcolm et al. 2007) and have been shown to overcome the underestimates of diver-based systems (Willis & Babcock 2000, Willis et al. 2000, Harvey et al. 2004b, 2005).

Single video camera systems have been used to measure the length-frequency distribution of fish assemblages in shallow- (Willis & Babcock 2000, Willis et al. 2000) and deep-water habitats (Love et al. 2000, Yoklavich et al. 2000). However, unless the target fish is close to the original point of scaling, significant measurement errors are introduced into the data (Harvey et al. 2002b). This issue can be partially overcome by using paired, parallel laser dots as scaling points (Love et al. 2000, Yoklavich et al. 2000). However, laser measuring systems using single cameras are limited to measurements of single fish in any one image and, depending on the requirements for measurement accuracy, are limited to measuring fish that are perpendicular to the camera system. Furthermore, it is impossible to make measurements of distance using a single-camera system unless a triangulating laser system is used (Caimi & Bessios 1994).

Stereo still photography has been used to determine the size, density and dispersion of schools of free-swimming sharks (Klimley & Brown 1983) and to measure the 3-dimensional structure of fish schools (Dill et al. 1981). Stereo-photogrammetric techniques have been used to monitor fish schools because of the advantage that accurate length estimates are obtained for individuals while not disturbing or removing the individual from the sample population. The advantage of stereophotography has been extended to paired video camera systems (Boland & Lewbell 1986, Krohn & Boisclair 1994, Li et al. 1997) to provide detailed information on school densities and swimming action from recorded image sequences.

Underwater stereo-video is a research tool that has been used to make very accurate, precise, non-invasive measurements of fish length (Naiberg et al. 1993, Harvey & Shortis 1996, Li et al. 1996, Petrell et al. 1997, Harvey et al. 2001a,b, Harman et al. 2003, Watson et al. 2005, 2007) and the distance and angle of a fish from the camera system (Harvey et al. 2002b). The use of accurate and precise stereo-video measurements of targeted morphometric parameters facilitates very accurate predictions of fish biomass (Petrell et al. 1997, Harvey et al. 2001c, 2002a). Accurate measurements of range and angle now permit line transect theory (Burnham et al. 1980, Buckland et al. 1993) to be objectively applied to surveys of reef fish. In addition, it is also possible to determine the swimming speed of fish (Petrell et al. 1997, Harvey et al. 2001c). The area or volume within which measurements or observations are made can also be calculated, allowing raw counts of fish recorded on videotape to be converted to numbers per unit area and for the unit sampling size to remain consistent, both spatially and temporally. The error associated with defining sampling units has the potential to substantially improve the ability of a sampling programme to detect spatial and temporal changes (Harvey et al. 2004b).

However, all applications of underwater imagery for studies of fish and epibenthic organisms suffer from common limitations. All underwater imaging techniques are constrained by the amount of light available and turbidity of the water column. The light levels available for the camera systems can of course be supplemented by the use of strobes or underwater lights, but this may have an impact on the behaviour of the subject of interest. Turbidity can be overcome by reducing the camera to subject distance, thereby limiting the amount of suspended material in front of the lens, but this commensurately limits the size of the object being investigated. All types of underwater imagery can be prone to systematic errors in the data obtained due to the inability to view the entire organism, to account for internal spaces of the organism or to accurately define the structure of the substratum below, for example, an epibenthic organism. Another consideration is that the extraction of 3-dimensional information requires stereo-image systems that are inevitably bulkier, more complex and more expensive than off-the-shelf single-camera systems, although the penalty of the second camera is reducing as advances in the technology realise less-expensive and more compact systems. Notwithstanding these limitations, the application of underwater imagery is unbounded as it can be applied very effectively via scuba diving, through the use of ROVs, towed bodies or drop camera systems (Bogorov et al. 1970, Vrana & Schwartz 1989, Woods et al. 1994, Leach 1998, Chong & Stratford 2002, Negahdaripour & Madjidi 2003, Abdo et al. 2006).

Other applications

While this review primarily examines the use of underwater stereo-imagery on fish and epibenthic communities, it would be an omission not to briefly discuss the use of underwater imagery in the study of marine mammals, infauna and planktonic organisms, as well as the physical attributes of the marine environment.

Mammals and sharks

Underwater imaging techniques have been applied in many research situations with marine mammals and sharks, from behavioural observations, to measurements of their swimming speeds, and even to morphometric measurements (Dudzinski et al. 1995a,b, Herzing 1996, Ridoux et al. 1997, Marshall 1998, Spitz et al. 2000, Nowacek et al. 2001, Calambokidis et al. 2007). Specific examples include observing the predatory behaviour of sharks hunting for squid (Smale et al. 2001), estimating the body mass of sea lions (Waite et al. 2007) and tracking individual dolphins within a group to identify social interactions (Brâger et al. 1999).

Infauna

Traditional methods of biological sampling of subtidal sediments involves trawling or collecting cores or grab samples. Rhoads & Cande (1971) demonstrated that sediment profile photography was an efficient technique for the *in situ* documentation of organism-sediment relationships. More recently, a profiling system (REMOTS), which incorporates a high-resolution video camera in place of the still camera, has been developed (Rhoads & Germano 1982, 1986, Rumohr & Schomann 1992, Rumohr 1995). Shortis et al. (2000) investigated the use of stereo-imagery to determine the size of surf clams based on the diameter of the inhalant siphon, potentially replacing destructive sampling techniques such as dredge surveys.

