Cephalopods

Ecology and Fisheries

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University of Aberdeen

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To Ann and Laura

Contents

Preface

Squid, cuttlefish and octopuses are a group of marine molluscs which have been recognised, illustrated and appreciated from ancient times, and are of great interest to fishermen, cooks and students of natural history. Most were described and named during the nineteenth century, but it was the technology of the late twentieth century that brought them to wider scientific attention, allowing a generation of anatomists and physiologists to use laboratory studies on cephalopods to investigate the principles of organisation and function in their nervous system. Now, underwater access by diving and submersible vehicles increasingly reveals the range and complexity of their normal life in the sea, oceanic and deepwater expeditions explore the full range of their habitats, and twenty-first-century techniques such as molecular biology and remote sensing are making new advances.

Widening investigations of the ecology of the seas and oceans have progressively revealed the major importance of cephalopods in the trophic structure of the marine ecosystem – as predators on many different animal types and as prey themselves for the larger fish, birds and mammals at the top of the ocean foodweb. Coastal hand-fisheries for cephalopods have always had local human importance, but man has joined the list of major cephalopod predators through large-scale commercial fisheries operating globally. These international fisheries take a large and still increasing share of the global take of living marine resources. The variety, scale and range of the fisheries make a major contribution to scientific knowledge of cephalopods at sea, and we feel that this fully justifies the integration of fisheries studies with traditional ecological approaches.

Both of us, over many years, have introduced students and researchers from different backgrounds to a variety of cephalopod topics, and we have felt the need for a general text covering the basis of cephalopod biology, the patterns of their life history, and their relevance in the changing ecology of the world ocean. Despite the wealth of information in the scientific literature, there are few viewpoints from which the student and marine biologist or fisheries scientist can see a broader picture and begin to navigate towards their own area of interest.

We have written this book for readers from backgrounds in biology, zoology, ecology, biological oceanography or fisheries, to help them become familiar with the themes of cephalopod biology and ecology, and to promote their greater integration into the mainstream of marine science. A particular challenge for all of us is the fluid state of the taxonomy and systematics of the group, and the changes that are likely to arise from application of the emerging molecular techniques in evolutionary and population biology. We have adopted a pragmatic approach to the problem of scientific names that we judge will suit the majority of readers, since it is a compromise between the terminology in general use and the more strictly correct forms.

Generations of marine biologists have found interest and excitement in the study of cephalopods and their work has been our source material for the writing of this book. To acknowledge this foundation, and to take full account of the diversity of modern studies, we have used citations from all periods of work, and drawn information and examples from most areas of the world. In undertaking this review we have been acutely aware of the increasing volume of new scientific literature – some groundbreaking and some repetitive. Inevitably, as soon as this book is in the hands of its readers it will already appear out of date, but new literature is readily found through modern bibliographic methods and set into the framework we have tried to assemble.

We hope to have reported our remit objectively, if selectively, and to have placed cephalopod ecology and fisheries into some overall perspective which will be useful as a basis for widening our understanding of the marine ecosystem as a whole.

Peter Boyle and Paul Rodhouse
Aberdeen and Cambridge

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Ian Rendell (Aberdeen) and Juliet Corley (Cambridge) undertook the major work of preparing the line illustrations, Jianjun Wang (Aberdeen) provided all of the distribution maps, and Lyndsay Brown (Aberdeen) and Nadine Johnston (Cambridge) provided considerable assistance with the manuscript and bibliography.

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Chapter 1

Introduction

Human interest in cephalopods is of long standing. The classical civilisations of the Mediterranean had a good knowledge of the various types. Descriptions of large cephalopods can be recognised at least back to Homer's *Odyssey* (~700 BC, Lane 1957). Aristotle (~330 BC), in the *Historia Animalium*, gave clear descriptions of many aspects of the lives of several species, including octopus and cuttlefish, and described such biological details as their specialised mating and egg-laying habits. Artistic representations of octopus, squid and cuttlefish are seen on the earliest glazed pots and mosaics of the Minoan Crete (~1650 BC), Greek and Roman cultures, and were even symbolically sculpted on to a ship's anchor found in the Cretan palace of Knossos.

From mediaeval times to the end of the nineteenth century, cephalopods were likely to be regarded with awe and suspicion by maritime populations as hostile sea creatures, capable of sinking ships and drowning sailors. Many of these stories probably resulted from fearfully exaggerated accounts of rare encounters with giant squids. Lane (1957), Cousteau & Diolé (1973) and Ellis (1998) provide popular introductions to the biology of cephalopods and fascinating insights into their interactions with people. Widely read authors have included encounters with fierce and gigantic cephalopods in classic adventure tales such as the *Toilers of the Sea* (Victor Hugo) and *Twenty Thousand Leagues Under the Sea* (Jules Verne). Fiction writers and artists continue to draw inspiration from cephalopods, and examples range from the aggressive giant squid in *The Beast* (Peter Benchley) and the venomous octopus pet belonging to *Dr No* (Ian Fleming), through to the erotic engravings of the Japanese woodcut artist Hokusai. Far from emerging from earlier dark ages of mystery and myth, modern popular culture still incorporates cephalopod images and characteristics into powerful and threatening monsters, as any student of fiction and film will recognise.

1.1 Class Cephalopoda

The cephalopods, commonly the octopuses, squid and cuttlefish, along with the vampire squid and *Nautilus*, comprise a well-defined class of Mollusca. As such, they share a basic body organisation with the bivalves, snails and chitons, and retain some of their most recognisable characters such as the file-like feeding organ (the radula) and the ability to secrete a shell. They appeared as a distinct class over 450 million years ago, and for much of the fossil record are very well represented by the heavy shelled nautiluses and ammonites. The loss of the external shell and evolutionary radiation into the subclasses recognised today occurred relatively late, and the living forms, in which the shell is suppressed or lost, originated less than 100 million years ago.

The cephalopods are probably most easily recognised by the many anatomical and biological features that they do not share with other molluscs. The common coastal species are large, abundant animals, actively swimming by powerful jet propulsion. In their abilities to operate off the bottom and fully use the three-dimensional space of the water column, in their shoaling and migration patterns, and their complex and versatile behaviour, the ecology of cephalopods is more realistically compared with that of the bony fish than the mainly benthic members of the other molluscan classes. Few other molluscs (some opisthobranch gastropods and a few pectinid bivalves) have evolved any sort of swimming capability, and there is nothing comparable to the use of the mantle musculature by cephalopods to produce a powerful and directed jet thrust. Effective though this method is for rapid propulsion, it is energetically much less efficient than the undulatory movement of fish, and many squid also use undulating fin movements for swimming.

Modern cephalopods (order Coleoidea, suborder Neocoleoidea) have reduced the form of the external shell of their ancestors to an internal structure or lost it altogether. In cuttlefish and their relatives, the shell remnant is now a chambered buoyancy organ enclosing a gas space capable of counteracting its weight in water and allowing the animal to hover weightless in space. In squid, the shell is further reduced to a supporting structure called the pen or gladius without any buoyancy function. These muscular squid are negatively buoyant and need to swim continuously to maintain their position. Many squid, mostly those in oceanic midwater, reduce the energetic cost of swimming by becoming watery and flaccid, and accumulating ammonium salts in their tissues or special compartments to counteract sinking. Although octopuses are primarily bottom-dwelling, there are some families that have become completely pelagic by adopting new buoyancy devices which retain a gas bubble. Living on the seabed, in midwater, or in the surface layers of the ocean, the arms and tentacles of cephalopods bear muscular suckers which serve primarily to catch and hold their prey. Collectively, the suckers can exert considerable force and, coupled with the flexibility and muscularity of the whole animal, can make a sizeable octopus or squid quite a formidable animal for a person to handle.

To control this active and mobile lifestyle, the molluscan nervous system of isolated ganglia (accumulations of nerve cell bodies) linked by nerve cords has evolved in cephalopods into a highly concentrated and differentiated brain. Consistent with their molluscan ancestry, however, the brain is organised around the oesophagus. The greatly increased mass of nervous tissue, now encased in a rigid cranium, significantly constrains the diameter of the oesophagus and the size of the food that can be swallowed. Unusually for large predators, cephalopods eat their prey in small pieces. Apart from its sheer volume, two capabilities of the nervous system stand out:

- the ability of the octopus to learn by experience, most clearly demonstrated by laboratory experiments teaching individuals to discriminate between sensory cues;
- the establishment of a sequential transmission system of giant nerve fibres connecting the brain to the mantle muscles in many squid, which ensures their rapid and coordinated contraction and maximises the escape response of the animal.

The tactile, chemical and visual senses of cephalopods are highly developed. Most obvious are their large eyes, which are capable of good image formation and visual acuity under water. Most of the coastal cephalopods and those of the upper layers of the ocean (epipelagic) are highly visual animals relying on their vision for prey capture and avoidance of predators. The skin of living cephalopods (except the nautilus) displays a remarkable system of mobile pigmented cells called chromatophores. These are under individual muscular control and are innervated from the brain to display precise, complex and actively changing patterns on the surface of the animal. This method of pattern expression by cephalopods is completely unique, and is one of their most surprising and impressive capabilities. Displays by the pigmented chromatophores are seen by the human observer as coloured patterns, but cephalopods themselves do not seem to be capable of colour vision and presumably they read these displays in black and white or shades of grey.

1.2 Cephalopod themes

As a group, the living cephalopods share common themes of life cycle, growth and reproduction that set the framework for their ecological interactions. The degree to which these themes are varied, and the detailed mechanisms of their expression, is mainly influenced by the divergent requirements of the habitat itself. Conditions on coastal sediments, for example, require quite different adaptations to those needed for the oceanic midwater realm. The octopuses, squid and cuttlefish have much in common with respect to their general biology, and the differences between individuals or families can be interpreted largely in terms of the requirements of the environment.

The class Cephalopoda includes the largest invertebrate animals known to be living at present or in the fossil past. Apart from the giant squid *Architeuthis*, there are many species reaching a maximum body weight of 50–60 kg, and the majority probably attain sizes of 0.1–10 kg. No other invertebrate class approaches these individual body sizes.

The large body size of cephalopods is reached quickly as a result of generally high growth rates. Not only are cephalopods universally predators, they selectively ingest only high-quality parts of their food organisms, rejecting most of those parts such as shell, carapace, bone and cartilage that are less digestible or nutritious. It is also clear that cephalopod digestion and metabolism is generally very efficient at converting food intake to body growth, and consequently they are capable of reaching adult body size and breeding condition at a young age (6–24 months after hatching for most of those for which data exist).

The sexes are separate and, unlike many gastropod and bivalve molluscs, no instances of sex change or hermaphroditism are known. At sexual maturity, male animals package sperm into specialised packets which are delivered to, or implanted in, the female during mating by one of the arms of the male which is specially modified for the purpose. In most cephalopods, the mature eggs are fertilised as the spawn mass is deposited by the female. The individual size and number of eggs is highly variable, and ranges from a few very large eggs (<30 mm long) attached to the seabed, to numerous (>1 million) small eggs drifting in the plankton. Compared with other molluscs, egg numbers are low, but individually they are of relatively large size due to the amount of yolk provided for the development of the embryo. The incubation period is highly temperature-dependent, and is completed by the hatching of a larval stage that, in most respects, resembles a miniature adult. There are none of the highly differentiated larval forms of the other molluscs. After breeding, the spawned adults die within a short time, and in those species with a highly synchronised breeding population this can result in conspicuous mass mortality.

The combination of high growth rate, early attainment of adult size and maturity, and mortality after breeding has attached the 'live fast, die young' epithet to the cephalopod life cycle. Exactly what is meant by breeding once (semelparity), and the degree to which mortality after spawning is universal is open to various interpretations (see Box 6.1). Certainly the growth rates of cephalopods in different habitats vary, and there is a variety of spawning modes that may release the eggs singly over a long period or in episodic batches, but for most of the cephalopods for which there are data, life is short and there is a single reproductive season.

1.3 Cephalopod ecology

Ecology is concerned with where organisms are found, how many occur there and why (Krebs 1972). It tries to take into account the interacting factors of evolution, genetics, physiology and behaviour, as well as the predictable and stochastic variables of the physical environment. Study of the ecology of organisms, therefore, ideally involves a holistic and multidisciplinary approach to biology and the environment, an approach all the more difficult to pursue in marine animals ranging throughout the ocean and beneath its surface.

Inevitably, taking a practical approach to cephalopod ecology involves some ordering and categorisation of the information arbitrarily imposed on what is actually a continuum of knowledge. Doing this imposes a spurious degree of structure and order on the subject that is exaggerated by the very incomplete knowledge of most species in the relatively inaccessible oceanic, mid- and deep-water habitats. Only about 650–700 species of cephalopods are definitively described and named. For many of these there are real uncertainties in the naming of species and the establishment of their relationships, with further difficulties arising from attempts to reconcile the conventional taxonomic and phylogenetic approaches with the newer molecular taxonomy. The form of words used for the various categories of ranking within the classification is also not always consistently applied, but in this book we have tried to adopt systematically correct terminology while using the popular names for groupings wherever possible.

The broad category of coastal and shelf species (Chapter 11) covers the relatively well-known species cephalopods, i.e. those most available to study and those that support most of the generalisations about cephalopods. They most obviously exhibit the shared characteristics of predation, which places them in the upper trophic levels of the ecosystem, and a short lifespan, leading to highly volatile populations responsive to changes in the physical and biological environment. These neritic forms share some degree of dependency on the seabed, and include truly benthic species such as *Octopus* and *Sepia*, with squid of demersal habits (family Loliginidae).

Members of the squid family Ommastrephidae, which comprise the bulk of world fisheries for squid, are associated with the productive and dynamic oceanographic features at the shelf edge and do not consistently fit into a simple neritic/oceanic subdivision. All ommastrephids have a pelagic lifestyle, extruding fragile neutrally buoyant egg masses at depth, releasing larvae into the surface plankton and making use of large-scale current patterns for larval transport and assisted migration of populations. Some of these are justifiably treated as true ocean dwellers (genera such as *Ommastrephes*, *Sthenoteuthis*, *Martialia* and *Dosidicus*) in Chapter 12. Other ommastrephids, although typically offshore in distribution, are frequently present over the shelf itself, taking advantage of rich feeding opportunities by following prey into shallow water and themselves becoming available to coastal commercial fisheries (e.g. *Illex*, *Todarodes*, *Nototodarus* and *Todaropsis*).

The offshore fauna of oceanic and deep-sea species encompasses the taxonomically diverse families of mesopelagic and the bathybenthic cephalopods together with large populations of epipelagic squid (see Chapter 12). This assemblage is far less well known, and there are fewer recognisable similarities of lifestyle between these taxa than with the coastal forms. As a consequence of our weaker understanding of their biology, and also of the much greater scale of the oceanic and deep-sea habitat, many important questions surround their ecology, interactions with the environment, life-cycle characteristics, production of biomass and roles in the trophic structure of the marine ecosystem of the oceans.

The ability to identify cephalopods and quantitatively estimate the consumption of them by higher predators through the persistence of their beaks in the predator's gut, vomit and faeces has led to great advances in understanding their role in marine ecology. Large populations of large fish, marine birds, whales and other marine mammals take a major proportion of their food as cephalopods. Studies on the links between predator and prey, and the scale of their trophic interactions, have made major contributions to marine ecology generally and the upper levels of marine life specifically.

1.4 Cephalopod fisheries

Humans have probably always taken advantage of the octopus and cuttlefish available in shallow water since coastal settlements were established in prehistoric times. However, we have little direct evidence of this since, unlike the gastropods and bivalves, cephalopods do not provide persistent remains to be discovered in the vast shell middens left by our ancestors. It is also true that, with very few exceptions, cephalopods are not present in estuarine waters, or bays having lower salinity, where many human settlements would have begun.

Today, throughout the world, many coastal human populations derive a significant proportion of their protein intake from locally caught cephalopod species. These so-called artisanal fisheries make a very important, but usually unrecorded and unquantified, contribution to the sustenance of some marginal communities. Even in areas with advanced economies, the artisanal, hand-fishing methods of capture by pots, traps and lures persist for the sake of tradition or preference.

Historically, the consumption of cephalopod products has been highest in the countries of south-east Asia. Countries such as Japan, Korea, Thailand, Taiwan and

China have been most prominent in the sale and trade of fished cephalopods and the development of specialised fishing methods, notably the use of jigging machines with high-intensity lights. These Asian countries still predominate in the commercial fisheries for cephalopods. It was the sudden decline in the availability of *Todarodes pacificus*, mainstay of the Japanese fishery, in the 1970s that accelerated the search for new resources and pushed the fishing fleets out into the open ocean and remote areas. This global demand for cephalopods has resulted in steadily increased landings, mostly of squid, to over 3.0 million tonnes annually, and encouraged entry into the commercial fishery of fleets from many countries. Massive amounts of frozen squid are stored and moved about as part of the international trade in marine products. Among European countries, Portugal, Spain, Italy and Greece are traditionally high consumers of cephalopods in their diet. In most of northern Europe, the Americas and Africa, *per capita* cephalopod consumption is low, but the increasing demand for oriental cuisine among these large populations is maintaining world demand for the product.

Worldwide concern over the level of exploitation of all marine resources has increased the need for scientific knowledge for assessment and management purposes. Because many of the major commercial stocks of cephalopods are exploited in distant-water and international fisheries, attention to them has come late, but increasingly, fishery-related studies are contributing an important stream of knowledge on the basic biology of cephalopods.

The life-cycle characteristics of cephalopods mean that their fisheries are intrinsically difficult to assess and manage. Rapid growth and a short lifespan means that there is little overlap of generations in the population, and that most large-scale fisheries in temperate waters are catching animals recruited earlier in the same year. In these circumstances, catch availability depends heavily on the timing of breeding and the coincidence of the new recruits with suitable conditions for growth and survival. Predatory interactions with fish, and competition with them for resources, have raised speculation that some of the increase in cephalopod catches have resulted from the depletion of fish stocks by over-fishing. In addition to the perceived need for fisheries to exploit their target population at a level sustainable in the long term, there are strong reasons to question the possible effects of large-scale subtraction of cephalopods on the food supply of their natural predators.

Chapter 2

Form and function

Summary: The cephalopods share basic features of body organisation with other molluscs. Characteristically, the molluscan shell is lost or highly reduced to an internal remnant (except in *Nautilus*), which in the sepioids still provides a buoyancy organ. Cephalopods are active mobile predators, swimming by means of jet propulsion and fin undulations, or rapidly scrambling by strong suckered arms. All cephalopods are predators, capturing and holding live prey with arms and tentacles (squids and cuttlefish). The basic feeding apparatus is a pair of tough horny mandibles ('beaks') and a typical molluscan radula. Octopuses have elaborate prey-handling mechanisms which involve injection of their prey with a cocktail of toxins and enzymes. Urine is formed by ultrafiltration, and the excretory cells surround the lateral venae cavae and parts of the return venous circulation. Respiration occurs through a pair of well-vascularised gills suspended in the mantle cavity. Oxygenated blood is coloured blue due to the copper-containing respiratory pigment haemocyanin. In addition to the muscular systemic heart, contractile bulbs at the base of each gill (the branchial hearts) and contractile blood vessels contribute to a strong blood circulatory system. As in other molluscs, the central nervous system is arranged around the oesophagus. It is highly developed and concentrated into a brain in which there is considerable division of function. Sense organs, particularly the eyes and organs of balance (statocysts), are highly developed. With the exception of nautiluses, all cephalopods have pigmented cells in the skin that are capable of expansion by muscular action and elastic retraction. This system of pattern formation by chromatophores, coupled with luminescent organs in deep-water animals, the capability for expulsion of ink clouds, and their extreme ability to alter shape and texture contribute to making the cephalopods among the most scientifically exciting of marine animals to study.

The purpose of this chapter is to provide a short overview of the biology of the living cephalopods. It is intended as an introduction to the group, which should be sufficient to inform the reader about basic aspects of the cephalopod anatomy and biology. It does not attempt to treat the many specialised aspects of cephalopod biology in detail, some of which are developed in later chapters, but will give access to the different fields of the literature.

As members of the phylum Mollusca, the cephalopods share certain basic features of their body organisation, especially with the gastropods. Molluscs typically produce a hard calcareous shell to protect the body, but the shell originally present in ancestral cephalopods is greatly reduced or lost in the modern forms, as it is in certain other molluscan lines such as many marine gastropods and the terrestrial slugs. The radula, a ribbon of chitinous teeth, is one of the most characteristic molluscan features. Although lost in the bivalves, it functions in gastropods and chitons as a versatile feeding organ for rasping or scraping. It is also present in most cephalopods, although its role in feeding may be subsidiary to other structures. Standard texts (Barnes 1980; Russell-Hunter 1979; Willmer 1990; Brusca & Brusca 1990) and selective reviews (Solem 1974; Yonge & Thompson 1976; Wilbur 1983–1988; Boyle 1987b, 1999) will give access to the general features of molluscan organisation and the special points of comparison between cephalopods and other molluscs.

Cephalopods are generally large animals. While some species attain only very small adult body sizes, such as the members of the family Idiosepidae (mantle length (ML), may be <10 mm), or *Octopus micropyrsus*, which lives in the holdfasts of giant kelp on the California coast (ML 20–25 mm), others reach exceptionally large sizes, with the North Pacific *Octopus dofleini* commonly over 50 kg in weight. Squids such as *Dosidicus gigas* and *Moroteuthis robusta* reach a mantle lengths of <1 m, and the occasional stranded specimens of the giant squid (*Architeuthis* sp.) are reliably estimated to be over 450 kg or >2 m mantle length (Roper & Boss 1982; Ellis 1998). They are also active and mobile animals. Squids swim constantly by jet propulsion, and they can 'hover' in midwater using lateral fins. Many species of deep-water squid, however, adopt a passive lifestyle, using accumulated ammonium salts and reduced body musculature to achieve neutral buoyancy (see Chapter 12). The octopuses are generally bottom-dwelling, normally active and exploratory in behaviour, although there are some wholly pelagic families (see Appendix B). All cephalopods are voracious predators and with few exceptions will take only living prey. These characteristics of size, activity and predatory habits mark them out from most other molluscs.

Many aspects of cephalopod biology and physiology have been the subjects of laboratory research. Apart from the intrinsic interest of their systems for colour change, luminescence, buoyancy, digestion, growth, reproduction, sensory reception and movement, etc., physiological preparations from the giant axons of squid nerves have proved exceptionally valuable in the study of the biophysics of nerve function. Commercial fisheries are operating on a global scale, and over 3 million tonnes of cephalopods are caught annually. Pilot trials to assess the potential of these fast-growing animals for commercial mariculture have also taken place. Detailed knowledge of cephalopod biology is still restricted to a relatively few species and locations. Insights into their life in the wild are limited, but are rapidly being improved through the use of underwater video by divers and submersible vehicles. Generalisations about their biology are certainly possible, but these are based on a narrow range of coastal species because the majority of cephalopods are offshore and deep-water animals that are difficult to capture and almost impossible to maintain alive in captivity.

The diverse interests in the group, ranging from physiology and biochemistry to ecology and fisheries, have led to a series of review books, workshops and special issues of journals, a selection of which will guide further reading in the cephalopod literature (Messenger & Nixon 1977; Wells 1978; Roper *et al.* 1984; Caddy 1983a; Boyle 1983a, 1987a; Nesis 1987; Gilbert *et al.* 1990; Okutani *et al.* 1993; Pörtner & O'Dor 1994; Hanlon & Messenger 1996; Payne *et al.* 1998; Voss *et al.* 1998a; Boyle *et al.* 2002).

2.1 Cephalopod forms

Cephalopods as a molluscan class are first found as distinctive fossil shells in upper Cambrian deposits (ectocochleate forms, Chapter 3). Some of these shells were very large, with coiled forms reaching 2 m across and straight shells extending from 20 mm to as much as 9 m long (Lehmann 1981). Owing to the good preservation of shell material, over 10 000 species have been described from fossils, including nautiloids (subclass: Nautiloidea), ammonites (subclass: Ammonoidea) and belemnites (subclass: Coleoidea, division: Belemnoidea). These early types are represented today by a few remaining species of the nautiloids only, and all of the ammonoids and belemnoids are extinct.