Plankton

The Underwater Video Profiler (Gorsky et al. 1992, 2000) and other high-resolution video systems (Welsch et al. 1991, Turner et al. 1993, Waite et al. 1997, Tang et al. 1998, Tiselius 1998) have been developed to examine phytoplankton aggregations and feeding behaviour in zooplankton and obtain visual records of planktonic organisms. These techniques also have been utilised in the study of sediment flocs and aggregations in estuaries (Van Leussen & Cornelisse 1993, Thomsen et al. 1996). The techniques can quantify particles as small as 280 μm and can be operated in water depths of up to 1000 m.

Geomorphology

Underwater imaging has also been applied to the study of physical attributes of the marine environment, investigating the substratum topography and complexity, temporal changes in the nearshore bedform patterns, and changes to beach topography (Barnes 1953, 1955, Swift et al. 1985, Forbes & Boyd 1987, Judge & Forbes 1987, Rumohr 1995, Holland & Holman 1997, Doucette et al. 2002, Ojeda et al. 2004).

Conclusions

This review of the status and trends in underwater stereo-image measurement has identified the development of imaging and photogrammetric techniques in marine biology and ecology and presented a summary of applications to illustrate the current state of the art. Despite the high levels of sophistication and automation in other applications of stereo-image techniques, underwater systems continue to use relatively straightforward measurement techniques. Manual measurement using on-screen presentation to human operators is still widespread, and stereo-photogrammetric geometry predominates for 3-dimensional measurement applications.

The lag in the adoption of advanced stereo-image technology is due primarily to the difficulties associated with operations in the underwater environment. Experience in marine science has shown that simple approaches to underwater measurement problems are generally successful, and increased task or equipment complexity has a greater tendency towards failure. Whilst stereo systems lack versatility in operational range and the size of objects that can be measured, stereo is the minimum level of complexity that enables measurement of 3-dimensional objects. This has naturally resulted in specific stereo-camera designs to meet specific underwater measurement tasks.

An additional factor is of course the attenuation of light through the water medium. All optical measurement techniques are limited to short ranges of several metres and can be restricted further in poor conditions, such as high-turbidity levels or backscatter from particulate matter when artificial lighting is needed. The water medium reduces contrast, decreases resolution and alters the colour of images. The refractive interfaces and the variability of the water medium place limitations on accuracy because of the need for additional modelling of light paths. Microvariations in the non-uniform water environment cannot be readily modelled and must be absorbed by the statistical variations in the measurement system, limiting the precision of measurements. Hence, any imaging system and photogrammetric geometry in water is unlikely to match the precision and accuracy of the equivalent configuration in air.

Whilst all of these factors limit the potential range of applications and accuracy of underwater stereo-image measurement, prospects for the future are very promising. The increased resolution and automation of digital still cameras and frame rate cameras used with direct-to-disk systems will improve the utility of underwater stereo-image techniques and broaden the potential range of applications. Photogrammetric measurement of biomass, especially in aquaculture, is an area in which there is a plethora of potential applications, driven by the need to manage marine resources. However, the greatest bottleneck preventing the wider use of stereo-images is the automation of measurement and processing. Whilst the qualitative use of video is widespread in marine science, stereo-image measurement is a relatively new tool that will be adopted for quantitative applications only if it requires a modest investment of time and resources. Advances in the automated or semi-automated recognition and measurement of marine fauna and flora species to generate size or biomass estimates will enable a substantive improvement in the accuracy and efficiency of applications such as habitat monitoring and stock assessment. Automation of measurement and analysis is the key to the increased use of underwater stereo-image techniques for marine biology and ecology.