Modern cephalopods (subclass Coleoidea: division Neocoleoidea), in which the shell remnant is greatly modified or absent completely, appeared relatively recently. The layout of the main organ systems of the living octopus, squid and cuttlefish follows a consistent plan, as shown in Figs. 2.1–2.3. The somewhat different layout of the nautilus is discussed in Chapter 4 (see Fig. 4.1).

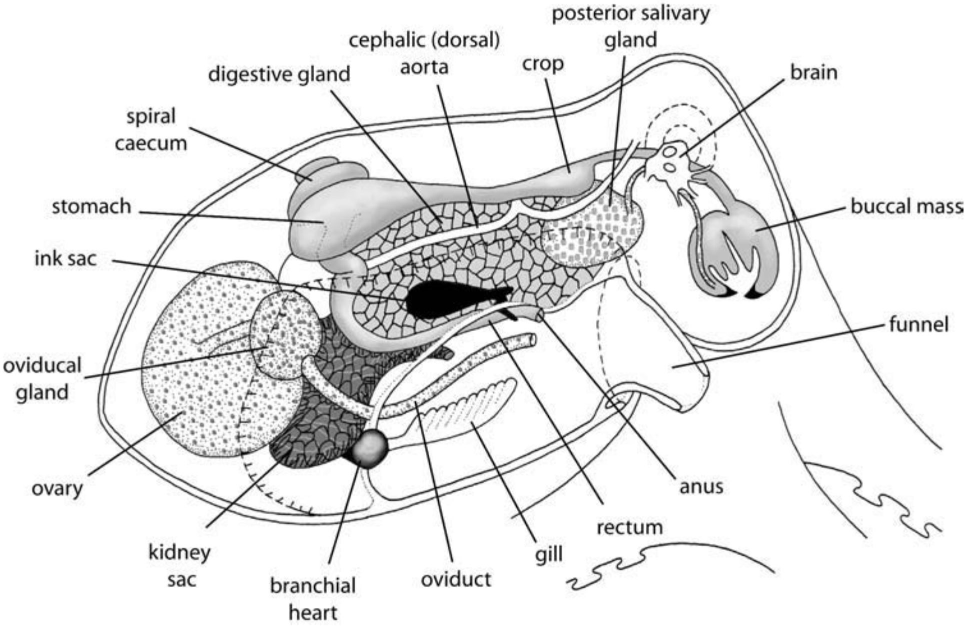

Fig. 2.1 Generalised anatomy of a female octopus (after Boyle 1999).

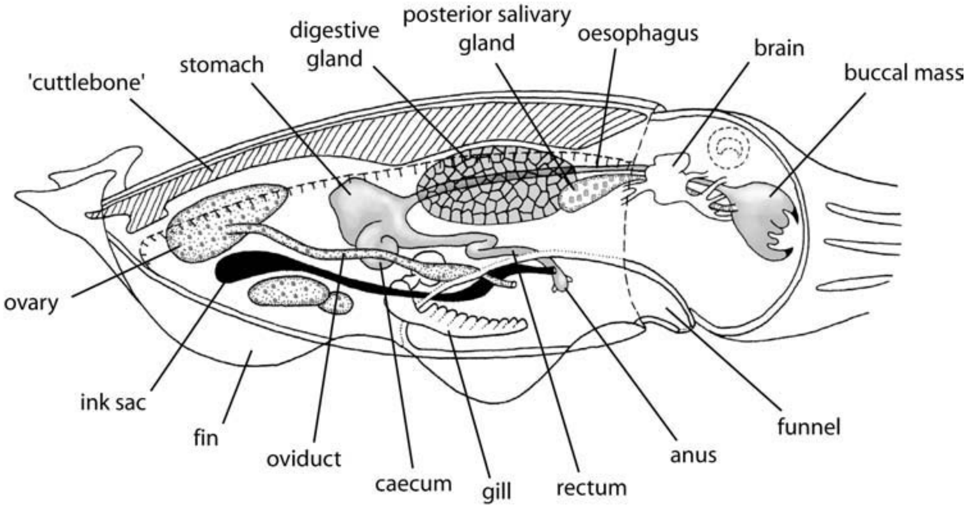

Fig. 2.2 Generalised anatomy of a cuttlefish (after Boyle 1999).

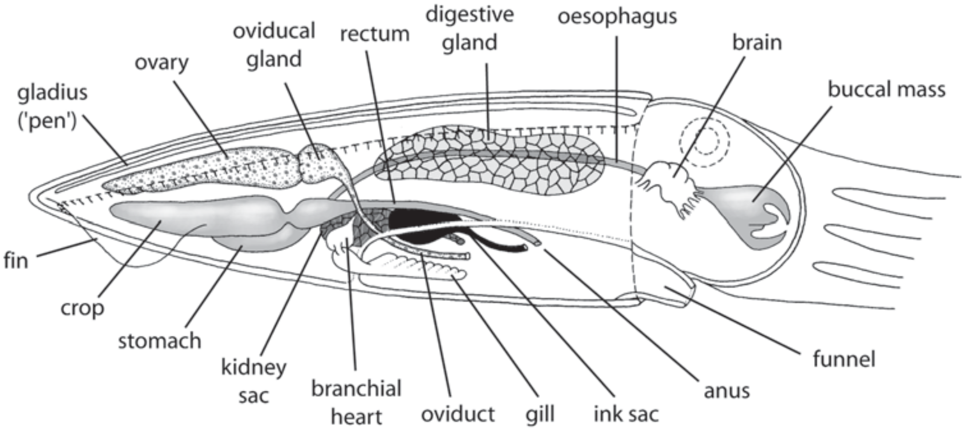

Fig. 2.3 Generalised anatomy of a loliginid squid (after Boyle 1999).

Approximately 650 species of living cephalopods are known, which is a small fraction of the total fossil fauna. The number of species recognised has not remained constant, and it is continually under revision from systematists as existing species are renamed, merged or divided and new species are discovered (Chapter 5). As with much of traditional zoology, the Latinised scientific names of many species are inconsistently spelt in the literature. Within this book we have tried to adopt consistent spellings that are in standard usage but variations on the original spelling will be found in literature. Many changes and updates to the classification and nomenclature are now to be found on authoritative websites. Sources such as the Integrated Taxonomic Information System (ITIS, www.itis.usda.gov); the Tree of Life (http://tolweb.org/tree) and Cephbase (www.cephbase.utmb.edu) will all provide useful portals to up to date systematic and biological information.

The number of species is rather unevenly distributed among genera and families. Voss (1977a) pointed out that two genera, *Octopus* and *Sepia*, were each credited with over one hundred species, whereas more than half of all described genera only support one named species. A few other coastal genera may have an appreciable number of species (e.g. *Loligo*), but the remainder are scattered throughout a large number of diverse families of mainly deep-sea distribution (see Appendix B). This has given rise to speculation that the original cephalopod fauna may have become restricted to the relatively unfavourable habitats of the deep sea (mesopelagic) through competition with the teleost fishes. Only when the lighter, faster, more active coleoid forms evolved were they able to re-invade the more productive coastal and upwelling marine zones. Many of the characteristics of common cephalopods can be interpreted in terms of competition and parallel evolution with fish (Packard 1972). Most of our knowledge of cephalopod biology has been gained from relatively few types that, although common and available, may not be particularly representative of the full range.

2.2 Jet propulsion

All cephalopods make use of a form of jet propulsion in addition to other forms of locomotion. This is achieved by the rapid expulsion of water from the mantle cavity, forcing the animal to move in the opposite direction through the water in a series of pulses.

In nautiluses only, jetting is achieved by the muscular retraction of the head into the terminal chamber of the shell, which displaces water through a fold in the edge of the mantle cavity (the hyponome, which is the functional equivalent of a funnel). In the coleoids, the mantle cavity is enclosed by a flexible muscular wall. There are several orientations of muscle fibres and connective tissue within the mantle musculature (Ward & Wainwright 1972; Shadwick 1994). The bulk of the muscle volume is orientated in a circular fashion around the mantle; thin longitudinal muscle layers aligned in the long axis lie at the inner and outer surfaces; and short radial fibres traverse the mantle thickness (Fig. 2.4).

Acting in a coordinated way, this complex muscular organ supplies the regular exhalent and inhalent ventilatory movements. The bulk of the circular muscle contributes the main exhalent phase of mantle ventilation, with simultaneous contraction of the longitudinal muscle sheets to resist elongation of the mantle. When the circular and longitudinal muscles relax, the inhalent phase takes place by elastic recoil of the connective tissue layers (Gosline & Shandwick 1983) and contraction of the radial fibres, which have the effect of thinning the mantle layer and increasing its area and consequently the volume contained (Gosline *et al.* 1983). Seawater is drawn into the mantle cavity around the sides of the head where the mantle is detached. When water is forcibly expelled, the relatively small cross-sectional area of the funnel gives the jet considerable force and propels the animal in the opposite direction. Estimates of the peak jet velocity achieved by cephalopods range between 2.9 and 6.9 m/s for octopus and cuttlefish, and between 6.7 and 11 m/s for squid (from a range of sources assembled by Shadwick 1994). The weight-specific peak thrust of the escape jet and the thrust per unit area of the circumferential muscle increases significantly with growth over the size range 5–40 mm mantle length in *Sepioteuthis lessoniana* (Thompson & Kier 2002). Several types of muscle fibre are described, which may be associated with fast and slow components of muscle movement (Bone *et al.* 1981; Kier 1991; Kier & Curtin 2002).

Pressure sensors implanted in the mantle of free-swimming *Loligo forbesi*, coupled with acoustic telemetered tracking of individuals, have shown that the energetic costs of jet propulsion in squid are several times greater than the equivalent swimming costs of fish (O'Dor *et al.* 1994). The funnel of the coleoids is also capable of being directed backwards as well as forwards and from side to side, giving considerable manouverability. Generally, the coastal octopuses and cuttlefish (*Sepia*) swim only when actively escaping or making hunting attacks. The coastal and many pelagic squids, however, are negatively buoyant in the water column and swim continually. Lateral fins in sepioids and squid have an important role in maintaining or controlling orientation during locomotion. Delicate undulatory movements of fins alone are also used for small movements or during hovering.

The relationship between the dominant mode of locomotion in squids and the geometry of body form is discussed by Wells (1994). The powerful, epipelagic jet swimmers

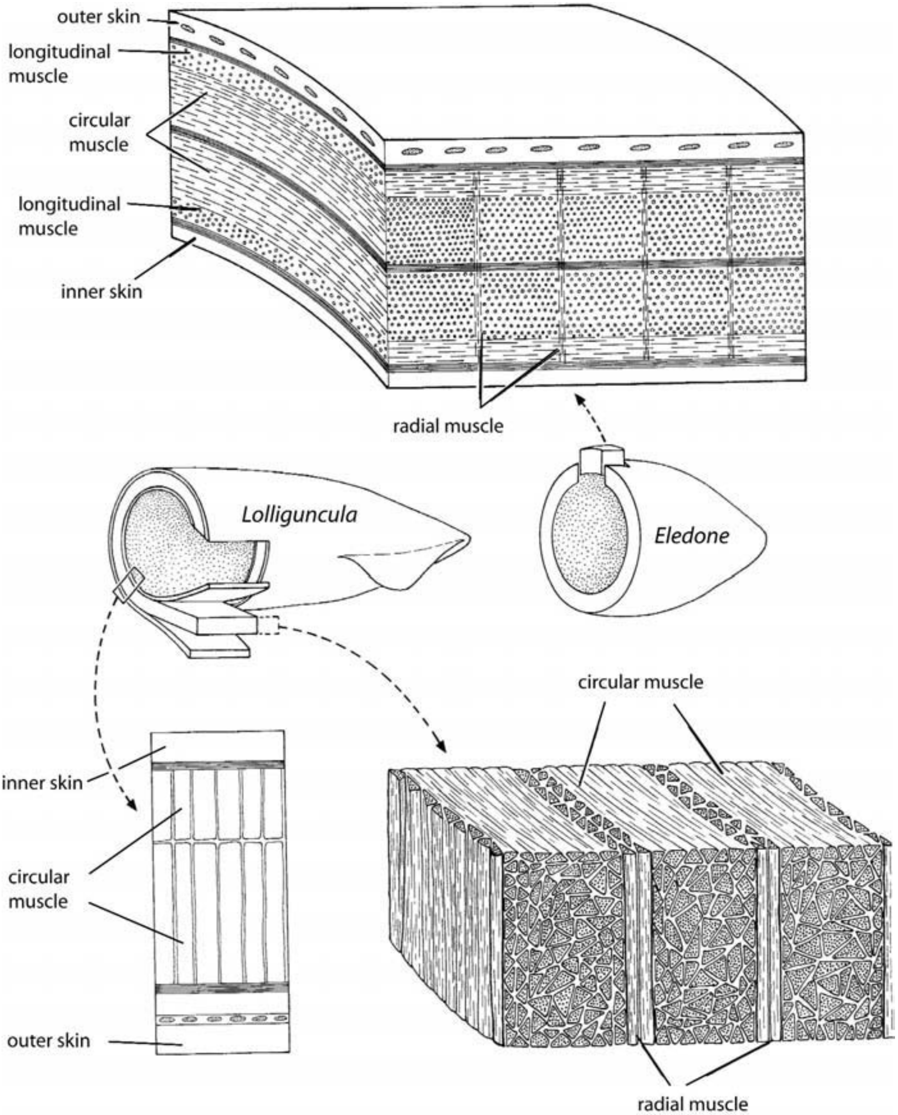

Fig. 2.4 The organisation of the muscle layers in the mantle of an octopus (*Eledone cirrhosa*) and a squid (*Lolliguncula brevis*). In octopus, the circular muscle is divided into two layers by connective tissue, and the nervous and blood supply to the muscle layers. This is sandwiched between thin outer and inner layers of longitudinal muscle bounded by a tunic of connective tissue. The muscle layers in squid are simpler, but the connective tissue is known to have a complex fibre orientation. In both species, radial muscle bands traverse the muscle thickness, inserting on the inner and outer tunics of connective tissue (after Boyle 1986b; Ward & Wainwright 1972).

such as *Ommastrephes* and *Todarodes* have short triangular fins, principally for stabilisation and manoeuvering; the coastal loliginids make greater use of slower, but more efficient fin swimming with their long undulant fins; and the many squid which have adopted ammoniacal neutral buoyancy have a much greater variety of less streamlined body form and fin shape (Fig. 2.5).

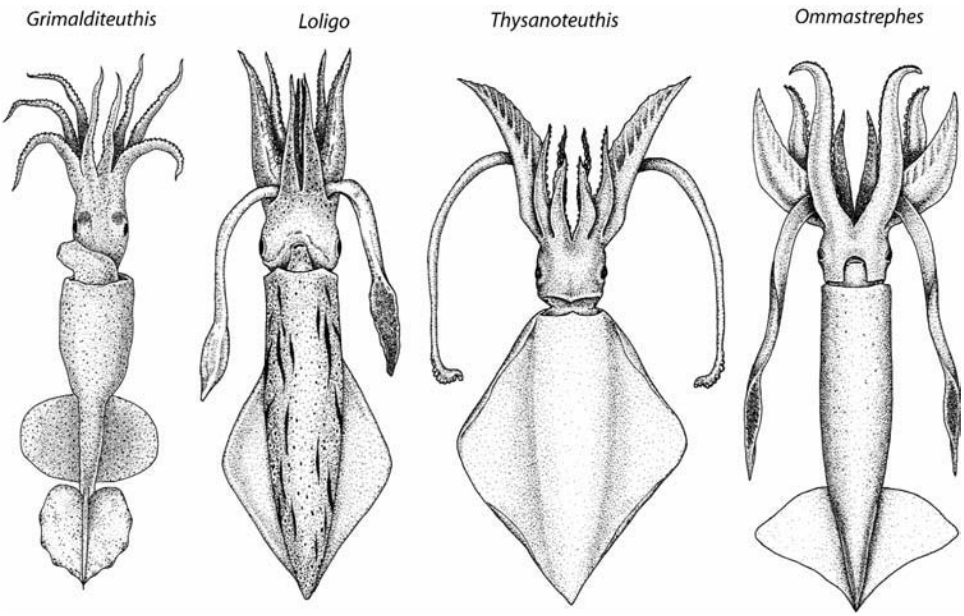

Fig. 2.5 Trends in squid shape and locomotion, showing comparisons between weak neutrally buoyant ammoniacal forms (*Grimalditeuthis*), active (*Loligo*) or sluggish (*Thysanoteuthis*) fin swimmers, and active jet swimmers (*Ommastrephes*). After Wells (1994).

The normal locomotion of the coastal octopuses is a fast relaxed scrambling over the bottom, or slower, exploratory walking using the arms and suckers. Muscle orientations in the arms (Kier 1982) and tentacles (Kier & Van Leeuwen 1997) of squid are complicated. The arrangement of antagonistic muscles acting on the hydrostatic spaces provided by the vascular system permit an unparalleled range and delicacy of movement. The suckers, which are arranged along the full length of each arm as a single (e.g. *Eledone*) or double (e.g. *Octopus*) row, can exert a powerful holding force on substrate or prey (up to 100 times body weight, Trueman & Packard 1968). The strength and speed with which arms and suckers can be used make the octopus both a powerful predator and a potentially difficult animal to catch and handle. Octopuses will also jet, especially when threatened.

2.3 Shell and buoyancy

The coiled shell of the nautilus is divided into a series of chambers by calcareous septa, or partitions. Sections of the fossil ammonites and nautiloids also show an internal series of partitions, and it is presumed that the role of the shell in living nautiluses is similar to that in the fossil groups. The shell is heavily calcified and protects the animal from predatory attacks by large fish. Evidence from broken and repaired shells, in both modern nautiloids (Ward 1987; Saunders *et al.* 1987) and fossil ammonites (Lehmann 1981), suggests that this was an important role for the shell, albeit not always completely effective.

The body of the nautilus occupies only the so-called living chamber of the shell, the largest and last to be formed. With growth, the shell enlarges at the free edges and internal partitions form successively. The space enclosed by the internal partitions of the shell is mainly gas space with some fluid (Box 2.1). The gas is a mixture closely

Box 2.1 Buoyancy control by gas spaces

In a series of classic studies in the 1960s, Eric Denton and colleagues at the Marine Biological Association of the UK in Plymouth discovered the basis of buoyancy control by variable gas-filled spaces in cephalopods (Denton 1974).

There are three living cephalopod types which use structures derived from the shell to contain a variable gas volume to counteract the weight of the animal in water and maintain neutral buoyancy. In *Nautilus* (Fig. A23), spaces enclosed by the inner chambers (camerae) of the strong external shell are partially gas-filled. A thin strand of living tissue from the animal compartment, the siphuncle, connects the chambers together by threading through the dividing septae (see Figs. 4.1 and 4.2). This well-vascularised tissue allows exchange to take place between the blood circulation and the cameral liquid.

The enclosed chambered shells of the pelagic *Spirula* (Fig. A37), although unrelated, are superficially similar to the *Nautilus* shell, with the chambers connected by a strand of living tissue. *Sepia* (Fig. A35), however, has the shell chambers realigned to form a flattened, laminated structure, the cuttlebone. Spaces between the laminae, supported by light calcareous struts, are partially gas-filled. In this case, the contained fluid lies against a siphuncular membrane covering the open ends of all the chambers.

In the shell spaces of each of these genera, the contained gas is a nitrogen-rich mixture derived from air, and has an average pressure of about 0.7 atmospheres. At any depth below the surface, the strength of the enclosing shell resists the hydrostatic pressure of the water column and maintains the volume of the gas space, without a significant change in pressure, down to a depth limit at which the shell fails (implosion).

Control of the volume of the gas space is achieved by pumping salts out of the cameral fluid across the siphuncular surfaces, establishing an osmotic pressure across the membrane that opposes the hydrostatic pressure tending to force water into the shell space. Fine control of the volume of the contained gas is achieved using osmotic forces, but this mechanism is unlikely to be used for significant vertical migrations. It can also be calculated that osmotic forces alone would be insufficient to maintain the gas space of these animals below about 200 m.

Squids which normally live in the water column at depths below about 500 m retain the lighter ammonium salts as a means of neutral buoyancy (see text).

related to the composition of air and contained at a pressure of around 0.7–0.9 atmospheres (Denton 1974). This gas space is normally sufficient to reduce the average density of the nautilus to that of the surrounding seawater (specific gravity 1.025–1.029). In other words, the positive buoyancy contributed by the gas space just balances the sinking tendency of the animal's tissues and the heavy shell. Since the rigid shell resists the hydrostatic pressure of the surrounding water, the pressure and volume of the contained gas space is independent of depth. Nautiluses can remain neutrally buoyant throughout their depth range without making significant changes to the mass of the contained gas. A strand of living tissue, the siphuncle, connects the body of the animal to the fluid columm contained in the chambers and allows minor adjustments of the gas space to be made by alterations in the osmotic differential between the body fluids and the chamber fluid (Denton & Gilpin-Brown 1966). The physiology of the cephalopod buoyancy system differs profoundly from that of the teleost fish (Denton & Gilpin-Brown 1971, 1973; Denton 1974).

All of the modern cephalopods (Neocoleoidea) have transformed the external shell into an internal structure without its original protective functions. Instead they rely on their abilities to alter the pattern and texture of the skin to disguise themselves to an extraordinary degree, and on rapid locomotion for escape. In sepioids, such as the cuttlefish *Sepia* and the open-ocean spirulid *Spirula*, the internal chambered shell also functions as a buoyancy device allowing *Sepia* to hover motionless before darting forward to strike a prey organism.

The squids have no gas-filled spaces, and most of the surface-living 'muscular' forms need to swim continually. The shell is reduced further to a chitinous rod, the pen or gladius, lying dorsally in the mantle, which gives rigidity during the convulsive contraction phase of jet swimming. A number of deepwater forms achieve neutral buoyancy by a reduction in the protein content of their tissues and an accumulation of a low-density solution of ammonium chloride either within the coelomic space or in vacuoles within the musculature and connective tissue (Voight *et al.* 1994, Chapter 12). Octopuses have a remnant of the shell represented by chitinous stylets located in the mantle on either side. These occur where the head retractor muscles insert into the mantle musculature and where they form an anchorage point for the muscles.

2.4 Feeding and digestion

All cephalopods actively catch and eat live prey, and a very wide range of prey items has been recorded (for reviews see Boletzky & Hanlon 1983; Nixon 1987; Rodhouse & Nigmatullin 1996). Generally, the cuttlefish and octopus take crustaceans living on or near the bottom, while squid eat mostly crustaceans and fish. In these shallow-water forms, hunting is essentially visual (Messenger 1968, 1977b; Hanlon & Messenger 1996). The cephalopod manoeuvres into a position from which it can strike at the prey by rapid extension of the paired tentacles coupled with a jet-propelled forward lunge (Kier & Van Leeuwen 1997). These tentacles are generally suckered only at the tips (tentacular clubs), unlike the eight arms which are suckered along their full length. Once trapped, the prey is drawn in towards the mouth and bitten into by the chitinous beaks (mandibles). Bite-sized pieces of flesh are swallowed. Squid feeding in a shoal of fish will often only take one or a few bites before releasing one and catching another (Bradbury & Aldrich 1969).