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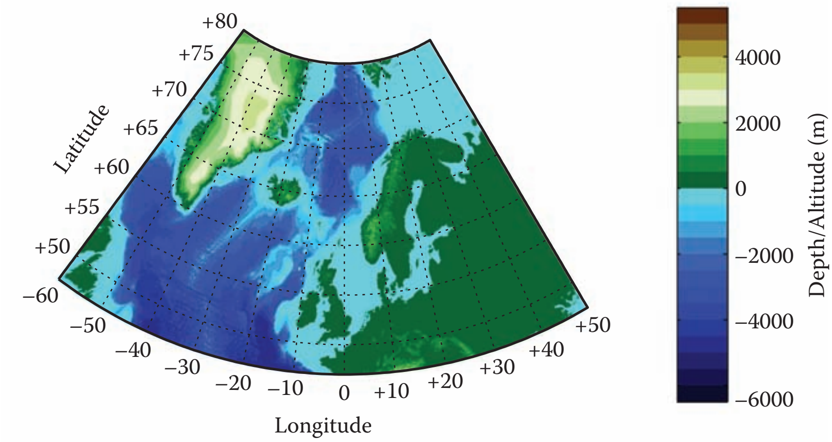
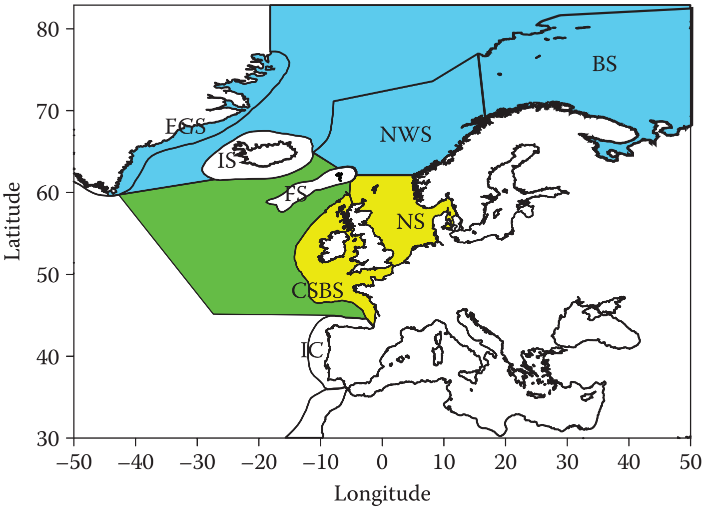
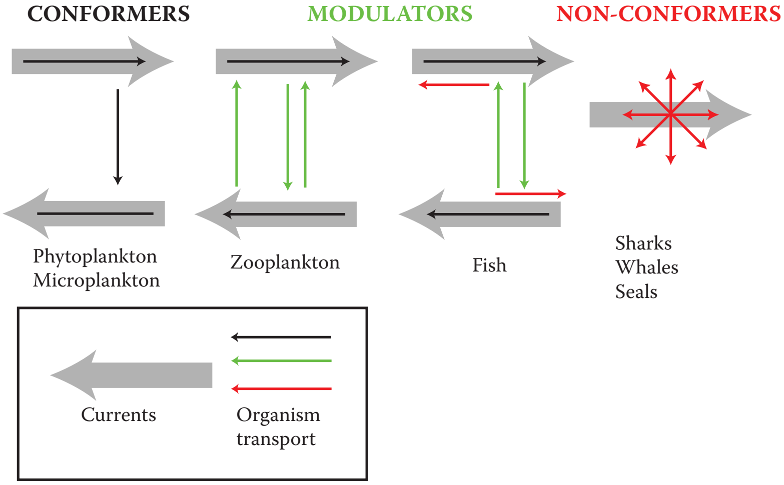


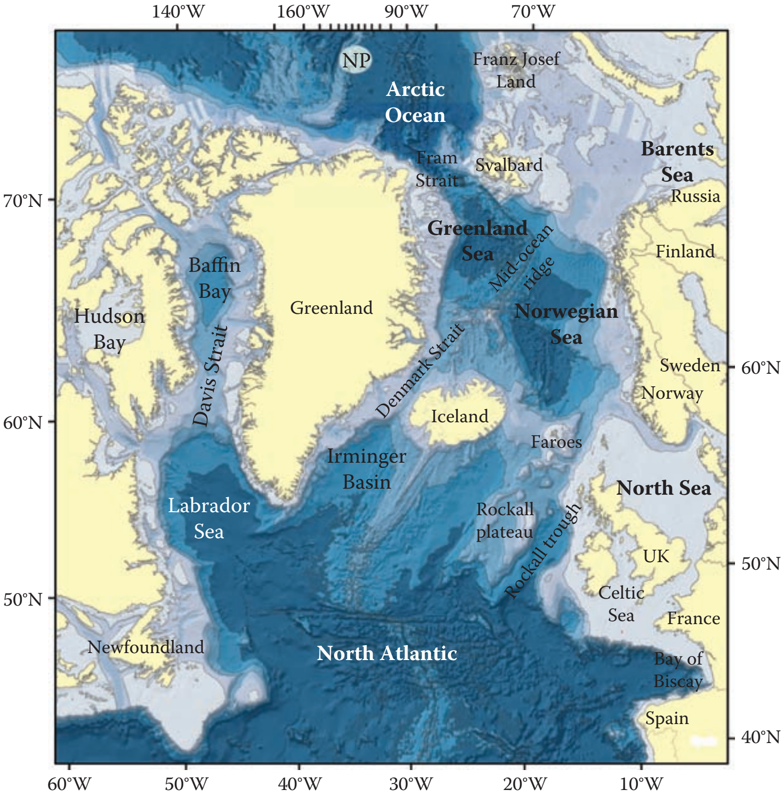
Colour Figure 1 Overall topography of the north-eastern Atlantic, elevations in metres from mean sea level (MSL). (Prepared from ETOPO2v2 data.)