Octopus and cuttlefish feed on a greater variety of prey species, and their diet is probably determined as much by prey availability as predator preference (Ambrose 1983, 1984). Large crustaceans such as lobsters and crabs are taken, and octopuses may be significant predators on commercial crustacean fisheries (Boyle *et al.* 1986). Molluscs, worms, fish and other groups are also frequent in the normal diet but are not commonly taken in aquarium studies. Octopus prey is located visually (Wells 1978), but chemical cues also probably have a role (Boyle 1986a; Chase & Wells 1986). Studies on the diet of cephalopods rely on a variety of sources of evidence. Conventional gut contents analysis is often not very productive because so much of the food is reduced to small particles at ingestion and is unrecognisable in the gut, but the use of serological analysis, using antisera raised to target prey species, has been used to test specific questions on diet (Kear 1992; Kear & Boyle 1992). There is a significant parasite fauna of the digestive tract of most cephalopods (Hochberg 1983) that gives insights into the relationships between the cephalopod and its diet (Pascual *et al.* 1996; Abollo *et al.* 1998; Brickle *et al.* 2001).

After capture by an octopus, crustacean and molluscan prey are dealt with in a lengthy and complicated way. Characteristically, flesh is removed from the exoskeleton or shell very cleanly (Wodinsky 1969; Arnold & Arnold 1969; Altman & Nixon 1970; Boyle & Knobloch 1981). This could partly be due to delicate movements of the beaks, radula and suckers, but it is generally accepted that octopuses also use secretions from the posterior salivary glands to immobilise the prey and to loosen tissues by extracellular enzymic digestion (Boyle 1990a; Grisley *et al.* 1996; Fiorito & Gherardi 1999). The saliva from the posterior salivary glands of octopuses contains a cocktail of bioactive compounds including: digestive proteases and chitinases (Grisley & Boyle 1990; Grisley 1993; Fiorito & Gherardi 1999); a tetrodotoxin-like toxin from the blue-ringed octopus from Australia, *Hapalochlaena maculosa* (Dulhunty & Gage 1971; Sutherland & Lane 1969); a compound which may be produced by bacterial symbionts (Hwang *et al.* 1989); and compounds with powerful haemolytic effects on vertebrate red blood cells (Key *et al.* 2002) (Box 2.2).

After ingestion, the already fragmented meal enters a rather short digestive tract consisting of a crop, stomach, caecum and intestine. Some digestion takes place within the lumen of the gut, but most digestion and absorption take place in the digestive gland (Boucher-Rodoni *et al.* 1987). This complex organ may also have a significant role in detoxification of heavy metal accumulations (Bustamante *et al.* 1998, 2002a, b). There is complex control of the passage of food through the gut (Semmens 1998, 2002; Best & Wells 1983, 1984). The entry of food particles into the digestive gland and the egress of excretory material into the gut lumen takes place through a pair of short ducts connecting the digestive gland to the junction of the stomach and caecum. Digestive excretion occurs by the release of pigmented material from digestive gland cells into the lumen of the gut. Long strings of pigmented faeces bound by mucus (the residues of the digestive process, usually pink–brown depending on diet composition) are released from the anus into the exhalent water flow from the mantle into the funnel. The active

Box 2.2 Toxins and prey handling

The octopuses have evolved a suite of elaborate prey-handling methods which enable them to cope with a wide variety of active prey species, mainly crustaceans such as crabs and lobsters, as well as molluscs, fish and worms.

Hunting with a combination of stealthy approach, exploration of likely habitats, and a concluding 'rush and grab', the prey is quickly overpowered and held in the arms. The exact sequence of the following events is unclear, but several organs are involved. These are mainly the *beak* (mandibles) and *radula*, a ribbon of chitinous teeth, the muscular *salivary papilla* which bears tiny teeth at its tip and may be protruded out of the mouth, and the paired posterior salivary glands which are the source of a cocktail of enzymes (proteases and chitinases) and other secretions injected into the prey via the salivary papilla.

In the penetration of a crab shell (Fig. 2.2.1) by the octopus *Eledone cirrhosa*, the prey is penetrated by a small hole, often on the carapace or in the eye, through which the salivary secretion is injected.

To collect pure saliva for study, the octopus is placed in a polythene bag (Fig. 2.2.2), the beak and radula bite through the bag (Fig. 2.2.3), the salivary papilla protrudes and the saliva is expressed (Fig. 2.2.4).

The prey is paralysed and the enzymes act rather specifically to release the prey tissues from the carapace. The carapace is disarticulated, and the meal extracted and chopped up by the beak and radula, and ingested.

The octopus reduces the risk of damage from large prey by immobilising them, and increases the efficiency of feeding and gain from the food by ingesting only a high-quality diet.

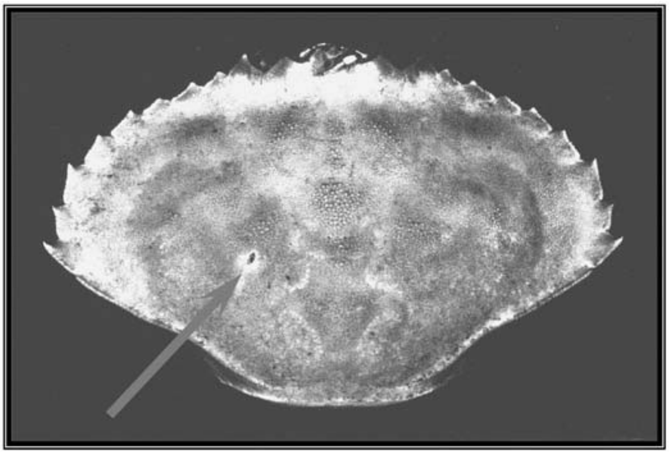

Fig. 2.2.1

Fig. 2.2.2

Fig. 2.2.3

Fig. 2.2.4

coastal cephalopods appear to make little use of dietary lipids for energy storage (Moltschaniwskyj & Semmens 2000), and the large digestive gland, at least in some loliginid squid, is excretory rather than for storing excess dietary lipid (Semmens 1998).

2.5 Excretion

The principal end-product of nitrogen metabolism in cephalopods is ammonia (NH_4^+), which is excreted in solution by several routes. Excretion from the blood system takes place through a well-differentiated renal system surrounding the venous return to the heart. Primary urine is formed by ultrafiltration from the blood in the branchial hearts into the branchial heart appendages, and via excretory tissue surrounding the lateral venae cavae (Schipp & Boletzky 1975). The main venous return from the anterior part of the body, the anterior vena cava, divides into two lateral venae cavae before entering the branchial heart on each side (Fig. 2.6). The excretory cells (kidney tissues) are grouped into flocculent masses (renal appendages) sited on fine diverticulae of the lateral venae cavae. The urine is formed, probably partly by ultrafiltration and secretion, into a coelomic pericardial space, where some resorption also takes place by the renal

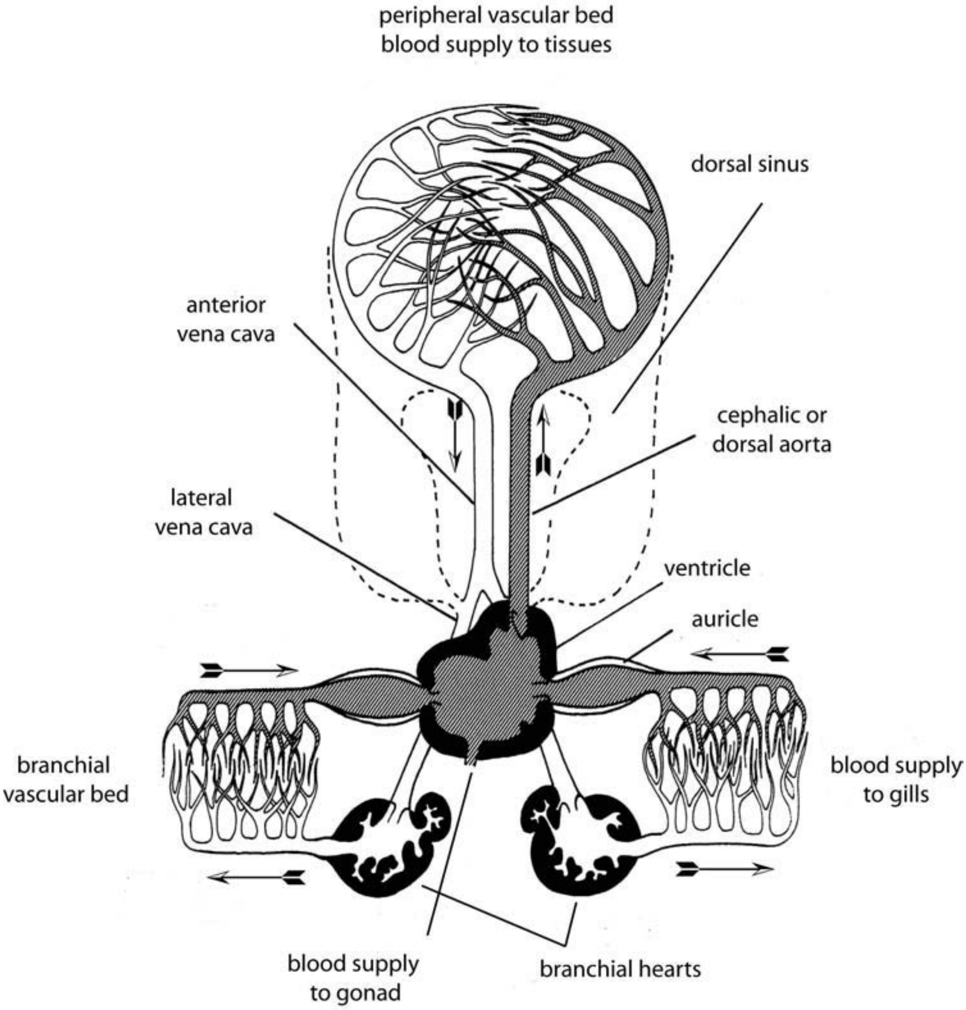

Fig. 2.6 Generalised cephalopod circulatory system (after Smith & Boyle 1983). The main contractile elements are the ventricle and auricle of the systemic heart, the branchial hearts supplying the gills, and their associated contractile afferent and efferent branchial vessels. The arrows show direction of flow in the main vessels.

appendages. From there it drains through a short duct and renal papilla and is released into the mantle cavity. Extrarenal excretion of ammonia via the epithelium of the gills directly to the seawater is significant, and octopuses can survive for significant periods by excretion across the gills only (Boucher-Rodoni & Mangold 1988, 1989, 1994).

A remarkable feature of the kidneys of cephalopods is their infestation by minute organisms, the dicyemid mesozoans, living among the lobes of renal tissue (Hochberg 1982; Furuya *et al.* 2002). The relationship is apparently symbiotic, causing no harmful effect to the host and providing the only known habitat for the mesozoans, and seems to be present throughout the class even in deep-sea habitats (Furuya & Hochberg 2002).

2.6 Respiration and circulation

Respiratory exchange with the environment occurs through well-vascularised gills suspended in the mantle cavity. In nautiluses there are two pairs of gills (tetrabranchiate), but in all the coleoids there is only a single pair (dibranchiate). Due to the orientation of gills within the lumen of the cavity, water flows between the lamellae of each gill in the opposite direction to the flow of blood through the tissue, a counter-current system that maximises the exchange of gases (Wells & Wells 1982).

Measurements of metabolic rates of cephalopods vary widely. This is partly because of the wide range of species and temperatures which are compared, and because of the inherent difficulty of obtaining a non-active or routine value for oxygen consumption in these animals. Figures collected from many sources suggest routine oxygen consumptions mostly in the range 100–500 ml $O_2/kg^{-1}h^{-1}$ for squid and 10–100 ml $O_2/kg^{-1}h^{-1}$ for octopuses (O'Dor & Wells 1987; Wells & Clarke 1996). The smaller number of estimates for cuttlefish and nautilus fall within the octopus range. Two factors substantially increase the metabolic rate. Swimming or other violent movements rapidly increase metabolic rate to 2–3 times the resting value, as does the energy demand of digestion in the 6–8 h following a meal.

Oxygenated cephalopod blood is a blue colour due to the presence of the copper-containing respiratory pigment haemocyanin in solution in the blood. This is a complex high molecular weight compound (whole molecule $3.5–4.0 \times 10^6$ daltons, and sub-unit molecular weight 340–400 K daltons) composed of individual functional units of 50 000 daltons (Miller 1994). The gas-binding of haemocyanin is less efficient than that of vertebrate haemoglobin which is contained within specialised blood cells (erythrocytes). Despite this, cephalopods exhibit the highest rates of aerobic metabolism among marine invertebrates, and there is a substantial body of knowledge on the performance of their haemocyanins (Bridges 1994; Pörtner 1994). Brix *et al.* (1994) divide the cephalopods into three broad groups of species based on the oxygen affinity of their blood (P_{50} value, i.e. partial pressure of gas at which the blood remains 50% saturated): the octopuses and some sluggish squid (P_{50} 10–20 mm Hg); fast-swimming squid ($P_{50} \approx 30$ mm Hg); and *Sepia* ($P_{50} > 30$ mm Hg). The relative ease with which oxygen unloading takes place is clearly an adaptive feature with wide ecological implications (Pörtner & Zielinski 1998; Pörtner 2002; Zielinski *et al.* 2000).

The circulatory system is a complex arrangement of vessels (arteries, veins and sinuses) through which the blood is driven by several contractile elements (Fig. 2.6). Venous return blood mostly collects into the anterior vena cava. This divides into two lateral venae cavae (surrounded by kidney tissue) supplying blood to either side of the contractile branchial heart, which supplies blood to the gills. The lateral venae cavae and the gills themselves are also contractile and probably contribute as much to movement of the blood as do the branchial hearts (Smith & Boyle 1983). From the gills, oxygenated blood enters each side of the auricle and into the heart (systemic heart). This powerful contractile organ is capable of high systolic pressures (Agnisola & Houlihan 1994). It pumps blood out to the tissues mainly through the cephalic aorta, but with lesser flows through the abdominal and genital arteries.

2.7 Nutrition and energy

Cephalopod growth rates, in captivity and in the field, are high. Figures for aquarium growth of many cephalopod species (mostly octopuses) have been collected (see Chapter 7). At small sizes (<10 g), instantaneous growth rates (percentage increase in body weight per day) are around 4–6% ranging up to a maximum of 12% (*Sepia subaculeata*). At body weights up to 100 g, growth rates are lower, but commonly in the range 2–4%. In part, these growth rates result from high gross growth efficiency, i.e. the conversion of food intake to growth. Many authors record growth efficiency values for octopuses in the range 40–60%, with extremes of 20–80% on a wet-weight basis.

Information on the nutritional and energy requirements for cephalopods (Lee 1994; Wells & Clarke 1996) establish that they depend mainly on protein intake as their principal energy source and to provide the basic requirements for somatic growth and reproduction (see Chapter 8).

Studies of growth and lifespan suggest that cephalopods of all types (except nautilus) are surprisingly short-lived. Direct evidence is often lacking, but the consensus opinion is that 1–2 years is the average lifespan for most of the medium-sized coastal species. In terms of food requirements, O'Dor & Wells (1987) calculate that octopods probably consume 2.5–3 times their body weight over a lifetime. Squid, in contrast, are calculated to need as much as four times their body weight during the first 9 months (O'Dor *et al.* 1980). Their consumption is inevitably higher owing to the energy demands of a more active lifestyle, and leads to interesting speculations about the fueling by cannibalism of the long migrations undertaken by many shoaling squid species (O'Dor 1998a).

2.8 Nervous system

The central nervous system of all cephalopods is a more or less compact mass of nerve cells forming the brain, linked to a series of peripheral ganglia. The brain is located between the eyes and is enclosed in a tough cartilaginous cranium. For *Octopus* it has been estimated by J.Z. Young (1967) that there are about $1–2 \times 10^8$ nerve cells in the brain and a further 8×10^6 peripheral receptor cells (excluding the eyes). A great deal of information is available on the neuro-anatomy of the system and the division of function between the many lobes (e.g. J.Z. Young 1971; Wells 1978; Hanlon & Messenger 1996; Shigeno *et al.* 2001a–d; Shigeno & Yamamoto 2002; Nixon & Young 2003).

In general terms, the sub-oesophageal areas of the brain are concerned with the control of groups of muscles. There are clear divisions of function between various lobes, and each of these areas can be identified as lower or intermediate motor centres. Groups of muscles known to be controlled from centres in the sub-oesophageal brain include those of the arms, mantle, head, funnel, fins and chromatophores. These divisions of function were originally established largely by experiments involving electrical stimulation of selected areas (Boycott 1961) coupled with the effects of nerve sections and degeneration (Young 1971). Higher motor centres, which coordinate the actions

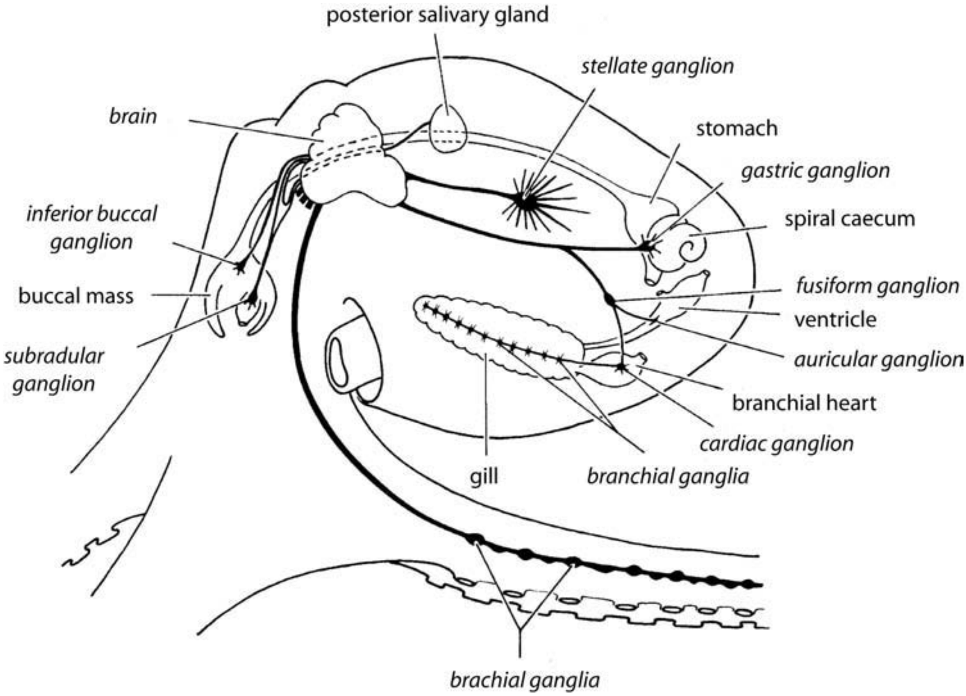

Fig. 2.7 Schematic layout of the brain and main ganglionic elements of the nervous system (labelled in italics) of octopus (after Boyle 1986b).

of several groups of muscles, are located in lateral and supra-oesophageal areas of the brain. Some regions are allocated to receptor information and analysis. Most notable of these are the optic lobes, which are large ganglionic masses located laterally on each side of the brain and receiving large numbers of small optic nerves. Many of the features of the neural organisation of cephalopods, and their anatomical and behavioural characteristics, bear comparison with those of the vertebrates (Young 1967, 1971; Packard 1972; Hanlon & Messenger 1996).

In addition to the brain, there is a series of peripheral ganglionic masses. These are very extensive and contain enormous numbers of nerve cells with functions which are restricted to the organ systems where they are located. For example, in *Octopus* there are an estimated 3×10^8 in the nerve cords of the arms alone. The main nerve cell groups (ganglia) in a typical octopod are shown in Fig. 2.7. It is important to note that this degree of peripheral nervous organisation confers some degree of local autonomy of movement. Thus, movements of the arms, mantle, buccal mass and chromatophores take place in isolation from the central nervous system, and this activity can continue for many hours after the death of the animal.

Of great interest to physiologists has been the giant fibre system of the squid. The nervous supply to the mantle musculature has the motor nerve cell bodies located in the stellate ganglion on each side (located on the inner surface of the mantle and connected to the brain by the pallial nerve). Fusing of the axons of the motor cells produces fibres with exceptionally large diameters of up to almost 1 mm (Young 1938; Martin 1977). In common with other invertebrates, the nerve fibres of cephalopods lack a myelinated sheath but, since in these animals the conduction velocity of nerve impulses along the nerve is proportional to its surface area, the giant fibres are capable of speeds of transmission comparable to those of the lower vertebrates. The exceptional size of these fibres made them attractive physiological preparations on which the earliest studies of transmembrane electrical potentials and the ionic properties of the axoplasm were made, leading to many important advances in understanding the basic properties of nervous transmission (e.g. Tasaki 1982).

In life, the giant fibre system of the squid and cuttlefish mediate the rapid escape-jetting response of the animal through a simplified nervous transmission sequence through three sets of fibres (Fig. 2.8). Arising in the magnocellular lobe of the brain, a single first-order cell on each side (approx 150 μm × 750 μm) gives rise to a short thick fibre that crosses over to the other side of the brain. At the crossover point (chiasma) the two fibres fuse (*Loligo peallei*) to ensure exact electrical synchrony. In the palliovisceral lobe of the contralateral side, each of these fibres makes an axo-axonic synapse with fibres of seven second-order giants which innervate the funnel and head retractor muscles and the stellate ganglion (via the pallial nerve), and from there to the mantle musculature (third-order giant fibres).

The significance of this system to the behaviour of squid is threefold:

- it is a simple direct method of triggering a supremely important evasive reaction;
- the increased rate of conduction of the giant fibres gives an appreciable gain in the speed of the behavioural reaction;
- gradation of the fibre diameter of the third-order giants allows differential rates of conduction to the full length of the mantle muscle and ensures its synchronous contraction. The giant fibre commonly referred to is the third-order giant axon which runs the full length of the mantle and is consequently of the greatest diameter. Commonly regarded as an inflexible all-or-nothing response mechanism, there is evidence that in some *Loligo opalescens* the response may be modulated by feeding experience (Preuss & Gilly 2000).

The complex structure of the large brain of all cephalopods is associated with the range and variety of their behaviour patterns, the requirements for nervous control of the flexible muscular body, and the processing of information from sense organs of advanced capabilities. The brain of the octopus has been the subject of a great deal of study. Octopuses, squid and cuttlefish readily attend to moving objects in their visual field. If the object is not too large, the cephalopod will advance and position itself for an attack; objects which are large, or otherwise threatening, will stimulate retreat or defensive displays. This attack–retreat axis of innate behaviour has been exploited in *O. vulgaris* to investigate their capabilities of sensory discrimination and capacity to learn by using pairs of stimuli associated with reward or punishment. The overall objectives of the work were:

- to discover the features by which similar stimuli might be discriminated and to evolve a general theory of pattern recognition;
- to reveal the characteristics of learning in *Octopus* in order to generalise about the nature of memory;

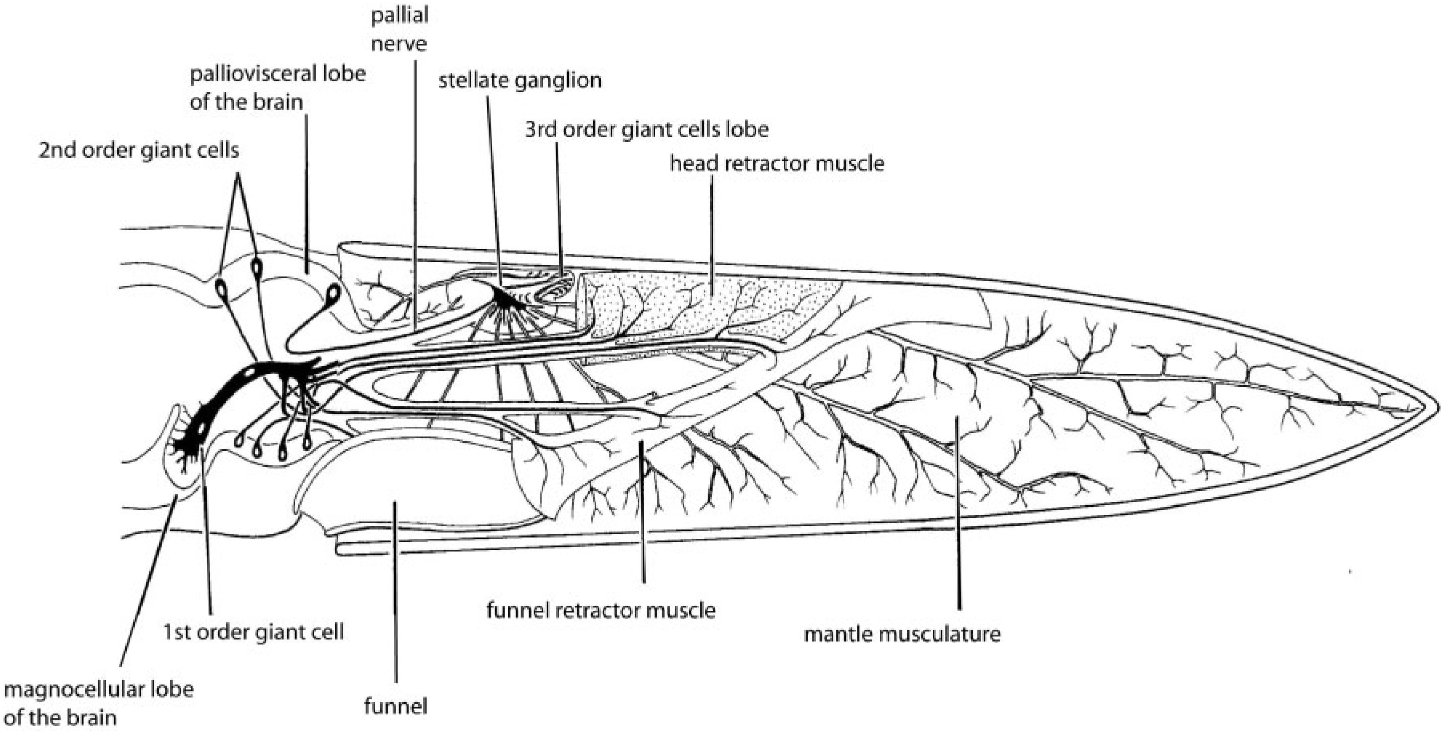

Fig. 2.8 Layout of the giant fibre system of a loliginid squid (after Boyle 1986b after various sources).

- to investigate the physical structure of the brain with respect to the localisation of specific functions and the organisation of the memory system.

In addition to an unparalleled level of detailed neuro-anatomical work on the *Octopus* brain and analysis of its conditioned responses to mostly visual stimuli (mainly by J.Z. Young and his co-workers, see Young 1971, 1991; Nixon & Young 2003), parallels drawn with vertebrate capabilities stimulated an important field of comparative analysis and neuro-ethology (e.g. Young 1964, 1978). The conclusion drawn from this body of work for the marine ecologist and student of behaviour is that for octopuses at least, a great deal of the behaviour of individual animals is conditioned by the past experience of that individual. This relatively large component of individually learned responses increases the variety of behaviour patterns in the field and must improve the success of the individual in its key activities of feeding and breeding. Most of our analytical understanding of cephalopod behaviour is derived from the artificial circumstances of the laboratory, and may be open to criticism of the techniques employed (Bitterman 1975). Observations from SCUBA diving in shallow water, and the increased availability of underwater video and manned and unmanned underwater vehicles, is now rapidly accumulating field knowledge at the descriptive level (e.g. Moynihan & Rodaniche 1982; Hanlon & Messenger 1988, 1996; Hanlon *et al.* 1994, 1999a, 1999b; Norman 2000; Hall & Hanlon 2002).

2.9 Sense organs

2.9.1 Chemotactile senses and olfaction

Molluscs generally have dispersed senses of touch and chemical sensitivity. The skin of cephalopods, particularly of the suckers and lips, is richly supplied with receptor cells responsive to tactile and chemical stimuli. Octopuses are responsive to a very light touch on almost any part of the surface, and may be taught to discriminate between objects which differ only in the quality of surface texture (Wells 1978).

Chemical senses are also associated with dispersed single-cell chemotactile receptors on the skin surface. In laboratory conditions, octopuses can discriminate between objects touched by the arms on the basis of chemical differences (Wells 1963; Wells *et al.* 1965; Chase & Wells 1986). Octopus and squid have localised pockets of ciliated cells on either side of the head which have been designated as olfactory organs (Woodhams & Messenger 1974; Emery 1975, 1976), and on histological evidence, areas of the brain are recognised as olfactory lobes (Messenger 1979). Chemical stimulation of the olfactory organ in *Loligo* elicits behavioural responses (Gilly & Lucero 1992) as well as electrical responses in the receptor cells (Lucero *et al.* 1992). A structurally equivalent sac of ciliated cells of presumed olfactory function, the rhinophore, is situated below the eye of *Nautilus* (Barber 1987). Responses to water-borne chemical stimuli have been described (Boyle 1983c, 1986a), and there is a general presumption that for the benthic octopuses and cuttlefish at least, chemoreception has a significant role in food-finding behaviour. Evidence for the role of chemical signals in reproduction is available for *Nautilus* to show that male odour release attracts females (Basil *et al.* 2002), and that pheromonal release from *Sepia* eggs has a role in attracting females to the spawning site and male sperm for egg fertilisation (Zatylny *et al.* 2002).

2.9.2 Eyes and vision

In contrast to other molluscs, cephalopods have highly developed, image-forming eyes. Visual input is of paramount importance to the behaviour of cephalopods living in lit regions of the sea, and possibly also to those in the dark regions where the significance of bioluminescent light has yet to be fully evaluated. Cephalopods have a pair of large camera-type eyes placed laterally (exceptionally dorsally) on either side of the head. In the living coleoids there is a highly refractile spherical lens which focuses light onto a retina of receptive cells (the nautilus operates on the different principle of the pinhole camera). All accounts of cephalopod behaviour, and experimental studies on prey capture (for a review see Hanlon & Messenger 1996), confirm the importance of the visual environment to cephalopods for orientation, prey capture, avoidance of predators, competition for mates etc.

Visual acuity is high (Packard 1969) but, after a history of uncertainty, octopuses have been shown to be colour-blind (Messenger 1979). This is a surprising finding among animals that appear to have evolved the most sophisticated system of colour control and pattern formation known. The evidence in support of this overall conclusion was summarised by Hanlon & Messenger (1996):

- the retina of most cephalopods has only one visual pigment with a single peak of spectral sensitivity (the Firefly squid, *Watasenia scintillans*, is exceptional with three visual pigments);
- the retina is not structured with multiple banks of photoreceptors which potentially could give colour vision by differential absorption of light;
- no change in the electrical response of the retina is produced by using light stimuli of different wavelengths;
- optomotor responses (tracking by the eyes of a moving visual stimulus) in octopus and cuttlefish are not stimulated by moving stripes of different colour hues when the stripes are matched for overall brightness;
- *Octopus* cannot be trained to discriminate between experimental cues differing only in colour.

The overall anatomy of the octopus eye is superficially similar to that of the vertebrate and there are many convergent optical properties (Jagger & Sands 1999), but fundamental differences in the layout of the retina are due to the way the eyes arise embryologically (Fig. 2.9). The vertebrate receptor cells (the rods and cones carrying the photosensitive pigment on modified ciliary membranes) are present lining the back of the retina. This receptor layer is overlain by several classes of interneurons (bipolar, amacrine and ganglion cells) which abstract information from the excited visual cells and give rise to nerve fibres running over the surface that eventually form the optic nerve connecting the eye to the brain. Optic nerves carrying neurally processed visual information from the two eyes cross over in the midline before entering the brain. In

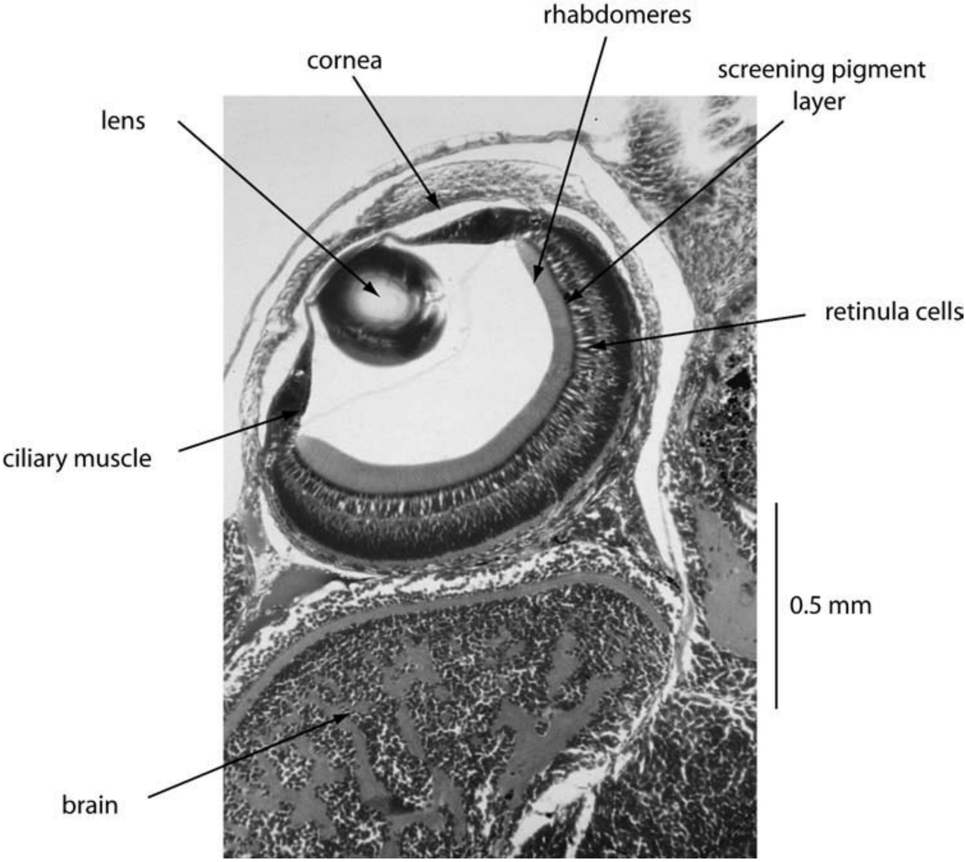

Fig. 2.9 Section of the eye of a late embryo of *Loligo forbesi*. The non-inverted retina is composed of retinula cells giving rise to rhabdomeres carrying the visual pigment. A screening pigment layer separating adjacent rhabdoms is extended during illumination. Nerve fibres from retinula cells from small bundles of optic nerve travel into the optic lobe of the brain. The distance between the spherical lens and the retina can be adjusted by the ciliary suspension muscles.

the octopus, the receptor (retinula) cells also line the surface of the retina. From the distal segment of each cell (projecting towards the lumen of the eye), tightly layered microvilli carrying the photoreceptive pigment project from two opposite sides (rhabdomeres) – the molluscan pattern of photoreceptor formation. Half of the rhabdomeres are orientated vertically and half horizontally with respect to the normal orientation of the eye, so the rhabdomeres of four adjacent retinula cells combine to form a rhabdom, which is geometrically square in cross section.

Each retinula cell also gives rise proximally to a nerve fibre, and these individual cell processes amalgamate into many small optic nerves which emerge from the back of the retina. A complex pattern of crossing over of these small nerves behind each eye transposes the inverted optical image on the retina and, maintaining its spatial relationships, projects it into the surface layers of the optic ganglion. These large and highly structured ganglionic masses, connected to the brain on each side by the optic tract, are the site of most neural processing of the visual image.

Key differences between the cephalopod visual setup and that of the vertebrate are:

- rhabdomeric (molluscan) structure of the retina;
- the visual image falls directly onto photoreceptor cells without intervening interneurons (in contrast to the inverted retina of the vertebrate);
- photoreceptor cell processes give rise to the optic nerves;
- the crossover of optic nerves at each eye preserve the spatial properties of the visual image;
- primary neural processing of the visual image occurs in optic lobes rather than in cells of the retina (as in vertebrates).

The strongly geometric pattern of the receptor cells of the rhabdom appears to confer greater sensitivity to visual stimuli with strong vertical or horizontal components. Visual images which differ quantitatively in their vertical or horizontal axes are easier for behavioural discrimination (see Wells 1978 for a summary of visual discrimination and learning in *Octopus*). The rectilinear geometry of the retinal organisation is probably also the basis for the discrimination of polarised light by cephalopods, which may be an important capability for breaking the countershading camouflage of silvery reflecting fish (Shashar *et al.* 2000).

2.9.3 Statocysts, balance and orientation

Encased within the tough cartilaginous cranium surrounding the brain is a pair of statocysts. The details of the structure are complex and vary among different cephalopod families. The basic layout is of a calcareous statolith (Clarke 1978), supported on a field of hair cells (macula), suspended in the fluid-filled cavity of the statocyst by the macula nerve. Gravity acting on the dense statolith exerts a directional force on the macula hair cells that continuously signals the direction of gravity and thus the overall orientation of the animal. A second field of hair cells (crista), also innervated to the brain, runs in a continuous strip around the inner surface of the statocyst in three orientations: vertical, horizontal and transverse. Movement of the suspended macula and displacement of the fluid of the cavity stimulate the orientated hair cells and sense the linear and angular acceleration of the animal in any direction.

In the organisation of the cephalopod statocyst there are many functional parallels to the structures of the vertebrate inner ear in the evolution of these structures. This highly evolved structure, which is far in advance of any other molluscan organ of balance and orientation, is responsible for much of the information necessary to monitor and control the orientation of cephalopods in three-dimensional space (Arkhipkin & Bizikov 2000).

2.9.4 Mechanoreception and hearing

In addition to their advanced visual system, cephalopods can detect disturbances in their local environment from small water movements. Cuttlefish, squid and at least octopus hatchlings have orientated lines of epidermal hair cells along the head and arms. The hair cells are precisely polarised to respond differently to direction of displacement, and are sensitive to water movements as small as 0.06 μm. At this sensitivity, the epidermal line system could detect a moving fish of 1 m in body length at a distance of about 30 m (Budelmann 1994). It is presumed that the system is valuable in conditions which are unsuitable for high acuity vision, and again there are clear functional parallels with a vertebrate system, i.e. the lateral line of fish.

Although cephalopods are sensitive to vibrational stimuli through this epidermal line system and the statocyst, it is not clear whether they 'hear'. Cephalopods are not known to possess an internal gas-filled cavity and associated sense organs which would fulfill a strict definition of a hearing organ. The calcareous brood chamber of the female pelagic octopus *Argonauta* is known to retain a bubble of gas, and another pelagic octopod, *Ocythoe*, similarly retains a gas bubble which contributes to buoyancy (Packard & Wurtz 1994). The low-frequency sounds that can be perceived by some cephalopods are due to particle motion detection rather than sound pressure (Hanlon & Budelmann 1987; Budelmann 1994).

2.9.5 Proprioception

Mechanically sensitive cells are known to be located within the blocks of somatic muscle in *Octopus*, where they are presumed to play a role in providing the sensory feedback necessary for the control of movement (Boyle 1986b). In *Loligo*, epidermal hair cells have been described as proprioceptors for relative movements between head and body (Preuss & Budelmann 1991). Little is known about these aspects of neural control in cephalopods, but the skill with which they handle objects and the precision of their body control in a three-dimensional environment argues for a high degree of proprioceptive feedback in monitoring and modulating muscular movement.

2.10 Colour

The pigmentation of cephalopod skin is contained within unique cellular chromatophore organs (Cloney & Florey 1968). These consist of an intracellular, elastic sac which contains the pigment, into which is inserted a series of 25 or so muscle fibres arranged radially, their distal ends being anchored in the connective tissue of the dermis. When these muscles contract, the pigment sac is expanded and imparts its colour to the skin surface. When the radial chromatophore muscles relax, the elasticity of the pigment sac causes it to retract to its smallest size. The pigment area is then too small to provide skin colour, and the animal appears white by reflection from the muscle surface. The coloured appearance of the cephalopod skin is extended and complicated by the presence of chromatophores of different pigment hues, and by static reflecting bodies deeper in the skin that can produce additional colours by differential reflection (iridophores) or scatter white light outwards (leucophores) (Hanlon & Messenger 1996, Box 2.3).

Much attention has been given to the neural processes underlying the control and coordination of the chromatophores (Messenger 2001). However, the sheer quantity of the elements involved, the detail and complexity of the system, the pattern variety

Box 2.3 Colour control and camouflage

The patterned and coloured appearance of cephalopods is due to complex arrangements of pigment cells and muscles, the chromatophore organs. Uniquely, the pigment cells of chromatophores can be actively expanded by contraction of the radially arranged muscle cells, returning to their smallest diameter by the elasticity of the pigment bag. Chromatophores may contain pigment of several colours (brown, red, yellow) and be arranged in several layers in the dermal skin.

Underlying the chromatophore layers is the white background of the musculature of the animal and static reflecting cells of two main types: the *iridophores*, crystalline layers reflecting interference colours by differential reflection (blue–green), and *leucophores*, amorphous masses of non-crystalline material reflecting all wavelengths (white) (Figs. 2.3.1–2.3.3).

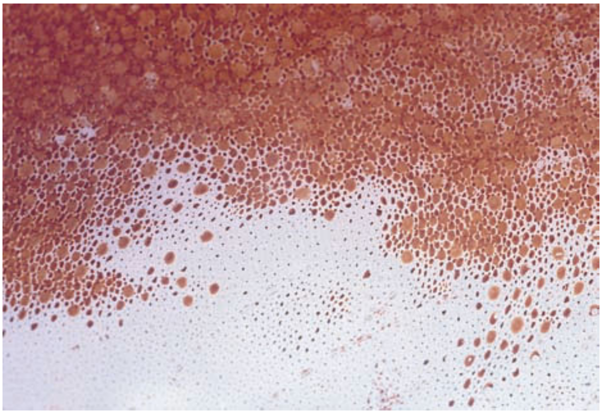

Fig. 2.3.1 Skin of *Todarodes sagittatus* with partially expanded chromatophores.

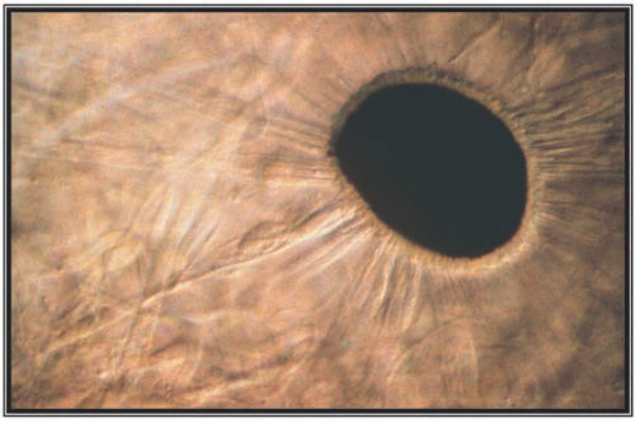

Fig. 2.3.2 Partially expanded chromatophore of *Eledone cirrhosa*.

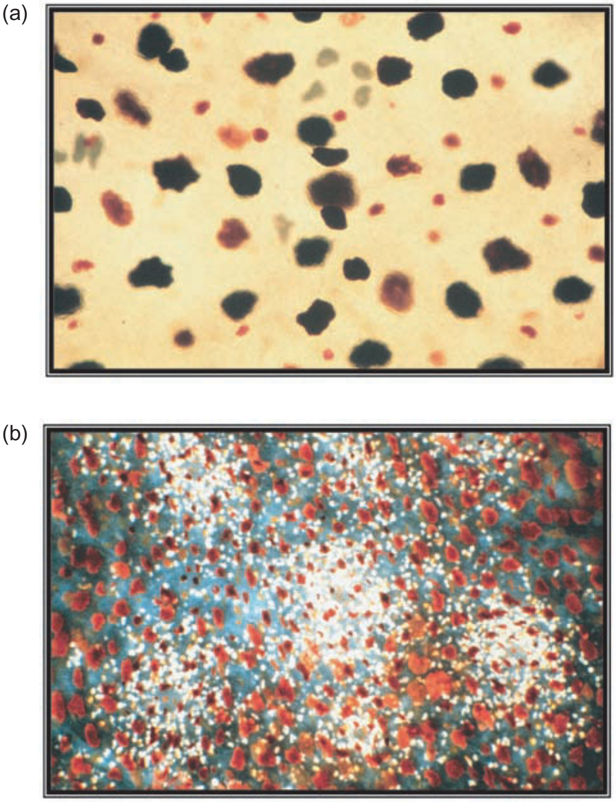

Fig. 2.3.3 Chromatophores, iridophores and leucophores in the skin of *Eledone cirrhosa* viewed under different conditions of illumination.

Chromatophores are controlled actively from the brain through direct innervation of their radiating muscles. They can be precisely controlled individually, or in groups (units) forming components of the overall pattern, and producing rapid and complex changes in the appearance of the animal by screening or revealing the underlying reflectors.

Chromatophore patterns function to camouflage the individual against its background and as part of feeding and reproductive patterns of behaviour. Present evidence suggests that both octopus and squid are colour-blind, and that at the normal depths at which they live, differential absorption of light by the seawater would strictly limit the colours reflected underwater. The information content of these patterns is therefore likely to be limited to patterns of contrast.

and its speed of change currently defy a comprehensive understanding of mechanisms involved. The increased availability of direct observation of living cephalopods underwater is producing many new detailed descriptions of their behaviour and its classification with respect to display and cryptic functions. The repertoire of pattern production is greatly increased by the addition of further coordinated elements generating

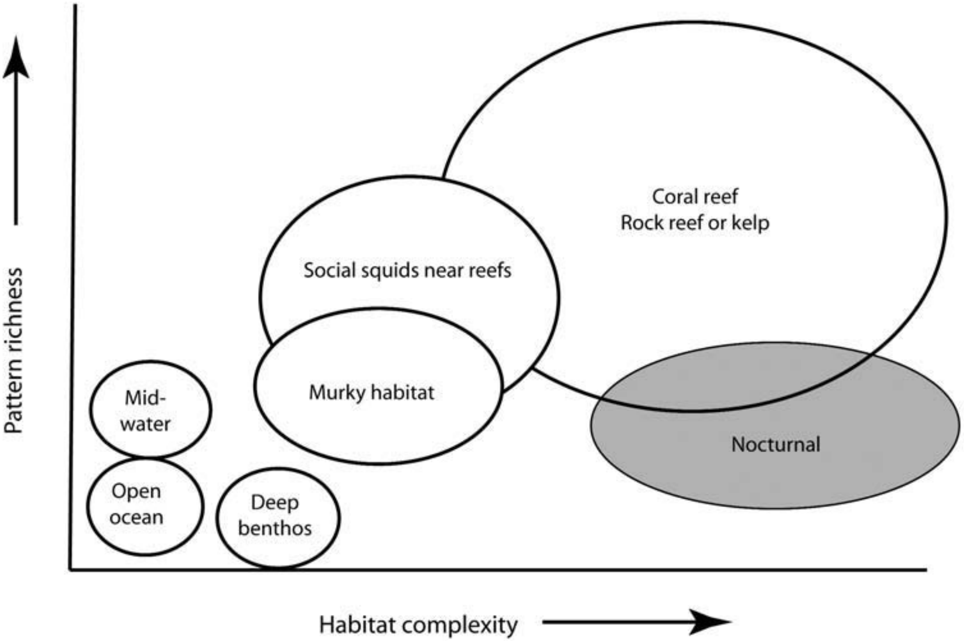

Fig. 2.10 Richness of body patterning according to the number of chromatic units recognised, classified by habitat complexity (after Hanlon & Messenger 1996).

modifications to the outline and texture of the animal by superficial skin muscles. The overall richness of pattern production is clearly related to the complexity and variety of the habitat and its associated fauna (Fig. 2.10).