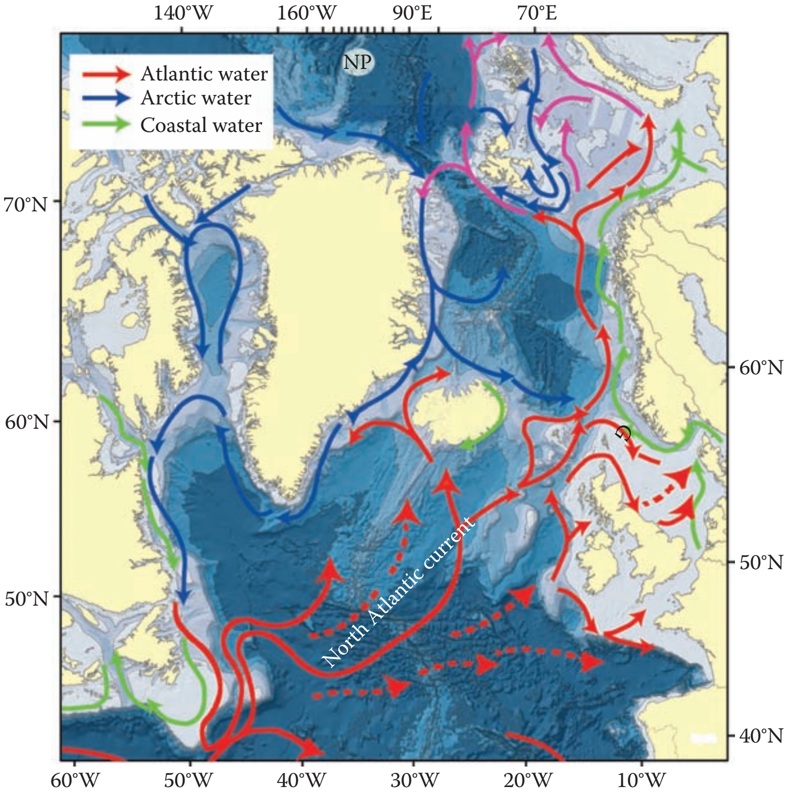
Colour Figure 2 Large Marine Ecosystems (LME) boundaries within the north-eastern Atlantic.



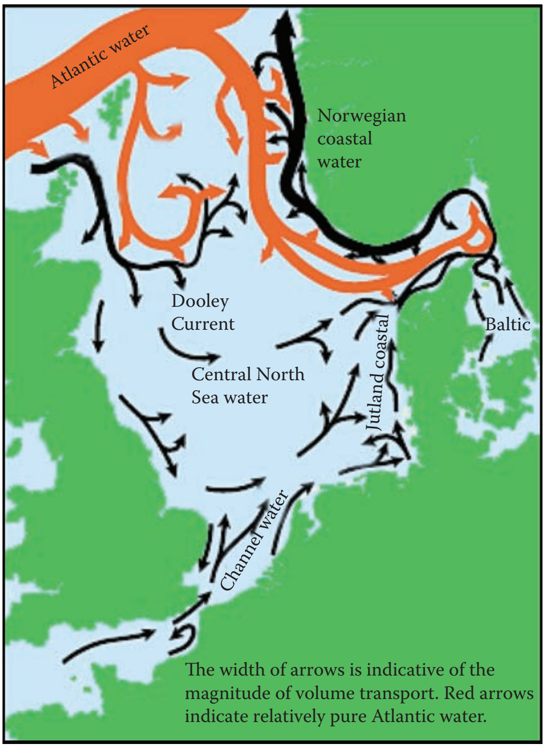
Colour Figure 3 Role of water currents for individual dispersal options.



Colour Figure 4 General bathymetry of the north-eastern Atlantic. NP indicates North Pole.

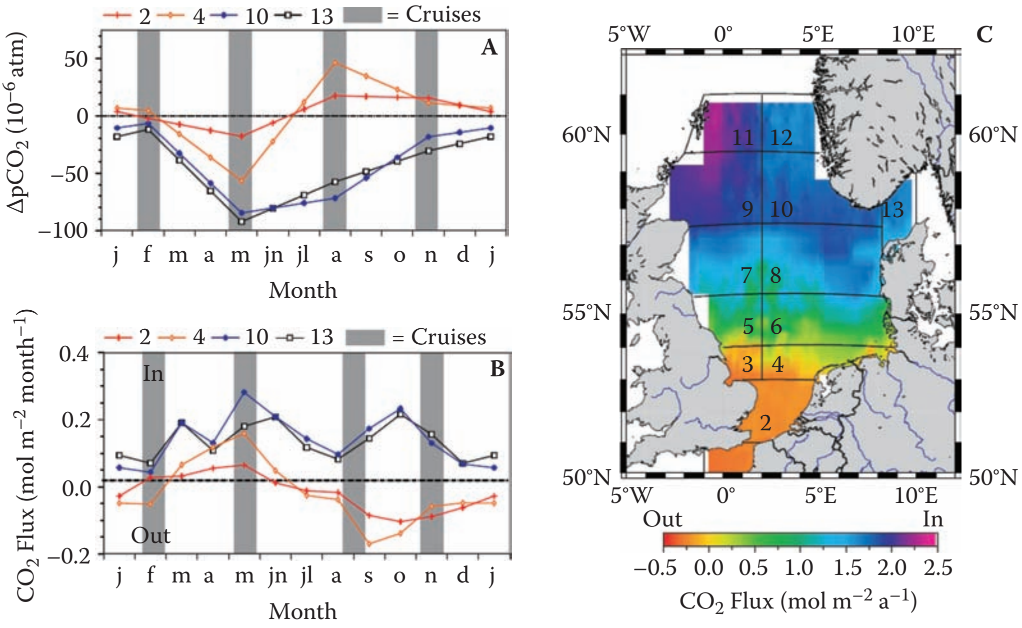


Colour Figure 6 The general pattern of oceanographic flows in the north-eastern Atlantic.