Luminescent organs are known from many neritic as well as mid- and deep-water cephalopod species (see Chapter 12). In many sepiolid and loliginid squids, light production is due to symbiotic bacteria located in pockets at specific sites which are characteristic for each species, or released into the water as a luminescent cloud. Little is known of the control and activity of these organs, but it is commonly held that they have a role in midwater camouflage (counter-shading) and/or intra-specific signalling.

2.11 Inking

Typically, all coleoids have an ink sac, but this is secondarily lost in some deep-water species and in one night-active shallow-water octopus *Ameloctopus*, presumably because the value of ink ejection is lost in the dark environment. The ink sac is a muscular bladder, actually formed as a diverticulum of the hind gut, located ventrally and opening into the anus close to the exhalent water flow at the base of the funnel. Discharge of ink (almost pure melanin) typically occurs when the individual is startled into an escape reaction or during active pursuit by a predator. Generally, the ink is not widely dispersed in the water, but tends to form a discrete dark mass composed of small mucus-bound particles. It functions as a discrete visual mass, probably holding the attention of a pursuer as a decoy while the cephalopod makes a rapid change in direction. This manoeuvre is often effective in gaining the extra few seconds necessary to make an escape. The fact that many deep-water cephalopods retain a functional ink sac is also interesting and perhaps indicates another function for the release of ink. In captivity, startled or stressed animals will frequently eject ink.

2.12 Reproductive system

In cephalopods, the sexes are separate (dioecious) and fertilisation is achieved by direct mating (see Chapter 9).

In the male, ripe sperm are packaged into spermatophores and stored in a special spermatophoric (Needham's) sac until mating occurs. In most species, the male transfers sperm to the female by passing ripe spermatophores along a muscular groove in one arm, the hectocotylus or hectocotylised arm, especially modified for this function at or before sexual maturity. The course of fertilisation then varies among different cephalopod types. Sperm may be held by the female in special pouches at the base of the arms, around the mouth, or within the mantle cavity (cuttlefish and squid), or enter the female genital tract and lodge in the oviducal glands (*Octopus*), or even pass into the ovary itself (*Eledone*). These mechanisms allow the possibility of opportunistic matings and sperm storage. The longest recorded interval between mating and egg-laying in octopus was for *Octopus tetricus* at 114 days (Joll 1976, 1977a), but we have no knowledge of how long sperm may be held by females of deep-water cirrate octopuses which apparently live for much longer and produce eggs over most of their lifespan.

Sexual maturation is under the control of hormone(s) released from small bodies called optic glands located on the optic tract (connecting optic lobes to the brain). At the onset of sexual maturity, there is rapid gonad growth, yolk formation in the ova and ripening of accessory glandular systems. In most of the coastal and epipelagic cephalopods, reproduction is seasonal and afterwards both males and females die, usually showing clear signs of muscle wasting and degeneration. The immediate causes of this apparently universal mortality are not understood, but it is as if the sequence of physical changes brought about by the optic gland hormone(s) cannot be reversed. Some direct evidence for this hypothesis is available from experiments in which the optic glands from mature octopuses were excised; their gonads regressed, while feeding and growth was resumed (Wodinsky 1977; Tait 1986). These consequences of reproduction are clearly of profound importance to the survival and lifespan expected of cephalopods in wild populations and in captivity. Variations to this pattern of monocyclic reproduction and short lifespan are found or suspected in deep-water benthic octopuses and a range of other species, and are discussed in more detail in Chapters 6 and 9.

2.13 Habitat and distribution

Cephalopods are exclusively marine. The squid *Lolliguncula brevis*, of the Gulf of Mexico, is one of the very few species known to tolerate seawater of lowered salinity (>16 S‰) but cephalopods generally must be regarded as stenohaline.

The few species of *Nautilus* have distributions in the Indo-Pacific region, typically in deep water off the reef edge (see Chapter 4). Although they are most common in water of 300–500 m, they are caught in traps between 600 m and the surface. They are relatively sluggish animals, relying on the strength of their shell for protection against predators. In the aquarium, eggs are attached to a hard substrate, and in the field the adults are found to have been eating benthic crustaceans and their moulted exoskeletons. Both of these observations suggest that their normal life is close to the bottom. There has been considerable interest in these animals, since they are representatives of a mainly extinct type, and have been successfully kept in aquaria. They are subject to significant fishing pressure in certain localities, and there is some concern for their conservation.

The octopuses (order Octopodida) are represented by a number of families, only one of which is bottom-dwelling. It is this family, the Octopodidae, which includes all of the species commonly available for studies in captivity. Coastal octopuses have worldwide distributions, they are epibenthic, living on or close to the bottom. Normally, they are associated with stony or rocky habitats where they can both shelter and find a wide range of invertebrate food sources. In fact, many octopus species also live widely distributed over mud or sandy bottoms in which they often bury. By reason of their natural use of holes and crevices, coastal octopuses are by far the most adapatable and amenable cephalopods to hold in captivity. In contrast, the deep-water cirrate octopuses (the suborder Cirrina) are known almost entirely from dead specimens.

Cuttlefish and bobtail squid (order Sepioidea, families Sepiidae and Sepiolidae) are also characteristic of coastal waters. Like octopuses they are active, bottom-dwelling predators. Instead of hiding amongst stones and rocks, they are able to bury themselves in the sediment, which they blow up using the funnel jet to excavate a depression and use the lateral fins to flick sand over their dorsal surface (Boletzky & Boletzky 1970). The best known genus, *Sepia*, is also able to hover above the surface, achieving neutral buoyancy in the water from the enclosed shell remnant, the cuttlebone. Cuttlefish are common in coastal waters of most temperate and tropical zones, but interestingly, the true cuttlefishes (family Sepiidae) are not found anywhere in either North or South American waters (Voss 1977a). Several families of the order Sepioidea are often loosely referred to as squids (Sepiolidae = bobtail squid; Sepiadaridae = bottletail squid; Idiosepiidae = pygmy squid; Spirulidae = ram's horn squid), but this is inaccurate, and the term squid should be confined to members of the order Teuthida unless qualified as sepioid squid.

The true squids (order Teuthida) are a very large and diverse assemblage of families which differ widely in habitat and distribution. Two sub-orders are recognised, both of which include species of importance to commercial fisheries. The Myopsida (the suborder Myopsina) are typified by squids of the genus *Loligo*. They are coastal squid, sometimes of great seasonal abundance. They attach spawned egg masses to a substrate and complete their life cycle in coastal water. The Oegopsida (sub-order Oegopsina) includes a great many families, ranging from obscure deep-water species whose biology is almost unknown, to genera such as *Todarodes* and *Illex* (family Ommastrephidae) characteristic of the high-velocity Western Boundary currents and areas of nutrient-rich upwellings, such as the edges of the continental shelf.

Ommastrephids are migratory over large distances, apparently releasing large, neutrally buoyant egg masses, and completing their whole life cycle in oceanic water. The squids also are active predators, hunting fish and crustaceans in the water column and on the bottom. This leads to large populations spreading over the continental shelf zones in annual feeding migrations, where they may be the subjects of important commercial fisheries.

Chapter 3

Origin and evolution

Summary: The cephalopods evolved in the Cambrian era from an ancestral benthic mollusc. Through the evolution of neutral buoyancy, they could occupy the water column and acquire a whole new adaptive zone, radiating into forms with little resemblance to their molluscan ancestors. The early cephalopods had a shell with gas-filled flotation chambers and a living chamber. As their dependence on the seabed decreased, the primitive molluscan foot became transformed into arms and tentacles and into the flexible muscular funnel capable of directing water derived from the powerful ventilation system for the gills to form a jet propulsion mechanism. It is clear that the arms and funnel arose from the primitive molluscan foot. For much of their evolutionary history, the cephalopods comprised mostly the shelled nautiloids and ammonoids, but in the Jurassic the coleoids, with a much reduced or absent shell, started to diversify, radiating and becoming predominant in the Tertiary. The living ten-armed and eight-armed squid and octopus may have arisen from a stem group, the Phragmoteuthida, which became extinct in the Jurassic. The cephalopods have probably been carnivorous since their early origins. The forms which dominate the fossil record are likely to have relied on slow-moving or sessile prey, and on their heavy external shell to resist predation. The radiation of predatory fish and reptiles in the Mesozoic apparently displaced the shelled cephalopods into deeper water, where the depth limits imposed by the low-pressure gas spaces in the shell directed evolution towards progressive shell loss. This was the starting point for the evolution of the modern coleoids (the Neocoleoidea), which then re-invaded shallow water. With the reduction of the shell the coleoids, other than *Spirula* and the cuttlefish, traded buoyancy for speed and consequently greatly increased their metabolic costs. These new demands were met by the evolution of more complex gills with increased diffusion capacity, higher-output hearts and faster digestive processes. As they swam faster and became more manoeuvrable, they evolved more sophisticated sensory systems, especially eyes, and larger brains to analyse and act on these capabilities. They also became faster growing and have adopted semelparous (unicyclic) reproductive patterns. Some living neocoleoids have secondarily become less active and use more efficient fins for slow swimming, and have buoyancy systems which are based on the retention of ammonium salts coupled with reduced musculature.

It can be helpful to consider the biology and ecology of the modern forms of living cephalopods in the light of knowledge of their evolutionary background.

3.1 Origins

The cephalopods arose from a shelled mollusc that evolved a buoyancy mechanism, and the first recognised species, *Plectronoceras cambria*, appeared in the fossil record in the late Cambrian period some 450 million years BP. The acquisition of buoyancy, which allowed the cephalopods to join the earliest swimming metazoans, such as jellyfish and primitive chordates, was undoubtedly the decisive evolutionary step during their early history. The molluscan ancestor from which they evolved was bottom-dwelling (benthic), and the evolution of a buoyancy mechanism released the cephalopods from dependence on the seabed, allowing them to adopt a pelagic existence. Apart from some small groups of pelagic molluscs (Gymnosomata, Thecosomata, Heteropoda and Janthinids) and a few nudibranchs such as *Glaucus*, the adult forms of all the other major molluscan classes still remain closely associated with the seabed. The ability to occupy the water column gave the cephalopods a new adaptive zone in which to evolve, provided enormous potential for radiation, and allowed the evolution of forms that bear little morphological or functional resemblance to their molluscan ancestors. Here we draw largely on reviews of cephalopod evolution and phylogeny using the conventional interpretation of phenotypes (Donovan 1964, 1977, 1993; Jeletzky 1966; Teichert 1988), as well as later work partially incorporating a cladistic approach (Anderson 1996; Engeser 1990; Doyle *et al.* 1994; Voight 1997; Young & Vecchione 1996; Young *et al.* 1998).

The cephalopods probably share a common ancestor with the Gastropoda. This would have had a simple cone-shaped shell similar to that of the extant monoplacophoran *Neopilina*. Buoyancy in the first cephalopods, the surviving nautiluses and the coleoids *Spirula* and *Sepia* is provided by gas-filled chambers (camerae) in the shell which are separated by thin walls (septae). Buoyancy control is achieved by moving fluid, the cameral liquid, into and out of the camerae, mostly via the siphuncle, which is a strand of living tissue which runs in a calcareous tube through the camerae (see Chapter 4). The likely link between the protocephalopods and the cephalopods has been found in the form of a fossil, *Knightoconus antarcticus*, from the Cambrian rocks of the Ellsworth Mountains, West Antarctica (Yochelson *et al.* 1973), which has a multiseptate conical shell but no siphuncle. Evolution of the earliest accepted cephalopods, such as the late Cambrian species *Plectronocerus* spp., from a possible ancestor like *K. antarcticus* would have required the addition of a siphuncle and a change in the curvature of the shell towards the ventral side of the body (endogastric curvature). No fossil forms are known which illustrate the evolution of the siphuncle, but it is possible that it evolved rapidly when, in an early form, a strand of tissue was retained in the first and subsequent camerae during growth, as the body moved forward at the time of septation.

A hypothetical early cephalopod from the late Cambrian, based on the *Plectronocerus* spp., is shown stylised in Fig. 3.1. The shell has an open living chamber in which the body of the animal lies, and a chambered part, or phragmocone, subdivided by septae which are interconnected by the siphuncle. It also shows the endogastric curvature of the shell (curved towards the ventral surface). The soft parts illustrated in Fig. 3.1 are purely hypothetical, since these have never been preserved in fossils of early cephalopods, but they suggest that the early arms or tentacles are homologous to the anterior of the foot of other molluscs. Twisting of the body (i.e. torsion, as distinct from spiral coiling of the shell), which is a major feature distinguishing the gastropods from the cephalopods (Yonge 1960), is notably absent. Some gastropods in the fossil record bear a resemblance to the early cephalopods in having chambered shells, albeit lacking a siphuncle, but the evolutionary step of torsion in the gastropods differentiated them from the cephalopods at an early stage in the evolutionary history of the two classes.

We can only speculate about the changes in locomotion that took place as the cephalopods evolved, but it seems likely that buoyancy evolved gradually and was accompanied by a reduction in the size of the foot as the need to move along the seabed declined. As dependence on the seabed decreased and the need to swim increased, early jet propulsion may have been aided by the foot rolling to form a nozzle in the lower mantle cavity where it was needed to direct the jet of water. The flexible siphon probably evolved from such an intermittently formed nozzle early in the evolutionary history of the cephalopods to provide a steering mechanism. The living nautiluses rely on retraction

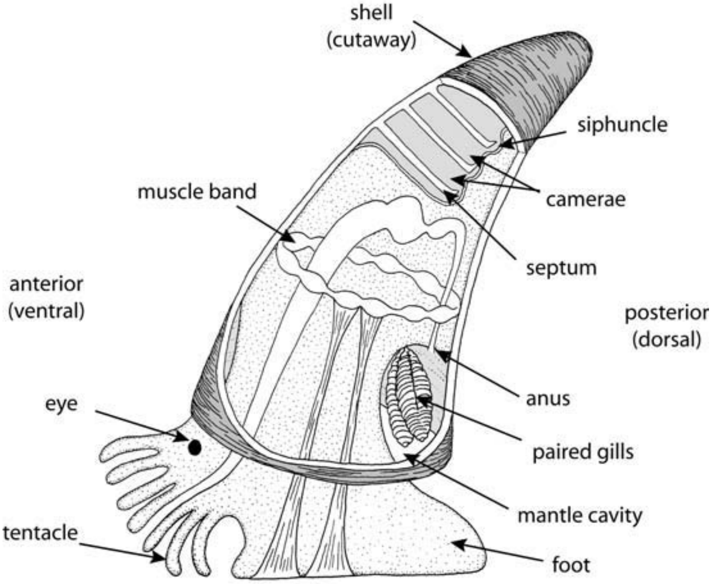

Fig. 3.1 Reconstruction of an early cephalopod (after Yochelson *et al.* 1973).

of the body into the final chamber of the shell to displace water expelled for locomotion (see Chapter 4). The evolution of an elongated, buoyant phragmocone was necessarily followed by curvature of the shell, and ultimately coiling (*Nautilus*). This change in orientation shifted the centre of buoyancy, allowing the animal to float in a stable position beneath the phragmocone.

The transition from a benthic to a nektonic existence, as the cephalopods evolved from their gastropod-type ancestors, placed demands on the respiratory system for more oxygen to support higher levels of activity. The need for a more efficient respiratory system was met in one of two ways by different evolutionary lines, either by the addition of a second pair of gills to increase the respiratory surface (the tetrabranchiate condition found in the living nautiluses), or by the evolution of capillary circulation and branchial hearts (sited at the base of each gill and characteristic of all the neocoleoidea) to enhance circulation within a single pair of gills (Yonge 1960). However, it is not known how many pairs of gills the fossil forms really possessed and, despite their value in phylogenetic studies (Young & Vecchione 2002), it is probable we will never know, as these flimsy structures do not appear often to have been preserved in fossils. It seems likely that the requirement for more efficient ventilation of the gills preceded the development of jet propulsion, because the need to ventilate the gills would have produced a more elaborate musculature in the mantle cavity, and it may have been this step that led to the evolution of the primitive mantle cavity into an expulsion chamber for jet propulsion. The active lifestyle of early cephalopods is also indicated from the evidence of squid statoliths in the fossil record (Clarke 1975).

The cephalopod beak is a major adaptation for carnivory and is unique among the molluscs. Although the oldest fossil beaks are from the Mesozoic (Yochelson

1971), their presence in all cephalopods suggests an early common origin. It is likely that primitive cephalopods possessed a small number of arms or tentacles, and that the larger number of tentacles in extant nautiloids is probably a derived condition. Certainly, X-ray images of Devonian nautiloids suggest that they had a relatively small number of tentacles (Zeiss 1969; Stürmer 1970). If this was the case, then modifications of the alimentary tract for carnivory must also have taken place at an early evolutionary stage, and included a U-shaped alimentary canal and a diverticulum for secretion and absorption (digestive gland).

3.2 Molluscan features retained by the cephalopods

Apart from the radula, there are few features of the modern cephalopods that are obviously of molluscan origin. In fact, the body plan is consistent with molluscan ancestry, but the molluscan ventral surface has become reduced. The anterior head, the ventral foot and the posterior mantle cavity all point in the same forward direction, and the dorsal visceral mass points backwards. The cephalopods have in effect become U-shaped, with the anterior and posterior ends bending towards each other. The foot, which in the primitive state lay between the two ends of the animal on the ventral surface, has effectively been rearranged as a series of arm pairs with dorsal extensions (Boletzky 2003) (Fig. 3.2). To explain the orientation of the cephalopods, Yonge &

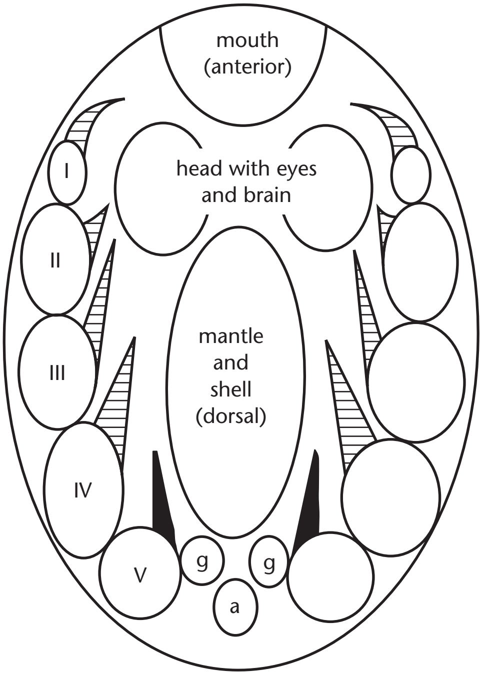

Fig. 3.2 Schematic representation of cephalopod characteristics at an embryonic stage corresponding to the advanced gastrula of the gastropods. The derivatives of the ventral foot are five pairs of arm rudiments (I–V) each with a dorsal extension giving rise to other body elements (after Boletzky 2003). g = gill; a = anus.

Thompson (1976) refer to the front end, which comprises the morphological anterior, ventral and posterior surfaces, and the hind end, which is morphologically the dorsal surface.

3.3 Diversification

The living cephalopods are dominated by the subclass Coleoidea that includes the squid, cuttlefish and octopuses which, although appearing relatively early in the fossil record, have only flourished recently in geological time. Throughout much of the evolutionary history of the cephalopods, the fossil forms with external shells, the Ammonoidea and Nautiloidea, were dominant. Grouping them as sister clades to the Coleoidea is done on the basis of the relationships between fossil and modern shell structures. It is inferred from living nautiluses that they had a similar body plan although, in the absence of evidence of soft parts, this cannot be proved.

3.3.1 Ectocochleates (shelled Nautilus and the fossil forms)

The evolutionary history of the cephalopods is illustrated in Fig. 3.3. The oldest family, the Ellesmeroceratidae, containing the *Plectronoceros* spp., arose in the late Cambrian and became extinct at the end of the Ordovician. Several other families then arose during the Ordovician, but these had largely disappeared by the end of the Palaeozoic, and it was the ammonoids and nautiloids (sub-classes Ammonoidea and Nautiloidea), arising in the Devonian, that radiated so dramatically in the Mesozoic. However, by the end of the Mesozoic the ammonites were extinct, the nautiluses declined during the Tertiary, and only two genera of nautilus, *Nautilus* and *Allonautilus*, survive to the present. During the course of their evolutionary history the ammonites diversified spectacularly during the Palaeozoic, and nearly became extinct at the end of the Permian and again at the end of the Triassic. Following each near extinction they diversified again (Kennedy 1977). Some ammonites grew to a very large size; the coiled forms reached diameters of up to 2 m, and some which became secondarily uncoiled or partially uncoiled reached lengths of several metres. Many species evolved complex shell sculpturing and, in the Mesozoic, the ammonites had highly convoluted sutures.

Geological evidence for the origin of the cephalopods in the Cambrian precedes that of the vertebrates by many millions of years throughout a period when there were apparently no other large aquatic metazoan animals. Throughout most of their geological history, however, they co-existed with other large organisms such as the extinct giant arthropods (Eurypterida) and early armoured fish (Ostracoderma and Placoderma) of the Silurian and Devonian. Later, throughout the Mesozoic, the great marine reptiles (Ichthyosaura, Plesiosaura) were pre-eminent, and are known to have preyed upon the shelled cephalopods. The potential for interaction between these predatory groups is a matter of fascinating speculation (Packard 1972). Major changes occurred in the cephalopod record over the last 63 million years (Tertiary). With the exception of *Nautilus*, all the shelled cephalopods disappeared and the Coleoidea radiated into solely soft-bodied forms. It may not be coincidence that this abrupt change in

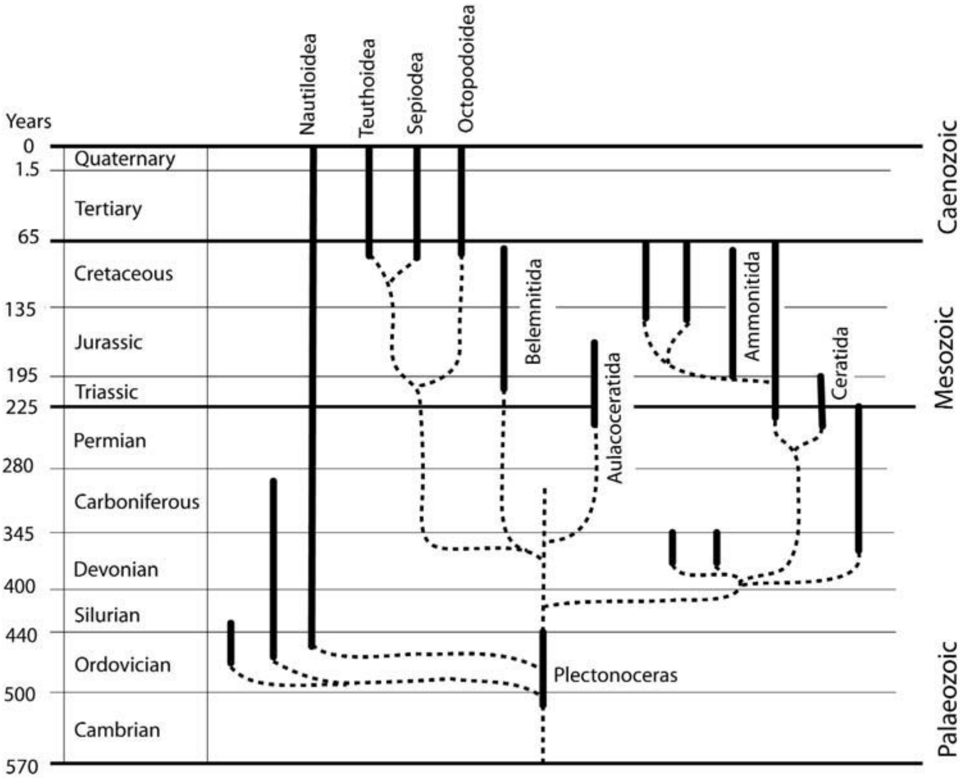

Fig. 3.3 A possible evolutionary tree of the living cephalopod groups, and fossil groups named in the text, displayed through geological time, indicated in years before the present (after Ward & Bandel 1987).

the cephalopod fauna occurred when the bony fish (Teleostei) radiated, diversified and became abundant in all aquatic habitats, and the toothed whales and dolphins became the largest marine predators. In later chapters we explore the ecological relationships between modern cephalopods, fish and marine mammals in terms of their trophic relationships (see Chapters 14 and 15), competitive interactions and occupation of habitat (see Chapters 11 and 12). It is not beyond the bounds of possibility to suggest that the demise of the armoured but slow-moving ectocochleate cephalopods at the end of the Mesozoic was linked to their inability to compete with fish for the most productive marine habitats and to resist the onslaught of superior predators.

A striking coincidence in the history of the cephalopods is the disappearance of the ammonites and belemnites at the end of the Cretaceous. A common feature of these two groups was their relatively small eggs and hatchlings, which generally measured 1–2 mm. These hatchlings were probably dependent on zooplankton for food. The ecological crisis characterising the K/T (Cretaceous/Tertiary) boundary may have reduced the zooplankton resource so drastically that the cephalopods producing the planktotrophic hatchings became extinct, while those producing bigger, lecithotrophic, eggs developing into benthic young survived.

3.3.2 Endocochleates (modern octopus, squid and cuttlefish without an external shell)

The coleoids (sub-class Coleoidea) are the endocochleate, dibranchiate cephalopods that include the living cuttlefish and squid, octopuses and devilfish, or vampire squids. As the sub-class incorporating all of the living cephalopods without an external shell, i.e. those with most significance to marine ecology and fisheries, the origin and history of the Coleoidea is of considerable interest.

They first appeared in the late Devonian (Bandel *et al.* 1983; Stürmer 1985) and started to diversify in the Jurassic but, apart from the fossil belemnites, major radiation of the group really only took place during the Tertiary. In the context of the evolutionary history of the cephalopods, the coleoids are an aberrant group because of the incorporation of the external shell, but they represent an expansion of a whole sub-class of molluscs into forms with vastly superior power and activity in which the remaining internal shell has become much reduced or lost altogether.

Fossils attributed to the early coleoid line are difficult to interpret, and may not all be derived from the same evolutionary source. Donovan (1977) defined them as forms that had a rostrum, or guard, surrounding the phragmocone and/or had a much reduced body chamber. The primitive common ancestor of the coleoids was endocochleate, with an entire body chamber and ten equal arms. Variations of the phylogeny of the Coleoidea, based on the presumed evolution of the arms and tentacles from a basically ten-armed ancestral form, are shown in Figs. 3.4 and 3.5.

Although most families of living coleoids are well defined, the phylogenetic relationships between them are controversial (R.E. Young & Vecchione 1996; R.E. Young

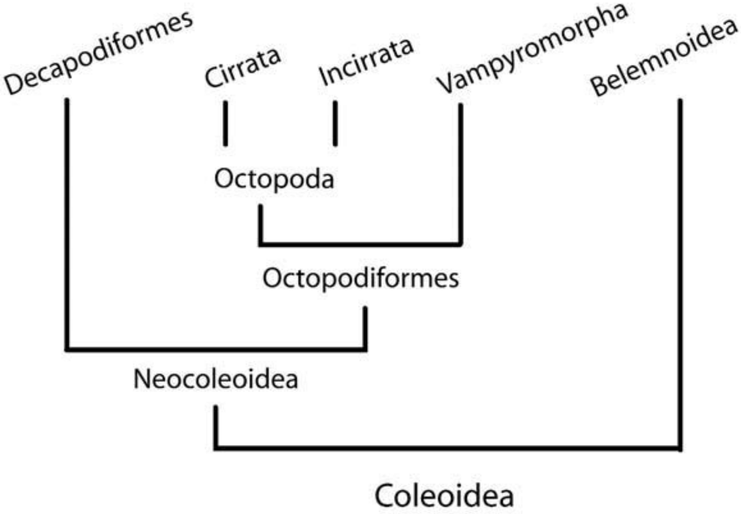

Fig. 3.4 A basic phylogeny and classification to the Coleoidea (after Young *et al.* 1998). The term 'Neocoleoidea' includes all living coleoids. 'Decapodiformes' replaces 'decapod' (commonly used in cephalopod literature and throughout this book) to avoid possible confusion with the crustacean group of the same name. 'Octopodiformes' designates the vampyromorph–octopoda clade (now, more consistently, the Octobrachia).

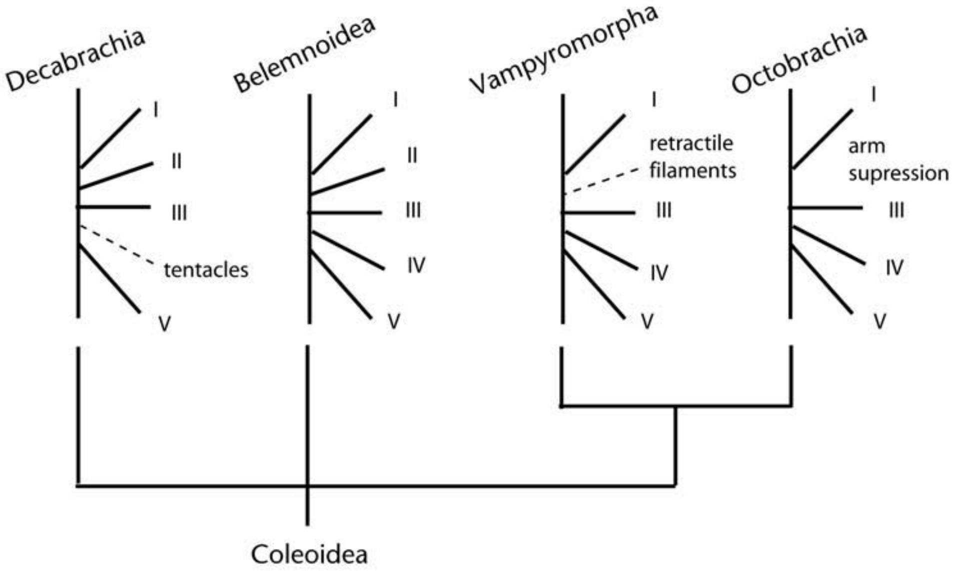

Fig. 3.5 Phylogeny of the Coleoidea showing the major groupings (super-orders) and schematically showing the expression and fate of the basic pattern of ten arms (after Boletzky 1999; Vecchione *et al.* 1999). See Appendix A for terminology.

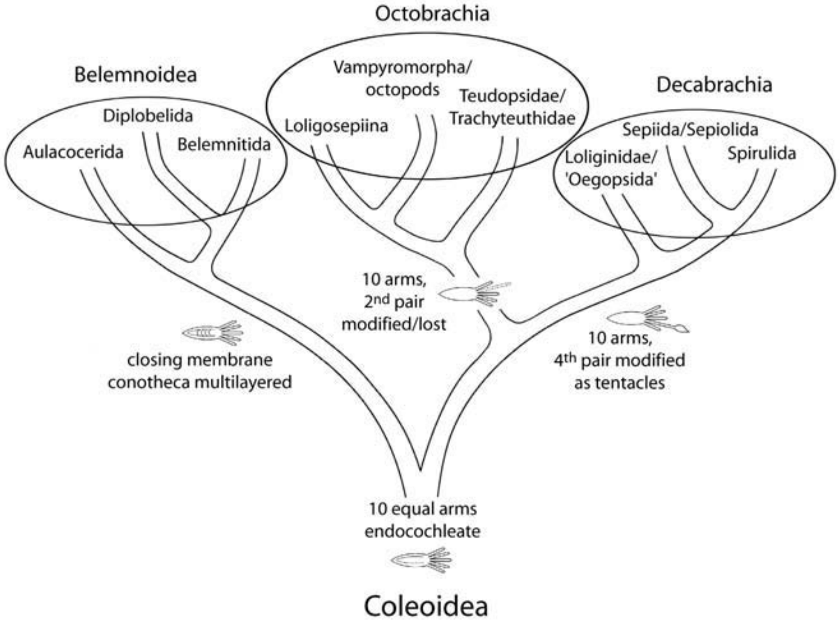

Fig. 3.6 Phylogram of the Coleoidea illustrating the major groups discussed in the text and based upon a ten-armed endocochleate cephalopod with an entire body chamber (after Doyle *et al.* 1994).

et al. 1998; Vecchione *et al.* 1999) and involve detailed arguments around the meaning of fossil characters extending well beyond the scope of this book. A phylogram illustrating the relationships of the major groups was suggested by Doyle *et al.* (1994) and is in common use (Fig. 3.6).

The Belemnoidea are an important fossil group typified by the belemnites (Belemnitida), abundant during the Jurassic and Cretaceous and becoming extinct by the end of the Mesozoic. The belemnite shell had three parts: (1) a small chambered phragmocone which provided buoyancy, (2) a solidly calcified rostrum which gave the body rigidity, probably acted as a solid anchoring point for the muscular fins, and possibly acted as a counterweight to the buoyant phragmocone allowing the animal to swim horizontally, and (3) a pro-ostracum, or vestigial body chamber, which provided the attachment for the mantle. It is only the belemnite rostrum that is usually found fossilised, and it was these objects that early collectors, in a flight of fancy, believed to be 'thunderbolts from heaven'. The belemnites were rapid jet-propelled swimmers, with triangular fins rather like some squid, arms that were armed with two rows of hooks, and relatively poorly developed jaws. Most were of modest size, but some exceeded 2 m in length. Although there were numerous belemnite species there was little adaptive radiation in the group. The Aulacocerida, which appeared in the Carboniferous and became extinct at the end of the Jurassic, were similar to the belemnites. They had conical phragmocones and a rostrum, but they differed from the belemnites in having a complete body chamber. The Diplobelida were a specialised group confined to the Mesozoic and were extinct by the end of the Cretaceous period.

The Phragmoteuthida are regarded by Doyle *et al.* (1994) to be the stem group of the ten-armed Decabrachia and the eight-armed Octobrachia. They first appear in the fossil record in the upper Permian and disappear in the Jurassic. The shell had a well-developed phragmocone with the siphuncle displaced towards the ventral surface, there was apparently no rostrum and there was a long pro-ostracum originating from about two-thirds of the diameter of the phragmocone. The phragmoteuthids had an ink sac, and arms bearing two rows of hooks. It is not known how they were orientated in the water, but without the calcified rostrum of the belemnites, their centre of buoyancy might have been towards the posterior, causing the long axis of the body to align vertically. Alternatively, Donovan (1977) suggests that the soft parts of the body extended posteriorly to the phragmocone, so that it lay in the central part of the body, and that a horizontal position may have been possible.

Under the 1994 scheme of Doyle *et al.* (Fig. 3.6), the Octobrachia include several extinct groups (Loligosepiina, Teudopsidae and Trachyteuthidae) as well as the living vampyromorphs and octopuses. The key derived characters of the Octobrachia are the presence of ten arms, the second pair of which have been modified or lost. The Loligosepiina appeared in the late Triassic and became extinct in the Tertiary. Soft parts of one species, *Mastigophora brevipinnis*, from the Oxford clay in England, and including the ink sac, have been found well preserved (Donovan 1983). They had a broad calcified pen (gladius) and no phragomocone, and appear to have had tentacles like the Decabrachia (Vecchione *et al.* 1999). The Teudopsidae and Trachyteuthidae had a relatively short history in the Jurassic/Cretaceous; they were similar to the Loligosepiina. Fossil vampyromorphs are found from the late Jurassic onwards (Bandel & Leich 1986). The gladius of the loligosepiids and *Vampyroteuthis* are similar (Pickford 1949), and it has been suggested that the vampyromorphs are a deep-sea relict of a form that evolved from the loligosepiids, a step that would probably only have involved losing the calcified gladius of the loligosepiids (Donovan 1977). The first fossil octopod, *Palaeoctopus*, appeared in the Cretaceous. This is interpreted as having eight arms with suckers and cirri, a posterior pair of fins and a gladius. An earlier eight-armed cephalopod, *Proteroctopus ribeti*, from the Jurassic may represent a stem group of octopods, but the true provenance of that particular fossil is also doubted by some specialists (Engeser & Clarke 1988; Young *et al.* 1998). The octopuses may have diverged from the Mesozoic vampyromorphs or Loligosepiina. Fossil argonaut brood (pseudoconch) shells, similar to the living form, appear for the first time in the Tertiary.

The Decabrachia of Doyle *et al.* (1994) include the squids and cuttlefish. The key derived feature of the Decabrachia is the presence of ten arms, in which the fourth pair have been modified as tentacles. Fossils that look like squid gladii are known from the Mesozoic, and a Jurassic genus, *Plesioteuthis*, has a gladius which is very similar to that of the living ommastrephid squid and has affinities with the gladius of the gonatid and onychoteuthid squids. Donovan (1977) has pointed out that the gonatids and onychoteuthids possess suckers modified to form hooks on the tentacles, which is also a feature of the phragmotheuthids, and may suggest a link between them. It is likely, however, that there was considerable opportunity for evolution of the squids during the Tertiary, when the appearance of new forms would have been accompanied by parallel and convergent evolution, and so the origins of the squids cannot be placed with any certainty. A fossil from the Devonian, *Eoteuthis elfriedae* (Stürmer 1985), has been tentatively identified as a squid, but more material is needed for a full evaluation (Teichert 1988). Tracing the evolution of the squids, which are rare in the fossil record, is probably unrealistic over such a long span of geological time. The evolutionary history of the living genus *Spirula* is not clear. It was originally thought to resemble the oegopsid squids (Huxley & Pelseneer 1886), and a possible link with an Eocene family the Spirulirostridae is recognised (Donovan 1977), but on the basis of the structure of the shell, Bandel & Boletzky (1979) suggest a close affinity with the cuttlefish.

3.4 Paleoecology

The ecology of most of the fossil cephalopods and their role in the ancient seas was probably very different from that of the living forms, which are important as predators, especially on crustaceans and fish, and as prey for numerous higher predators (Clarke 1996a, b). The ectocochleate forms, which dominated the diversity during much of the history of the cephalopods, were probably relatively slow-moving and preyed on sluggish or sessile prey. In turn, they relied on their heavy external shell to protect them from predation, and probably developed avoidance patterns of behaviour to escape the attentions of predators.

3.4.1 Life-history strategies

The life-history strategies of the fossil forms has been dealt with in detail by Ward & Bandel (1987). Reconstruction of their developmental history suggests that all fossil cephalopods, in common with the living forms, underwent direct development without specialised intermediate or larval forms. As with the living representatives, there appears to have been a range of developmental strategies based on either small or large egg size, a feature which can usually be determined in well-preserved fossils from the size of the protoconch. Small egg size is considered to be the primitive character state (Engeser 1990). The ammonites had small eggs of about 1 mm in diameter, while the nautiloids generally had relatively large eggs over 2 mm diameter. Living nautiluses have very large eggs and are known to breed over a number of years (see Chapter 4), but there is little to indicate whether the fossil cephalopods were single or multiple spawners.

3.4.2 Depth distribution and locomotion

The vertical distribution of fossil types can be inferred to some extent from the stratigraphy of fossil beds and a knowledge of whether they were preserved in shallow- or deep-water deposits. Depth limits have also been estimated from calculations of the implosion depth of the different low-pressure buoyancy systems of the fossil shell forms (Westermann 1973), and the habitats of several fossil cephalopods have been inferred in this way. The morphology of the cameral compartments of the ammonite shell suggests that they could pump cameral liquid sufficiently fast to allow density-driven vertical movement (Engeser 1990), although in a neutrally buoyant animal the redirection of the water jet by the funnel would move it in any direction with little effort. In the absence of soft parts, there is little reliable information on the locomotion of the extinct cephalopods other than the inferences to be made from living nautiluses (note that in the living nautiluses, the functional equivalent of the coleoid funnel is an incompletely fused tube – the hyponome).

The evolution and diversification of the cephalopods may have been closely linked to their depth distribution and depth limits. Packard (1972) concluded that adaptive radiation and speciation by the fishes and reptiles in shallow water displaced the cephalopods into deeper water. The depth limits imposed by the low-pressure gas spaces in the shell then directed evolution towards shell reduction, and eventually shell loss, in the coleoids. Subsequently, the coleoids were able to re-invade shallow water and survive alongside the shallow-water vertebrate predators and competitors. Alternatively, Aronson (1991) has suggested that both the ectochleates and the endocochleates originally inhabited a wide depth range, and that radiation by the vertebrates eliminated the slower-moving ectocochleates from shallow water. The living nautiluses can exploit zones of low oxygen tension for temporary refuge and feeding by slowly using up the oxygen present in the buoyancy chambers (Boutilier *et al.* 1996). Given their similar morphology, it is likely that the fossil ectocochleates were also able to do this, which would have given them an advantage over the fishes in low-oxygen environments.

3.4.3 Feeding ecology

The presence of beaks in both the nautiloids and the coleoids strongly suggests a very early common origin for this biting structure and implies that the cephalopods have been predatory since their origins. The primitive cephalopod probably resembled the living coleoids in having relatively few arms or tentacles (Flower 1955). The ammonites may have been incapable of hunting and killing large prey, and might have used their jaws as shovels for feeding on the seabed (Lehmann 1981), and there is evidence that, in common with modern cephalopods, they were sometimes cannibalistic. However, Donovan (1993) has emphasised that in spite of the large body of knowledge on ammonite fossil remains, much of the biology of the living animals remains a mystery. It is not known how they swam, what they preyed on, or how they caught their prey, and there is no more information available about the belemnites or the other rarer fossils.

3.4.4 Role as prey

There is precious little information in the fossil record about predation on cephalopods in ancient seas, but on the basis of the scant data available, Lehmann (1981) has concluded that ammonites at least were consumed by mosasaurs (extinct reptiles), turtles and other marine reptiles, fish, crabs and some other cephalopods.

3.4.5 Physiological ecology

The evolutionary development of the cephalopods has been accompanied by major physiological changes. The living ectocochleate cephalopods (nautiluses) are slow moving, and analogy suggests that the same was true for their fossil ancestors. The external shell limited the volume of the mantle cavity and hence the capacity for high-speed jet propulsion. With the internalisation and ultimate loss of the shell, the coleoids traded-off buoyancy for speed and consequently greatly increased the metabolic costs of jet-propelled locomotion (Wells 1994). To meet these energetic costs they evolved gills with increased diffusion capacity, hearts with a higher output of blood, and faster digestion processes. With the ability to swim faster and with more manoeuvrability, the coleoids also evolved more sophisticated sense organs and larger brains. In addition, they became faster growing and adopted the semelparous (unicyclic) reproductive strategy. Some of the coloeids later reversed these evolutionary trends to some extent and became less dependent on jet propulsion by evolving larger fins, which provide more efficient locomotion – at least for routine activity. Some coleoid families, notably the ‘bathyscaphoid’ cranchiid squid, have evolved new means to neutral buoyancy by retaining relatively light ammonium chloride in the coelomic fluid and reducing muscle mass. Others such as the mastigoteuthid squid have become ammoniacal and jelly-like, having evolved watery vacuolated muscle tissues containing high concentrations of ammonium salts (Denton & Gilpin-Brown 1973).

3.5 Evolution of the cephalopod shell

Donovan (1964) concludes that the earliest shells, or orthocones, were simple septate structures with a siphuncle. They were at first cyrtoconic (gently curved), but later became coiled into a tight spiral, or nautilocone. Similar structures evolved at least

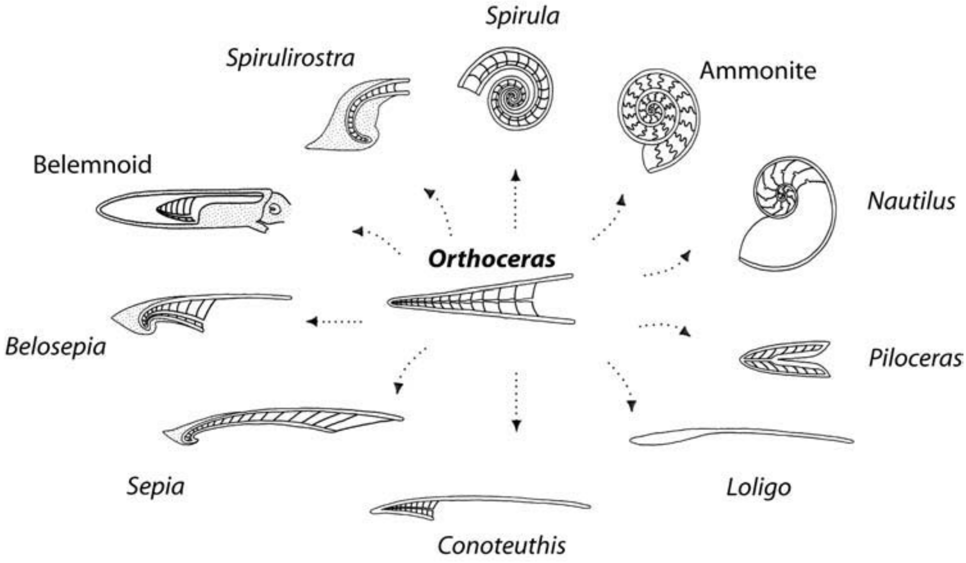

Fig. 3.7 Derivation of various fossil and modern forms of the cephalopod shell or shell remnant from the primitive fossil 'orthocones' of the *Orthoceras* type (after Morton 1958). Evolutionary relationships are not suggested.

twice in the evolutionary history of the cephalopods, once in the Ordovician and again in the Devonian. Uncoiling also took place, most notably in the ammonites, which evolved open coils, gastropod-like spirals and even straight shells. The earliest orthocones were endogastric (coiled ventrally), but exogastric coiling (coiled dorsally) appeared soon after and, in different evolutionary lines, changed from one shell form to the other, which suggests that this feature was not very important biologically. The appearance of the belemnite rostrum (although preceded by cameral deposits in the ectocochleates) was an important evolutionary step that possibly provided a counterbalance to the buoyancy of the straight phragmocone, enabling the animal to adopt a horizontal posture (Fig. 3.7). It was conditioned by the change from an external to an internal shell, which in turn allowed a muscular mantle to evolve. Subsequent evolutionary changes to the shell were the loss of the phragmocone, and finally, reductions to the remaining uncalcified shell framework of the ancestors of the squids and octopuses. This change probably only happened once in evolutionary history judging by the uniformity of the gladius in the present-day squid. The gladius in these squid provides some stiffness to the mantle, and is morphologically and functionally homologous to the belemnite pro-ostracum (except for the conus).

Among the living cephalopods, chambered shells are confined to the nautiluses, cuttlefish and spirulids. The nautilus shell is external, whereas the spiral shell of the spirulids and the straight cuttlebone are internal. Although the shells of nautiluses and spirulids are superficially similar in being coiled and having large chambers, that of the former is exogastric and that of the latter is endogastric. Although the cuttlebone is straight and has small chambers, it is closely related to the shell of the spirulids (Bandel & Boletzky 1979).

3.6 The cephalopod lineage – a cladistics approach

Phylogenetic systematics, or cladistics, is the method of classification of living organisms that makes use of lines of descent, rather than phenotypic similarities, to determine evolutionary relationships. The cladistic approach allows the systematisation of a major taxonomic group such as the Cephalopoda. It starts by considering the living groups, for which more taxonomic characters are generally available than for the fossils, so allowing phylogenetic relationships to be firmly established. In cladistics, taxonomic characters are polarised into plesiomorphic (primitive) and apomorphic (derived) characters. This approach groups organisms strictly on the sequential recognition of common ancestors for monophyla (the inclusiveness of each monophyletic group being based on the relative time of common ancestry). Although practitioners claim that the palaeontological record is too incomplete to reconstruct phylogenies, the fossil record is often used to the determine minimum age of taxa, or species, as well as the chronological sequence in which different taxonomic characters evolved. The cladistic approach facilitates the reconstruction of the stem species of a group, i.e. the latest common ancestor.