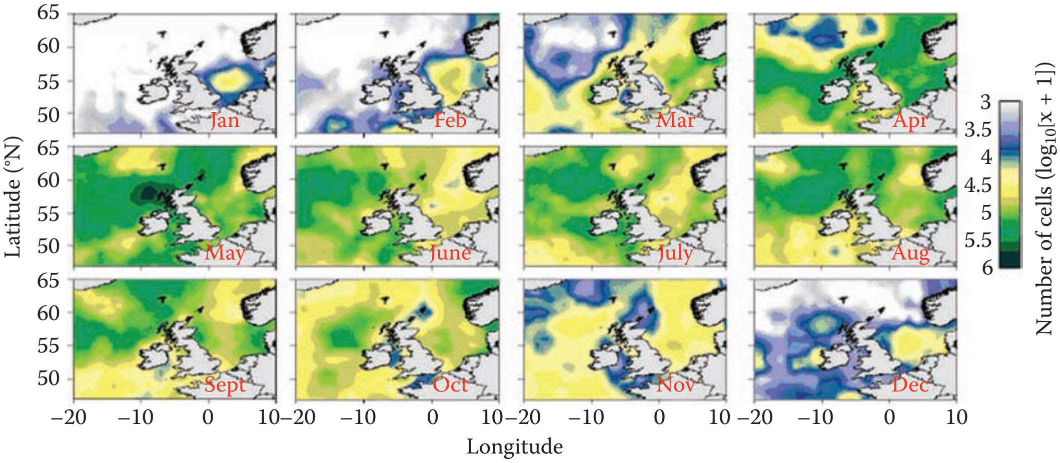


The width of arrows is indicative of the magnitude of volume transport. Red arrows indicate relatively pure Atlantic water.

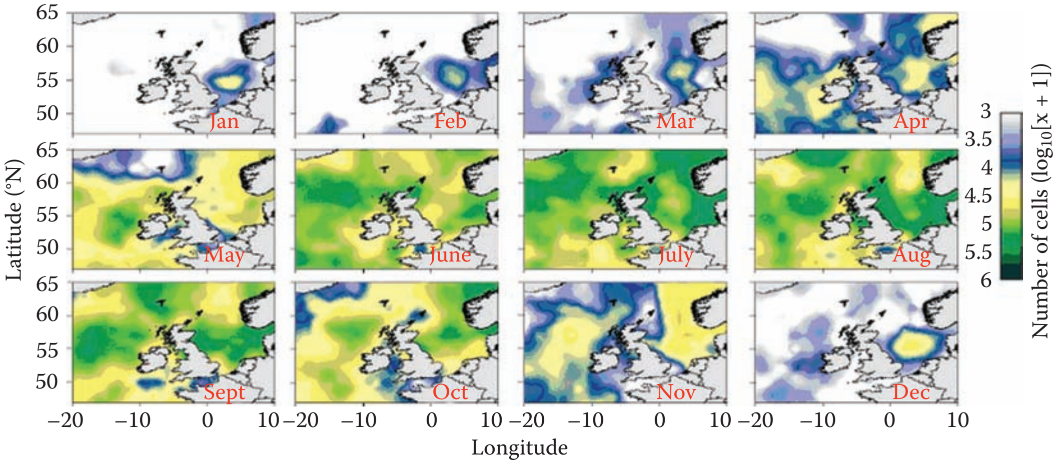
Colour Figure 7 Schematic diagram of general circulation in the North Sea. (After Turrell 1992. Reproduced with Crown permission.)



Colour Figure 10 Annual cycles of air-sea partial CO_2 pressure differences (A) and calculated fluxes (B) for selected areas in the North Sea, with shading indicating periods of observation. The spatial pattern of air-sea CO_2 fluxes across the North Sea is shown in C. Note positive values for CO_2 flux indicate absorption from air to sea.