Using cladistics, Engeser (1990) reconstructed a cephalopod phylogeny using conventional characters such as shell morphology, but he also included novel characters such as reproductive strategies and developmental strategies of the buoyancy system. This approach produced a somewhat different phylogenetic picture from that obtained by conventional palaeontological reconstructions, but one which is not fully accepted by other taxonomists (Anderson 1996; Doyle *et al.* 1994; Young & Vecchione 1996; Young *et al.* 1998). It suggested that cephalopods are a monophyletic sister group of the gastropods. It also suggested that there are two distinct evolutionary lines in the cephalopods, the Nautiloidea and the Neocephalopoda (Coleoidea). These lines have a hypothetical common ancestor which can be reconstructed as illustrated in Fig. 3.8. Engeser (1990) also concluded that the fossil *Knightoconus* should be considered to be a cephalopod, i.e. a representative of a stem-lineage, and not a monoplacophoran with a chambered shell as was previously thought.

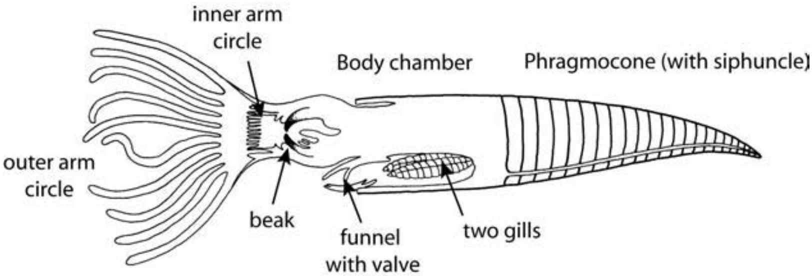

Fig. 3.8 Reconstruction of the hypothetical ancestral cephalopod (after Engeser 1990), the latest presumed common ancestor of *Nautilus* and the Coleoidea.

Chapter 4

Nautilus: the survivor

Summary: The pearly nautilus is a survivor of the previously abundant ectocochleate (shelled) cephalopods. Although the modern species are not of ancient origin (1–5 million years), they are direct descendants of the fossil forms. The shell is chambered and mostly gas-filled to provide near-neutral buoyancy. The five extant species are limited to the tropical Indo-Pacific ocean, where they are characteristic fauna of the outer reef face. Distributed vertically over a normal depth range of 70–500 m, they migrate closer to the surface at night. They appear to be mostly scavengers relying on chemoreception for food detection. They consume a high proportion of crustacean moults in their diet, and perhaps are also opportunistic predators. They are slow growing, taking from about 5–6 years to 11–15 years (depending on species and locality) to reach sexual maturity. Total longevity is unknown, but it is presumed that adult animals breed seasonally for several years after maturity (polycyclic). Fecundity is low with 10–20 large (25–30 mm) eggs per breeding season. In conditions of low oxygen concentration, the nautilus can suppress its anaerobic metabolism to 4–8% of that of the rate at normal oxygen levels, and this capability is the basis for an energy-conservative lifestyle. Consumption fisheries are limited to local markets in the Philippines and New Caledonia; capture for the shell trade and the supply of live specimens for aquarium display is quantitatively more significant.

The only representatives of the early evolution of cephalopods, the externally shelled (ectocochleate) forms, survive to the present as the pearly nautilus. Until 1997, all the surviving species were grouped within the single genus *Nautilus*. A second genus, *Allonautilus*, is now recognised (Ward & Saunders 1997), but we will refer to all representatives of the family Nautilidae as nautilus or pearly nautilus. The large chambered shells of these animals are very well known from drifted specimens, and are prized as museum exhibits and domestic ornaments throughout the world. The interest aroused by their unique lifestyle and evident links with the evolutionary past of the cephalopods (see Chapter 3) has resulted in a large body of popular and scientific literature. Although often popularly characterised as a living fossil (Wells 1986; Davis 1987), genetic evidence from the living nautiloids suggests that the living species originated only between 1 and 5 million years ago (Woodruff *et al.* 1987).

There are many apparent biological differences between the nautiloids and the modern coleoids (Neocoleoidea), most obviously highlighted by the endocochleate (reduced or absent internal shell) body forms of the octopuses, squid and cuttlefish (Fig. 4.1). Living nautiluses have narrow distributional and ecological ranges, and the significant fisheries for them are highly localised. For the purposes of this book we have chosen to treat them as a special case and to restrict our coverage to the main elements of the biology of the group, i.e. the significant differences in lifestyle between nautiloids and the coleoids. The key literature sources used are the reviews by Ward (1983, 1987), the contributed volume edited by Saunders & Landman (1987), and the integrated ecological and physiological studies of O'Dor *et al.* (1993) and Boutilier *et al.* (1996).

Five species of *Nautilus* were recognised by Ward (1987). The most studied, *N. pompilius*, is widely distributed in the tropical Indo-Pacific ocean. This species is highly

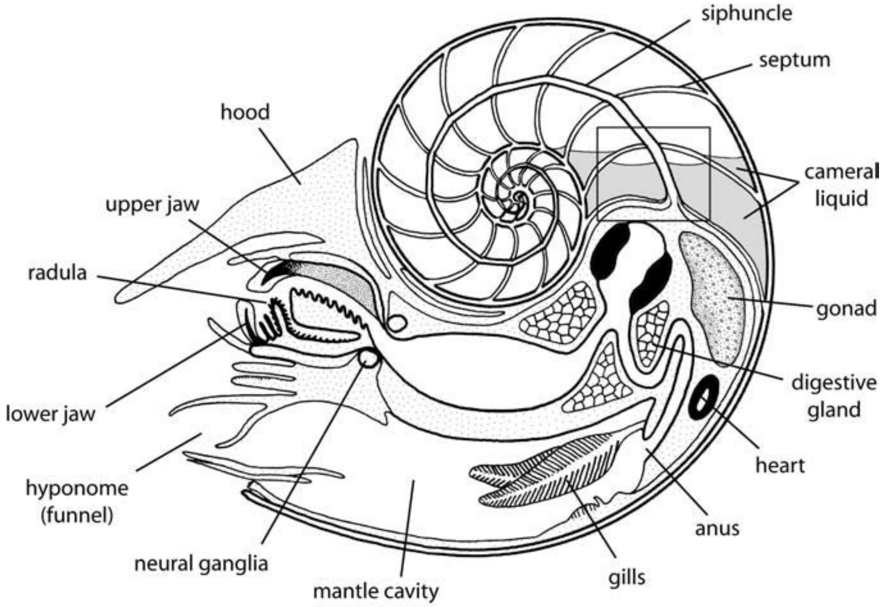

Fig. 4.1 The major morphological components of the shell and soft parts of *Nautilus macromphalus* (after Ward *et al.* 1980). The square outline indicates the region covered by Fig. 4.2.

variable in size and colouration throughout its range (Ward 1987; Woodruff *et al.* 1987; Swan & Saunders 1987). The other well-established species, *N. macrophalus* (New Caledonia) and *N. scrobiculatus* (Northern Australia, Papua New Guinea), have much more limited distributional ranges. The latter species is now assigned to a new genus as *Allonautilus scrobiculatus* (Ward & Saunders 1997) to accommodate the thickly encrusting periostracal layer and wide open umbilicus of the shell. Ward (1987) points out that *N. stenomphalus* from northeastern Australia (Sowerby) and *N. belauensis* from the Philippines (Saunders 1981b) differ only slightly from *N. pompilius*. The status of dubious or questionable species (*N. rupertus*) is discussed by Saunders (1987).

4.1 Form and function

This brief account of the biology of the nautilus is based largely on the *Natural History of Nautilus* by Ward (1987), who in turn makes clear the considerable debt owed to the many early studies, notably the anatomical works by Appelhöf (1893), Griffin (1900), Keferstein (1865), Owen (1832) and Willey (1902).

4.1.1 Shell

The shell is a strong, planispiral structure made up largely of calcium carbonate deposits within a proteinaceous matrix. Like the shells of other molluscs it is composed of three main layers. There is an outer periostracum, which is entirely proteinaceous. In most adult specimens of *N. pompilius* and *N. macromphalus* this is thin or worn away to reveal the calcareous shell beneath, but in *Allonautilus scrobiculatus* it is much thicker and persists throughout life. The periostracum in this species gives rise to leaves of material extending from the surface and giving the shell a furry appearance. The bulk of the shell is composed of the middle layer of calcium carbonate deposited in a prismatic crystal form (long calcite crystals orientated normal to the shell surface). In this layer, the pigment ornamentation of irregular lines is laid down at the time of growth. The innermost layer, next to the soft tissues, is made up from the nacreous aragonitic form of calcium carbonate. These flat, sheet-like crystals, interleaved with organic conchiolin, give a characteristic reflective sheen to the inside surface of the shell and justify the common name of pearly nautilus.

The distinctive shell of the nautilus must not be confused with the calcareous egg case of the pelagic octopod *Argonauta*. This structure is often referred to as the paper nautilus. Its fragile structure is unchambered and is produced by, and held by, two modified arms of the mature female egg-laying octopus. The superficially similar external shape has historically led to confusion between the two structures and speculation as to whether it may have been modelled on the shells of dead ammonites available to the ancestral argonauts as egg shelters (Naef 1921–23; Young 1959), an idea convincingly rejected by Young *et al.* (1998, Chapter 3).

4.1.2 Buoyancy

The shell space of the nautilus is subdivided into a series of chambers by thin but strong calcareous septa. These chambers, called camerae, are formed sequentially throughout growth, and consequently they are progressively larger towards the aperture of the shell. The coiled, subdivided portion of the shell is termed the phragmocone to distinguish it from the final open portion of the shell, the body chamber. Contact is maintained between the body chamber and the cameral chambers by the extension of a strand of vascularised living tissue, the siphuncle (Fig. 4.2). In life, the most recent

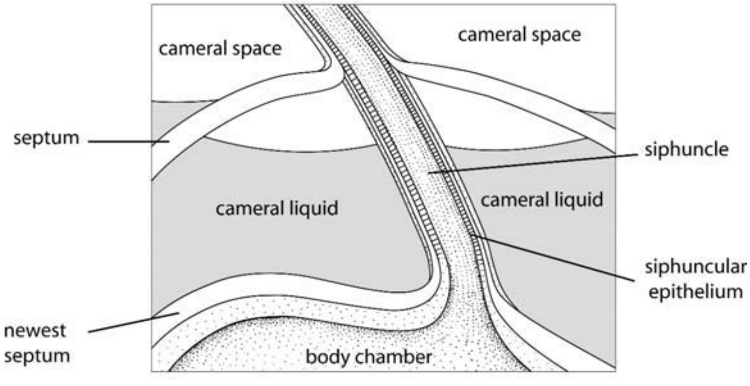

Fig. 4.2 Schematic view of a section of the phragmocone of *Nautilus* showing the relationships between the body chamber, septa and cameral spaces (after Ward *et al.* 1980). The location of this section is shown in Fig. 4.1.

camerae are only partly gas-filled, and their connection to the body of the animal by the siphuncle is the means by which the relative distribution of the gas and fluid in the chambers is maintained.

The body of the animal occupies the final body chamber. It is anchored firmly to the shell by a pair of powerful retractor (adductor) muscles, and sealed against the last-formed septum by the muscular sheet of the septal mantle. Shell growth in the nautilus, as in all molluscs, is a function of the mantle tissue and occurs by accretion only at the shell edge. As the body cavity enlarges due to shell growth, a new septum is formed at the back of the body cavity. Each camera formed is initially fluid-filled; only later is it partially pumped out, the fluid volume being replaced by a nitrogen-rich gas mixture. This process of sequential chamber formation involves the detachment of the septal mantle from the previous septum, after which it must be pulled forward to create the space for new camera formation. The new septum must form behind the mantle in its new position. An even more remarkable aspect of growth and chamber formation is that the massive retractor muscles must be released from their insertion areas on the inner shell surface and re-attached further forward in the body compartment. Optical and transmission electron microscopy of the attachment site of the retractor muscles onto the inner shell wall of the body chamber shows a peculiar membrane junction which seems to be physically weak and adapted for this periodic detachment/reattachment (Isaji *et al.* 2002). The detailed mechanisms of this process have been subjects of a large volume of research (see Denton & Gilpin-Brown 1966; Denton 1974; Greenwald *et al.* 1980; Greenwald & Ward 1987; Ward *et al.* 1977; Ward & Martin 1978; Ward 1979; Ward *et al.* 1980), as well as speculation and controversy about details of the mechanisms and their relationship to ecology and growth; a debate eloquently expounded by Ward (1987).

Growth in pearly nautilus continues until the final body size is reached and the animal sexually matures at an age of 5–6 years. Unlike other molluscs, the process of growth by sequential chamber formation is complicated by the maintenance of neutral buoyancy (see Box 2.1). Owing to growth, and the addition of tissues and shell material denser than seawater, the maintenance of neutral buoyancy requires continuous adjustment of the gas volume contained in the shell. This process, first elucidated in the classic work of Denton & Gilpin-Brown (1966), involves the withdrawal of fluid from the newly completed camera by osmotic forces generated at the interface between the siphuncle tissues and the cameral fluid, and its replacement by a nitrogen-rich gas mixture at a pressure of 1 atmosphere (see Greenwald & Ward 1987; Ward 1987 for reviews). Clearly, the structure of the shell must be strong enough to resist the hydrostatic pressure of the water column. The implosion depth at which the shell is crushed by the pressure of the water column is usually estimated to be in the range 700–800 m (Saunders & Wehman 1977).

4.1.3 Locomotion

Although normally neutrally buoyant, *Nautilus* may make frequent, perhaps daily, vertical migrations between the surface and depths of several hundred metres, with an estimated maximum depth of about 600 m. Whether these vertical movements across the slope can be generated from adjustments in the fluid/gas balance of the shell compartments has frequently been discussed. On balance, the rate at which adjustment could take place and the volume of fluid available for movement (Heptonstall 1970) appears to make this mechanism for vertical migration improbable (Ward 1987). Up and down movements in the water column are driven by directional water jets from the funnel-like tissue fold (hyponome), while just sufficient gas is maintained in the shell for neutral buoyancy.

The void of the mantle cavity is filled with seawater and only partly separated from the surrounding sea. Contractions of the retractor muscles pull the head into the shell, displacing water from the mantle cavity through the hyponome. This is the functional equivalent of the funnel of the coleoids and serves to form a directional jet of expelled water. A jerky swimming motion is thus achieved by weak jet propulsion (Chamberlain 1988). The gills (paired on either side, the tetrabranch condition) occupy the inner part of the mantle cavity and are aerated by this water movement (Bizikov 2002). As in other molluscs, the mantle cavity also receives the faeces and the products of excretion, and contains the genital openings.

4.1.4 Head and eyes

The head encloses a large and muscular buccal mass. There is a pair of heavy chitinous beaks which are reinforced with calcified deposits along their cutting edges, and a wide radula of simple teeth. The central nervous system is concentrated in the head behind the buccal mass and surrounds the oesophagus. It is not as large or compact as that of the coleoids, but still shows considerable subdivision of parts and presumably function (Young 1965, 1987). Large cup-shaped optic lobes lie on either side of the brain and are connected by optic nerves to a large stalked eye on the side of the head. Compared with those of the coleoids these are primitive structures. There is no lens, and the eye appears to function on the basis of a pinhole camera, focusing light on the retina through a narrow pupil of average diameter 2 mm (Hurley *et al.* 1978). The pupil is capable of adjustment in diameter (Barber & Wright 1969), and the eye itself can be slowly moved to compensate for changes in the position of the animal, but the lack of a lens and the fact that the eye is open to seawater probably results in very poor image quality. The possible use of vision by nautiluses in the deepwater habitat is still uncertain (Barber 1987; Muntz 1987).

4.1.5 Tentacles and their functions

The head bears numerous tentacles of a form quite different from those of the neocoleoids and without any suckers. Three groups of tentacles are distinguished. There are four pairs of ocular tentacles, which are small weak appendages arising just in front of, and behind, the eyes. Bidder (1962) demonstrated their reaction to the presence of nearby food, and postulated a chemosensory function for them. The second group of 19 pairs of digital tentacles is subdivided by Bidder (1962) into three functional groupings, also based on their reaction to food: an outer ‘alert’ group, probably also chemosensory, a middle ‘search’ group which contacts the food, and an inner ‘feeding’ group which transports the food to the mouth. Both ocular and digital tentacles are morphologically differentiated into two distinct portions, i.e. a narrow distal section, or cirrus, which can be completely retracted into a proximal sheath. Although no suckers are present on the cirrus, these distal portions of the tentacles are highly adhesive owing to the presence of numerous fine grooves orientated across the long axis. The remainder of the total of 90 or so tentacles are the labial tentacles surrounding the mouth region. In both sexes some of these are modified for use during copulation. In males, a group of labial tentacles on either side is highly modified to form two copulatory organs involved in sperm transfer to the female. The larger of these, on the right or left side of the body, is the spadix, which may grow to comprise 6–7% of the soft body weight of the male (Ward 1987). It is paired with the smaller antispadix on the opposite side. The large size of these organs accounts for the increased cross-sectional width of the shell in mature males.

4.1.6 Skin colouration

The whole head region is overlain by a hood of tough connective tissue that merges with the bases of the marginal and some of the digital tentacles. Attached to the surface of the last shell chamber by a flexible layer of black tissue, the hood protects the surface of the head and closes the aperture of the shell when the animal retracts into the body chamber. In this respect it is functionally equivalent to the gastropod operculum. The reddish-brown pigmentation of the skin surface of the hood, head and tentacle is not contained within cells under active control. There are no true chromatophores in nautiluses, and no rapid changes in colour pattern are possible.

4.2 Ecology

4.2.1 Geographic and depth distribution

The shells of nautiluses remain buoyant after death, and consequently may be carried well outside the distribution area of the main populations. The main areas for living nautilus species, and the extended range of drifted shells and drifted living individuals are shown in Fig. 4.3. The capacity for ocean-scale drift by the shells clearly has the potential to confuse present distributional records, and has led to a commonly held view among palaeontologists that that the distribution of nautilid (order Nautilida) shells in fossil beds are of little palaeobiogeographic value. However, Chirat (2000) argues that, with some exceptions (*Aturia*), post-mortem drift was not significant in disturbing the fossil record.

The bulk of the ecological information available on modern nautilus has been obtained from *N. pompilius* in the Philippines (reviewed by Hayasaka *et al.* 1987) and Palau in the Western Caroline Islands (Saunders 1987). Other sites which have proved accessible for scientific studies on nautiluses includes Fiji, several sites around Papua New Guinea, off Lizard Island on the Great Barrier Reef of Australia, New Caledonia, the Samoas and Tonga (reviewed by Saunders 1987). Information from scientific trap

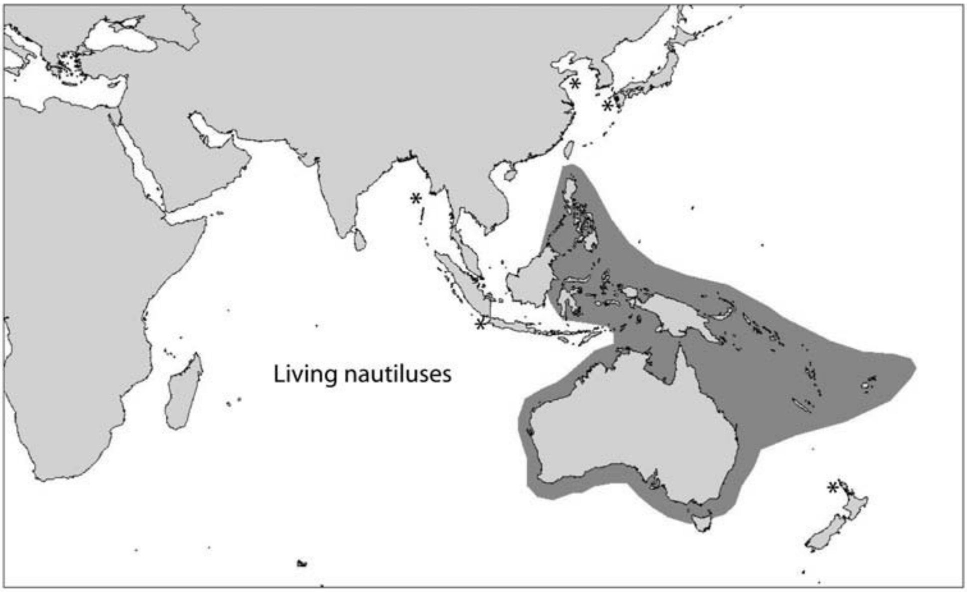

Fig. 4.3 The main area of distribution of living populations of nautiluses based on live capture records. Exceptionally, occasional live individuals have been found elsewhere (shown by * on the map), but empty shells are recovered throughout the western Pacific and Indian Oceans, where the buoyant shells are transported by the main oceanic current systems (after House 1987).

surveys has been supplemented by still and movie photography in baited traps (Saunders 1984b, 1985), tagging and recapture programmes (Saunders 1981a, 1983, 1984a, 1985), acoustic tracking and telemetry of tagged animals (Carlson *et al.* 1984; O'Dor *et al.* 1993; Ward *et al.* 1984) and localised intensive fisheries (Haven 1972, 1977a, b).

Nautilus belauensis in Palau is characteristically a reef-slope inhabitant ranging in depth maximally from the surface to about 500 m, but with a preferred depth range of 150–300 m (Fig. 4.4). A benthic scavenger and opportunistic predator, it relies on chemoreception to detect food sources, probably using regular vertical migrations to sample chemical trails (O'Dor *et al.* 1993). The preferred lower depth range is probably set by the requirements of maintaining the neutral buoyancy mechanisms against increasing hydrostatic pressure, as well as vulnerability to predators such as large teleost fish or sharks. The maximum possible depth is set by the risk of shell implosion or siphuncle rupture. The upper limit varies with the geographical area and with season, the animals being active and closer to the surface at night, and is probably set by a temperature maximum of about 25°C.

Tagging studies have shown that nautilus is capable of lateral movement along the reef face for distances up to 150 km over a year (Saunders & Spinoza 1979). Individuals tracked by telemetry travelled at rates of 0.45–0.60 km/day (Carlson *et al.* 1984). Integrating lateral and vertical movements over shorter (daily) intervals, O'Dor *et al.* (1993) estimated actual rates of travel up to 4.3 km/day. Most studies agree that there is a regular vertical migration to shallower water at night.

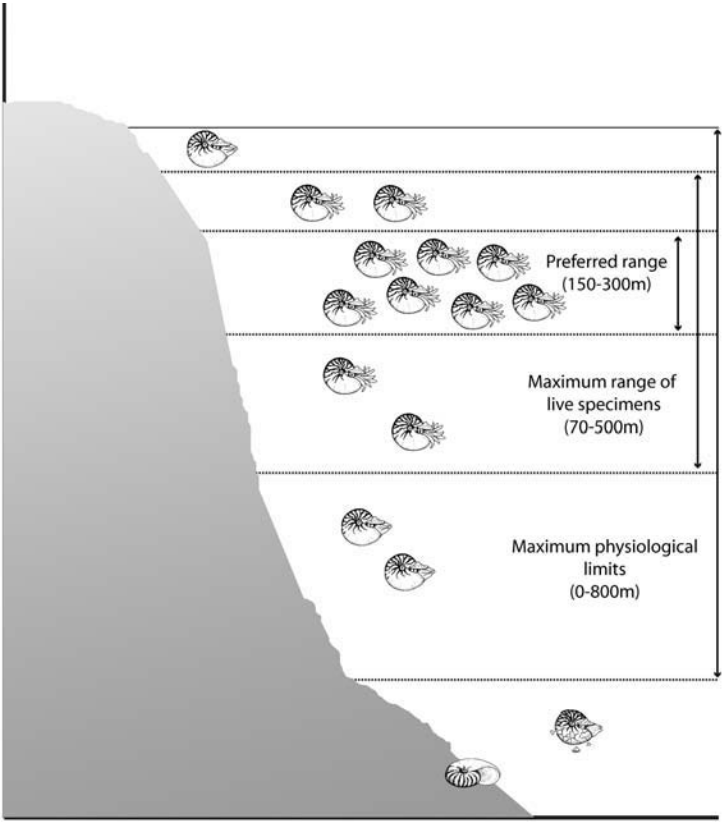

Fig. 4.4 Summary of the preferred habitat range of *Nautilus belauensis* in Palau (after Saunders & Ward 1987).