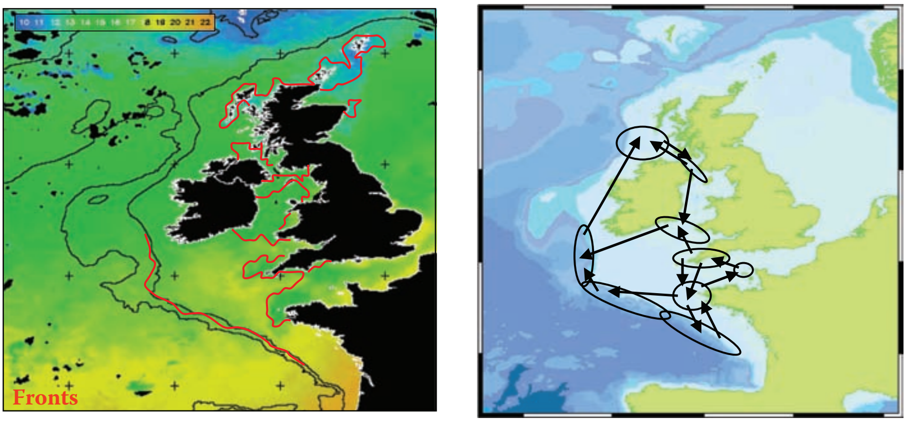


(A) Spatial distribution of diatoms



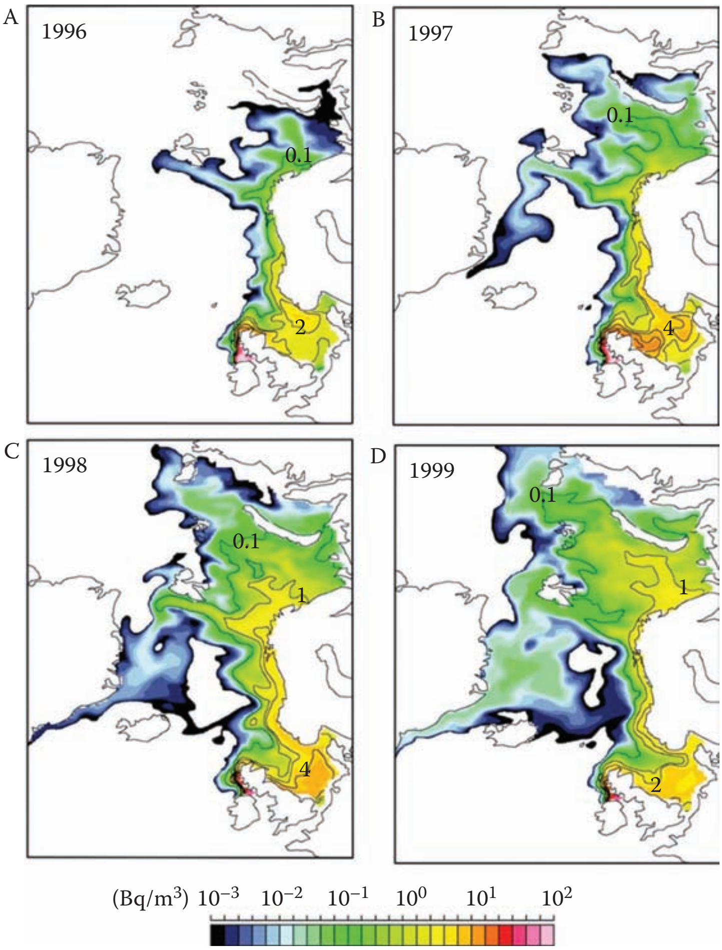
(B) Spatial distribution of dinoflagellates

Colour Figure 8 Mean monthly spatial patterns of (A) diatoms and (B) dinoflagellates in the north-eastern Atlantic during the period 1958 to 2003. (From McQuatters-Gollop et al. 2007a. With permission of Inter-Research Science Center.)

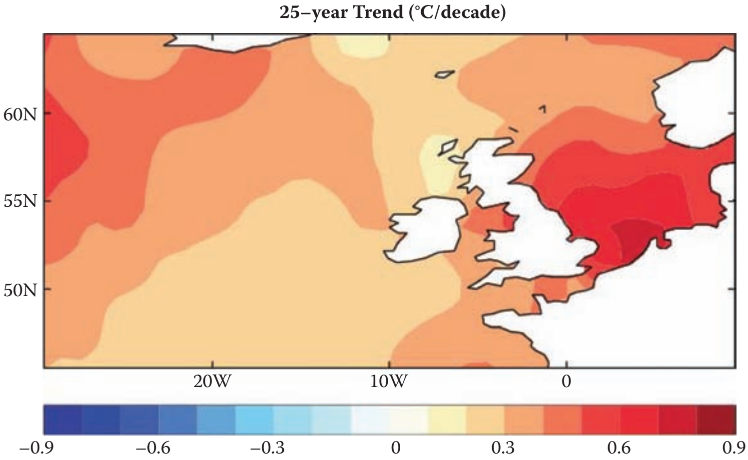


(A) (B)

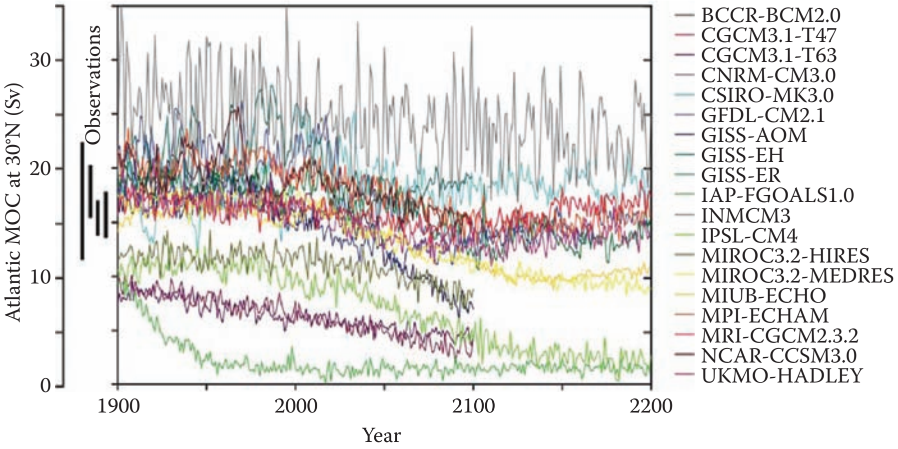
Colour Figure 15 (A) Tidal and shelf break fronts (red lines) on the European shelf and (B) the generalised movement patterns of "tracked" basking sharks between these productive regions. Remote-sensing image is a monthly composite of sea-surface temperature during August 2002 from AVHRR on National Oceanic and Atmospheric Administration (NOAA) satellites. (From Sims et al. 2005. Reproduced with Crown permission.)



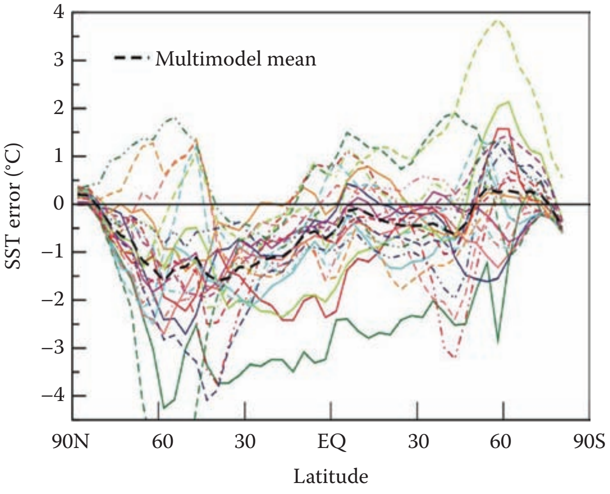
Colour Figure 16 Simulated distribution of ^{99}Tc (Bq m^{-3}) in surface water, from the North Atlantic/Arctic Ocean sea ice model (NAOSIM), in September (A) 1996, (B) 1997, (C) 1998 and (D) 1999 (isolines: 0.1, 1.0., 2.0 and every 2.0 Bq m^{-3}). Model simulations were broadly in agreement with observed concentrations. Elevated releases from the Sellafield nuclear fuel reprocessing plant into the Irish Sea began in 1994 due to the startup of the enhanced actinide removal plant (EARP) facility. (Karcher et al. 2004. With permission from Elsevier.)



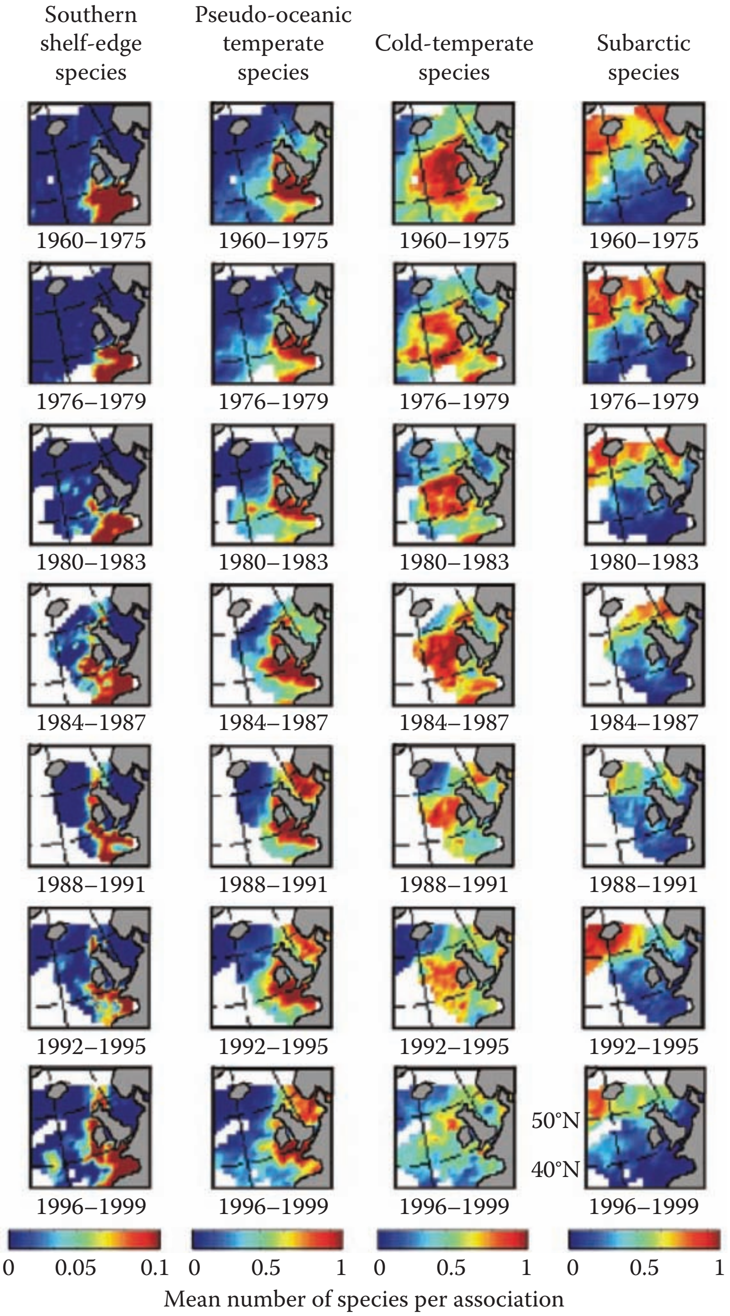
Colour Figure 17 The 25-year trend in sea-surface temperature (°C decade-1, 1982–2006) for the north-eastern Atlantic. (Holliday et al. 2008. Reproduced with Crown permission.)



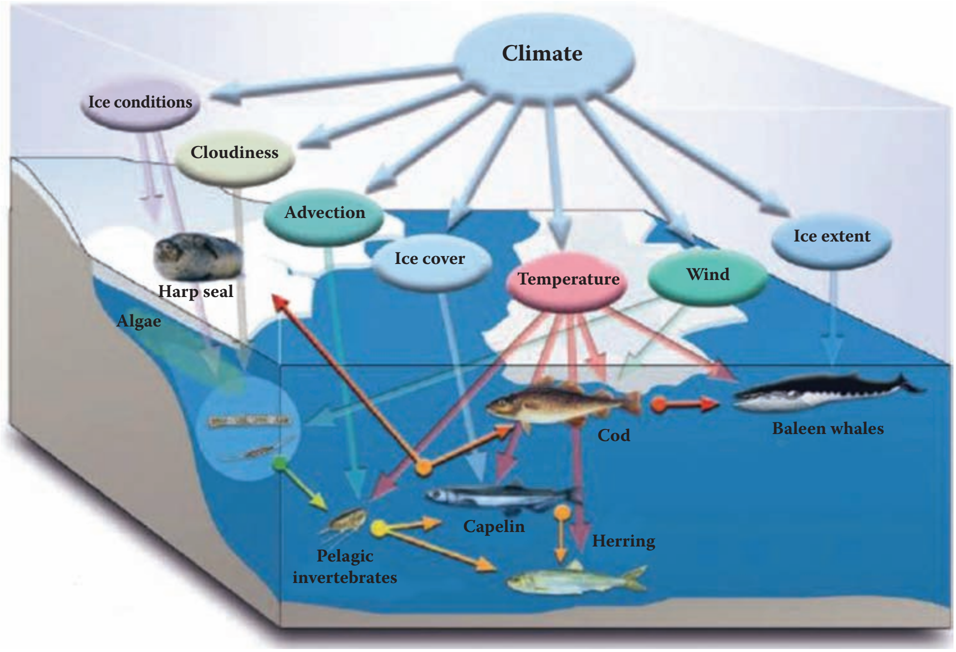
Colour Figure 19 Evolution of the Atlantic meridional overturning circulation (MOC) at 30°N in simulations with the suite of comprehensive coupled climate models. (From Meehl et al. 2007, Figure 10.15, p. 773. With permission.)



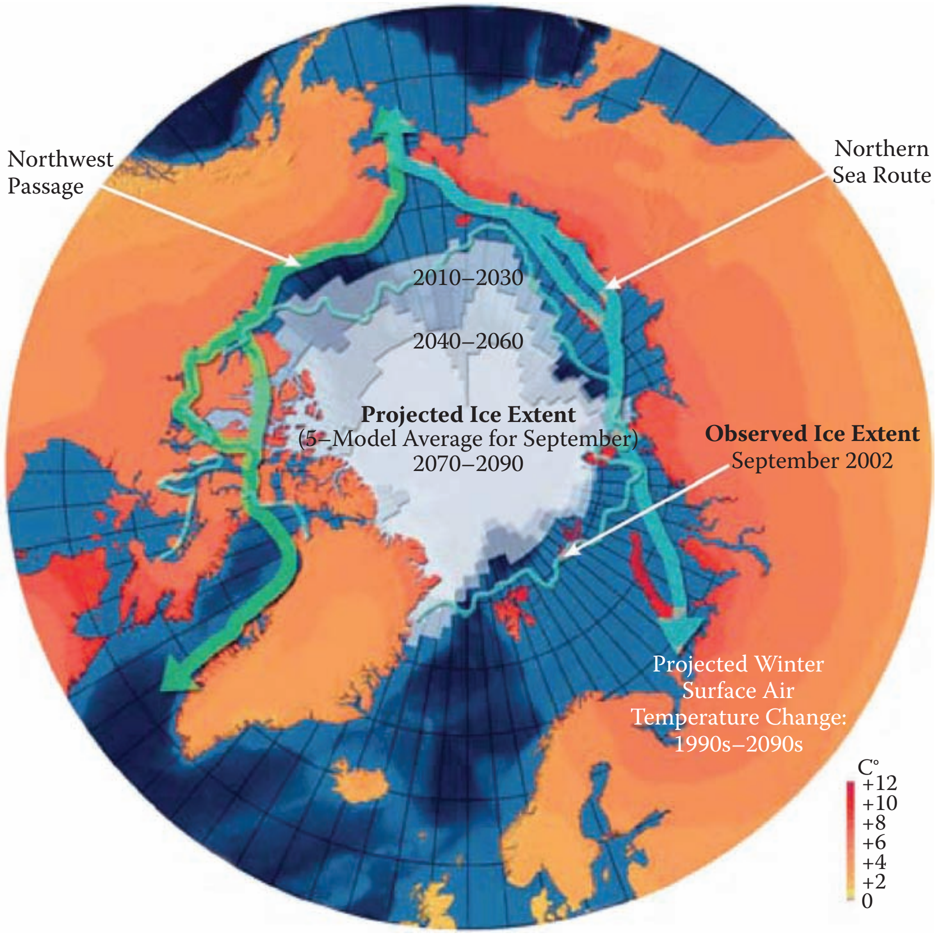
Colour Figure 20 Annual mean, zonally averaged SST error, simulated minus observed climatology for a number of atmosphere ocean general circulation models (AOGCMs). (From Randall et al. 2007, Figure 8.8, p. 614. With permission.)



Colour Figure 22 Long-term changes in the mean number of calanoid copepod species per association from 1960 to 1999 from Continuous Plankton Recorder (CPR) records. (From Beaugrand et al. 2002. With permission of AAAS.)



Colour Figure 24 Interactions of climate change factors with biological components of the Nordic and Arctic Seas ecosystem. (Reproduced with permission of Cambridge University Press.)



Colour Figure 25 Potential navigation routes in the Arctic. (Arctic Council 2006. With permission.)

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