4.2.2 Food

There is relatively little information on the diet of nautiluses. A major problem with diet determination has been that most specimens have been caught in baited traps, and the crop contents tend to represent the composition of the bait in the trap. Diver-caught specimens of *N. macromphalus* in New Caledonia (Ward & Wicksten 1980) had fed mostly on reef crustacea, particularly the common hermit crab (*Aniculus aniculus*), but there was some evidence of the presence of fish in the diet. In the aquarium conditions of Waikiki (Carlson 1987), shrimp (*Heterocarpus laevigatus*), fresh fish and crustacean pieces are readily eaten, and live deep-sea crabs (*Thelixiope* spp.) are rapidly located and killed. Smaller live crabs (*Scylla serrata*) and shrimps (*Saron marmoratus*) were not captured. The consumption of the exoskeleton moults of lobster and other crustacea has been seen many times in the wild (Magnier & Laboute 1978; Ward & Wicksten 1980), and they are accepted quickly by aquarium-held animals (Carlson 1987).

Using computer tomography techniques, Westermann *et al.* (2002) traced the movement of food through the gut and the timing of different phases of digestion in living

Nautilus pompilius. Like other cephalopods, ingested food reached the stomach in small pieces and was then stored in the expandible crop. It reached the midgut gland (digestive gland) 3 h after intake and the rectal loop after 5 h. The total time lapsed between food intake and gut evacuation was about 12 h, which is comparable to nectobenthic sepioids and benthic octopus, but significantly slower than that reported for loliginid squid. On structural grounds (Ruth *et al.* 1999) there is some evidence to suggest that the midgut glands are involved in excretory activities as well as digestion. Owing to mining activities of its mineral soils, the coastal waters of New Caledonia are particularly enriched in trace elements such as Co, Cr and Fe, which contaminate benthic invertebrates such as bivalves and gastropods. Bustamante *et al.* (2000) showed that *N. macromphalus* from the reef had metal concentrations much higher than those of cephalopods from coastal waters, and more similar to those of the local invertebrates, and that the highest levels were found in the digestive gland, and renal and pericardial appendages.

4.2.3 Predation

Despite their heavy, protective shell, the pearly nautilus is subject to predation. Triggerfish (*Balistoides viridescens*) have been witnessed by divers attacking live nautiluses in midwater and damaging the shell. Healed injuries to the shells of live-caught specimens infer that attacks by fish are common (Saunders *et al.* 1987). Somewhat surprisingly, it seems that octopuses frequently attack and kill nautilus. Tucker & Mapes (1978) first observed that shell specimens offered for sale as souvenirs by dealers frequently had boreholes in the shell of the type associated with octopus predation. Many of these were apparently sub-lethal attacks, i.e. the shell was not completely pierced by the borehole. Subsequently, boreholes have been found in nautilus from many areas, and these attacks seem to be a normal hazard of life (Fig. 4.5).

4.2.4 Growth

The complications of understanding the growth process in nautilus have been mentioned already:

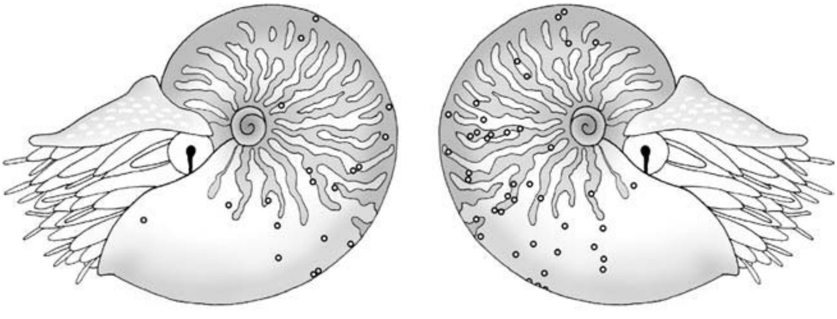

Fig. 4.5 Composite diagram of the distribution of octopus boreholes (∘) on the left and right sides of *Nautilus*, showing the concentration in the area of the posterior portion of the body chamber, approximately over the location of the retractor muscles and viscera (after Saunders *et al.* 1987).

- an increase in the mass of the soft body parts is accompanied by an accretion of shell at the aperture, forming a spiral of increasing radius;
- the animal periodically moves forward, vacating a space at the rear of the body cavity which is then sealed off as the next cameral chamber by formation of a new septum;
- near-neutral buoyancy is maintained throughout while the mass increases.

Throughout most of the growth period the septa are secreted at equal angular intervals, contributing to the regular formation of the spiral shape. Shell growth at the aperture is also incremental, and a series of 'growth lines' can be seen on the shell surface and in sections of the shell. Neither of these signals of discontinuous shell growth can be precisely related to time intervals and hence used to study age and growth rate. Comprehensive reviews of growth issues are available in Ward (1987), Landman & Cochran (1987) and Collins & Ward (1987).

Direct estimates of growth rate have been made using release–recapture of tagged animals (Saunders 1983) and captive aquarium specimens (Ward 1987). Indirectly, growth rates have been inferred from the decay rates of the radioactive nuclides of lead and polonium incorporated into the shell. The ratio of ^{210}Po (half-life 138 days) to ^{210}Pb (half-life 22.3 years) has been used by Cochran *et al.* (1981) and Cochran & Landman (1984) to date the formation of sequential septa on the assumption that the ratio of the elements in seawater does not vary. Landman & Cochran (1987) combined estimates for rates of apertural growth obtained by both methods and for two species (*N. belauensis* and *N. pompilius*) for a range of shell diameters from 55 mm to 210 mm (Fig. 4.6). These show apertural growth estimates of as much as 0.45 mm/day in the smallest animals, falling to 0.1 mm day as the shell diameter approaches 200 mm, when growth ceases. Only the largest sized animals were reproductively mature. The duration of individual chamber formation is variously estimated to be between >100 days and <1 year.

The wide range of estimates of apertural growth rate and chamber formation reflects the different methodologies used and the real differences between species and localities. Nevertheless, all evidence currently available suggests that nautiluses take years to grow to full size and reach reproductive maturity: minimally 2.5 years for *N. macromphalus* in aquarium conditions (Martin *et al.* 1978) to a maximum of 15 years for *N. belauensis* based on the growth of recaptured animals (Saunders 1983).

4.2.5 Reproduction

The onset of sexual maturity in *Nautilus* is preceded by characteristic changes in shell development, which suggest that growth to maturity is programmed (Collins & Ward 1987). Sexual maturity develops after the formation of the final, more closely spaced septum and the completion of the phragmocone. It is accompanied by cessation of the deposits of brown pigment in the still-growing shell margins, and progressive broadening of the body chamber eventually to accommodate the mature reproductive organs. Collins & Ward (1987) estimate that the process of sexual maturation takes about 3 years from beginning to end, during which time the relative size of the gonad will have

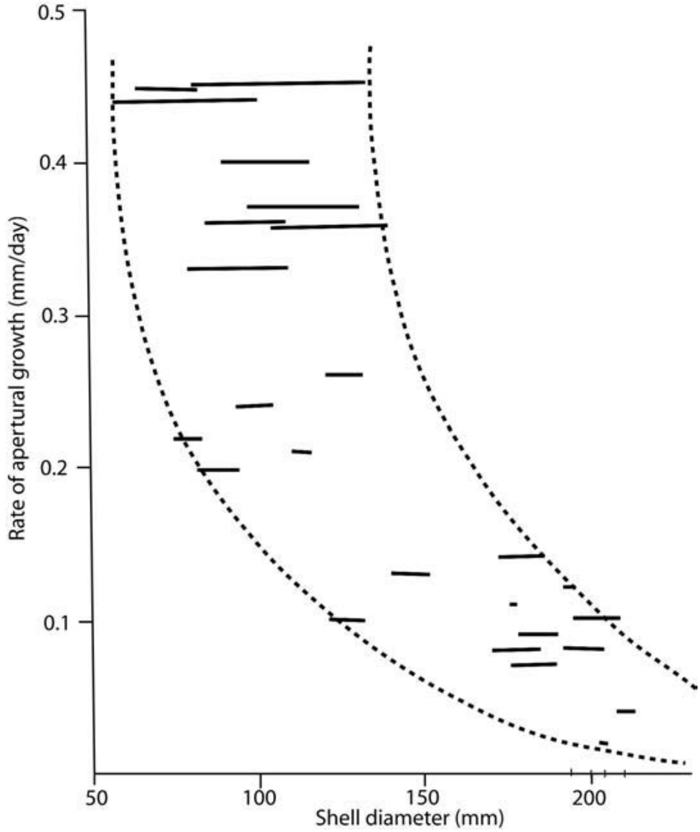

Fig. 4.6 Rates of apertural growth (mm/day) for *Nautilus* at a range of shell sizes (mm diameter), based on original studies by several authors compiled by Landman & Cochran (1987). Indicative curves enclosing the range of growth rates at different sizes are shown.

grown 100-fold from 0.06% to 6% of body weight. In males, the accessory reproductive organ (spadix) grows from 0.55% of body weight to 7.7%, and this accounts for the sexual dimorphism of shell shape (wider in males).

Like the neocoleoids, the nautilus is dioecious (separate sexes) and does not change sex throughout its life (Haven 1977b). Mature male sperm are packaged into spermatophores and stored in the spermatophoric sac. Later they are moved through the mantle cavity into the buccal area ready for copulation, head to head, with the female. The eggs laid by the female are individually enclosed in a thick double capsule, 25–35 mm in length and weighing up to 4 g. Although live eggs have not been recovered in the field, numerous eggs have been laid in aquarium conditions. Eggs are laid seasonally, and Hamada *et al.* (1978) reported the greatest number laid by a single female to be only 11. Although there is no direct evidence from the field, it is presumed that once mature, the reproductive life of the adult lasts for a number of seasons and that, in contrast to all of the coleoids, reproduction in *Nautilus* is polycyclic. Even so, with perhaps only 10–20 eggs per breeding season, the lifetime fecundity will be low.

The exhibition and breeding of pearly nautilus in captivity have been pioneered by public aquaria in tropical regions. The Noumea Aquarium in New Caledonia, the

Yomiuri-Land Aquarium in Japan and the Waikiki Aquarium in Hawaii each in turn played leading roles. Nautiluses readily mate in aquarium conditions, and chemoreception by the female is important in mate-finding (Basil *et al.* 2002). Females seek out a secluded space to deposit eggs. Norman (2000) reports that on average each female will lay about 1.5 eggs per month throughout the year, and will continue to do so for several years. Although numerous eggs were laid in aquarium conditions, none hatched and they were generally thought to be infertile because no embryos could be found. It is now known that nautilus embryos can take up to a year to develop and hatch at 21–24°C. This is the warm end of the temperature range over which the adults are distributed, and it is suggested (Norman 2000) that eggs may be deposited naturally on the slopes of coral reefs in shallower water rather than in the cold deep waters at the base.

4.2.6 *Activity*

Activity levels in the wild (O'Dor *et al.* 1993) and the special features of the respiratory and circulatory systems (Boutilier *et al.* 1996) show that pearly nautilus can survive very low oxygen concentrations and is adapted for a low-energy lifestyle. It achieves this by suppression of the anaerobic metabolic rate to as low as 4–8% of that at normal oxygen concentrations, coupled with some reliance on anaerobic energy production (Boutilier *et al.* 1996). This low-energy strategy contrasts with that of the coleoids (Wells & Clarke 1996), and allows nautiluses to remain active in deep-sea environments with low oxygen levels, maintaining itself as a scavenger with probably rather intermittent opportunities to feed. The argument is taken further by Wells (1999) to suggest that the ability of nautilus to remain intermittently aerobically active at low oxygen tensions has been an important factor in its continued survival. Progressive oxygenation of the oceans led to its fossil relatives, the nautilids and ammonites, becoming trapped between depth limits imposed by the buoyancy mechanism and the increasing competition from fish predators and competitors in the shallower water.

4.3 Fisheries

The interest to fisheries for human consumption is limited to local markets in the Philippines (*Nautilus pompilius*) and New Caledonia (*N. macromphalus*). They are caught by means of traps baited with fish or meat at 60–240 m depth in the Philippines and 300–400 m in the Coral Sea, New Caledonia (Roper *et al.* 1984). Trapping for scientific purposes, Norman (2000) described average catch rates of five *N. pompilius* per trap set at 200–250 m off Osprey Reef, Coral Sea, which is a seamount rising to the surface from water over 100 m deep. Although meat is eaten locally, much more significant is their traded value as shell specimens for the tourist trade (on sale worldwide) and for live displays in major public aquaria.

Chapter 5

Biodiversity and zoogeography

Summary: The classification and grouping of cephalopod species is in a relatively unsettled state. There is a poor fossil record of the living forms, many are difficult to catch and specimens are often damaged, leading to loss of taxonomic characters and poor representation in museum collections. Global interest in biodiversity in relation to global change, and the development of molecular genetic markers, has brought a renewed interest in the field, but still over 50% of the cephalopod fishery catch is not identified to species. New species continue to be found, and there are probably many more awaiting discovery. There are two sub-classes of living cephalopods, the shelled Nautiloidea and the Coleoidea, which includes all other living families. The simplest classification of the Coleoidea recognises four orders: the cuttlefish and related families (Sepioidea), squid (Teuthida), vampire squid (Vampyromorphida) and octopuses (Octopodida). More detailed classifications differ in how the Sepioidea and Octopodida are subdivided. Advances in molecular genetics are providing clarification of relationships at various taxonomic levels.

Many cephalopod genera are monotypic, whilst two (*Sepia* and *Octopus*) are species-rich. Genera with many species are from coastal waters or deep benthic habitats, while the low-diversity genera are largely mesopelagic. The cephalopods are all marine, are rarely present in water of lowered salinity, and are found from the polar regions to the tropics. They are present in virtually all habitats from the surface layer of the ocean to 5000 m. Perhaps because of the unsettled state of the taxonomy there has been relatively little work on broad biogeographic patterns in the class. On the continental shelves the sepiids and loliginids occur from the tropics to cool temperate waters, but not in polar seas, and the sepiids are absent from the New World; the ommastrephids are associated with western boundary currents and coastal upwelling regions. In the open ocean, the biogeography of the pelagic squid is broadly similar to that of other pelagic forms, and there are warm-water, cool-water and widespread groups; deep-living species generally have wider geographic distributions than near-surface forms. Among the octopuses, the older groupings (clades) are widespread in the remnants of the former circumequatorial Tethys Sea, whereas more recent lines are restricted to particular areas. Deep-water octopods inhabit cold waters, and their distribution seems to be related to high-productivity regions.

Cephalopod classification started with Aristotle in the fourth century BC. He distinguished between octopus and squid and, significantly, placed them within a group including the shelled molluscs. In the eighteenth century, Linnaeus divided the cephalopods into shelled and unshelled forms, but this distinction was later dropped. Throughout the nineteenth century developments in cephalopod classification continued to be made until the 1930s, when the basic scheme used today was finally settled (Table 5.1).

Species descriptions that are still largely accepted today started with the publication of D'Orbigny's *Histoire Naturelle* in 1848, which contained accounts of some 16 genera and 129 species. There were then two periods from 1879 to 1886 and from 1907 to 1936

Table 5.1 Early cephalopod workers and their contributions to systematics (compiled from Voss 1977a).

Workers	Date	Contribution to cephalopod classification
Aristotle	4th century BC	Identified the decapods and octopods and placed them in the class 'Malakia'
Linnaeus	1758	Split the cephalopods between the 'Vermes Testacea' and the 'Vermes Mollusca'
Schneider	1784	Abandoned Linnaeus' division of the cephalopods
Cuvier	1798	Gave the class the present name: Cephalopoda
Leach	1817	Reinstated Aristotle's Octopoda and Decapoda
Owen	1832	Divided living cephalopods into two sub-classes: Tetrabranchiata and Dibranchiata. Placed all fossils into one or other of these. Divided the Tetrabranchiata into two families: Nautilidae and Ammonitidae
Bather	1888	Proposed the three groups of equal status, independent of gill number, that are used today: Nautiloidea, Ammonoidea and Coleoidea
D'Orbigny	1845	Split the squid into two sub-orders: Oegopsida and Myopsida
Reinhardt & Prosch	1846	Split the octopuses into the Pteroti and Apteri
Hoyle	1886	Split the octopuses into the Lioglossa and Trachyglossa
Grimpe	1917	Split the octopuses into the sub-orders accepted today: Cirrata and Incirrata
Naef	1921/23	Re-classified the cephalopods, providing the starting point for modern classification
Pickford	1939	Modified the dibranchiates by adding the Vampyromorpha

when large numbers of species were described. The first period was dominated by the work on deep-sea species by Steenstrup, Hoyle and Verrill, as well as the early work of Pfeffer and Joubin. The second period was the time when the results of two particularly important expeditions were produced. An important account of the cephalopods of the *Valdivia* Expedition was published by Chun in 1910, and a monograph of the oegopsid squid by Pfeffer (1912), was based on the cephalopods caught by the German Plankton Expedition. Following that, Joubin, Naef, Robson, Sasaki and Berry brought the number of known species up to about two-thirds of those recognised today. An overview of these early contributions to cephalopod systematics can be found in Voss (1977a).

For two decades after the 1930s there was a lull in the development of knowledge of the cephalopod species, and then in the mid-1950s new interest started to develop which has continued with the introduction of new biochemical and molecular techniques. Several important keys and guides for identification have been produced over this time (Roper *et al.* 1969, 1984, 1985; Okutani 1973, 1995; Nesis 1987; Sweeney *et al.* 1992; Voss *et al.* 1998a, b).

5.1 Current status

By comparison with the situation in other major groups of animals, cephalopod systematics is in a relatively unsettled state. There are several reasons for this, starting with the fact that there is a lack of any substantial fossil record for the recent cephalopods. The limitations of scientific sampling gear for capturing fast-swimming species that have excellent vision has meant that many species are rare in scientific collections. Many of these captured specimens are damaged, leading to loss of taxonomic characters, and others are only known from the small early-life stages that are easier to catch (Voss 1977a). These early stages are often sufficiently different from the adult to cause confusion in the literature, where genera and species have been created on the basis of different life stages. Many descriptions have used a number of characters without any critical assessment of their value or reliability for systematic purposes and, at least until recently, there has been little study of cephalopod comparative anatomy to support the development of any phylogenetic classification of the group since Naef's monumental work (1921–1923). Systematics generally became an unfashionable area of biology over the last 20–30 years of the twentieth century and attracted only a relatively small proportion of research funding. However, recognition of the importance of biodiversity in a changing global ecology has created renewed interest in the subject at a time when molecular biology is providing powerful laboratory tools for taxonomists, and new computer software packages give sophisticated support for complex cladistic analyses. Cephalopod systematics is therefore enjoying something of a revival at an exciting time for the field of systematics in general.

The generally poor state of knowledge of cephalopod taxonomy has implications for the understanding and management of their fisheries (Vecchione *et al.* 2000). Over 50% of the global cephalopod catch recorded by the Food and Agriculture Organisation of the United Nations (FAO) is not segregated into single species categories, and this significantly reduces any value the data may have for population assessment (Boyle & Boletzky 1996; Chapter 17). The commercial fisheries exploit the most diverse families, namely the ommastrephids, loliginids, octopodids and sepiids, and lack of taxonomic knowledge has been highlighted in several fisheries (Roper 1983). In New Zealand, the fishery for the little known ommastrephid *Nototodarus sloanii* was well developed in the 1970s before it was realised that another species, *Todarodes filippovae*, which is similar in general appearance, was being taken as a by-catch. Furthermore, subsequent research, including allozyme studies, revealed that in fact two species of *Nototodarus* were present in the catches (Smith *et al.* 1981), a distinction simultaneously described from conventional taxonomic characters (Kawakami & Okutani 1981). In another case, Voss & Ramirez (1966) showed that an octopus fishery in Mexico, assumed to be exploiting *Octopus vulgaris* Cuvier 1797, was actually exploiting *Octopus maya*. Given the restrictions to gene flow that have been shown to exist for octopuses over quite small distances (Allcock *et al.* 1997), and which may well apply to cuttlefish and loliginid squid as well, more instances of mistaken identity in fisheries catch, or of fisheries exploiting undescribed species, are likely to be found. Good taxonomic knowledge of exploited species is a fundamental prerequisite to understanding stock structure for management purposes, so there are likely to be important taxonomic questions to be tackled in the future.

The cephalopods are a problematic group for morphological study because they have soft bodies with few hard parts. The preserved specimens therefore exhibit fewer reliable taxonomic characters, and the fragile pelagic ones are also likely to be damaged by capture. Differences in external texture and pattern, habitat partitioning by use of substrate characteristics, and differences in diurnal behaviour have been shown to be important species differences for shallow-water octopuses (Roper & Hochberg 1987, 1988; Norman & Hochberg 1992; Norman & Sweeney 1997; Norman 2000). The use of these characters in conventional systematics is presently limited to the relatively few cases where they can be positively linked to traditionally examined museum specimens. In spite of the problems, systematists have generally accepted that a conventional description of taxonomic characters, however difficult, remains the best approach to cephalopod taxonomy (Roeleveld 1988). This view was recently reinforced by Ogden *et al.* (1998), who tested meristic data on several Antarctic octopus species using multivariate statistics, and found that using this approach, it was not possible to discriminate below the level of genus. Recently, cladistic analysis has highlighted the need for more taxonomic characters to be used in cephalopod systematics, and novel features such as arterial branching patterns and muscle anatomy have been used, for example, in the analysis of octopus phylogeny (Voight 1997). The problem of intra-specific groupings in many cephalopods, distinguished by breeding season, locality, or size at reproduction, has been highlighted by Nesis (1998b), who concluded that no single methodology was reliable, and that a fully integrated approach, using all available methods, was the way forward.

Given the current status of cephalopod systematics, it has to be emphasised that any system of cephalopod classification is part of an on-going process, and it should be remembered that many problems remain unresolved. Although progress has been made in recent years, the field is still in an unsettled state. At present there are only about 700 described species of living cephalopods compared with some 17 000 fossil species (Brusca & Brusca 1990), but new species are regularly reported in the scientific literature. A single expedition to the Antarctic by the German research ship *Polarstern*, for example, caught at least seven new species of the Antarctic octopus genus *Pareledone* (Allcock *et al.* 2001). A simple extrapolation of the number of species of *Pareledone* plotted against the number of hauls in Antarctic Peninsula waters suggests that in deep water, new species await discovery in this region alone.

5.2 Taxonomic characters

The main morphological features used for taxonomic purposes in the cuttlefish, octopus and squid are shown in Figs. 5.1–5.3. Any serious attempt to identify cephalopods requires a detailed knowledge of the external and internal morphological characters, the bases for which are found in the works of Hoyle (1886), Robson (1929, 1932), Voss (1963), Adam & Rees (1966), Voss & Williamson (1971), Roeleveld (1972), Okutani (1973, 1980), Okutani *et al.* (1987), Roper *et al.* (1984), Nesis (1987) and Voss *et al.* (1998a, b) for information on adult morphology, and on juveniles see Sweeney *et al.* (1992). A detailed and comprehensive account of standardised methods for measuring and describing cephalopods is given by Roper & Voss (1983). This supplies guidelines for the recording of new or unusual material.

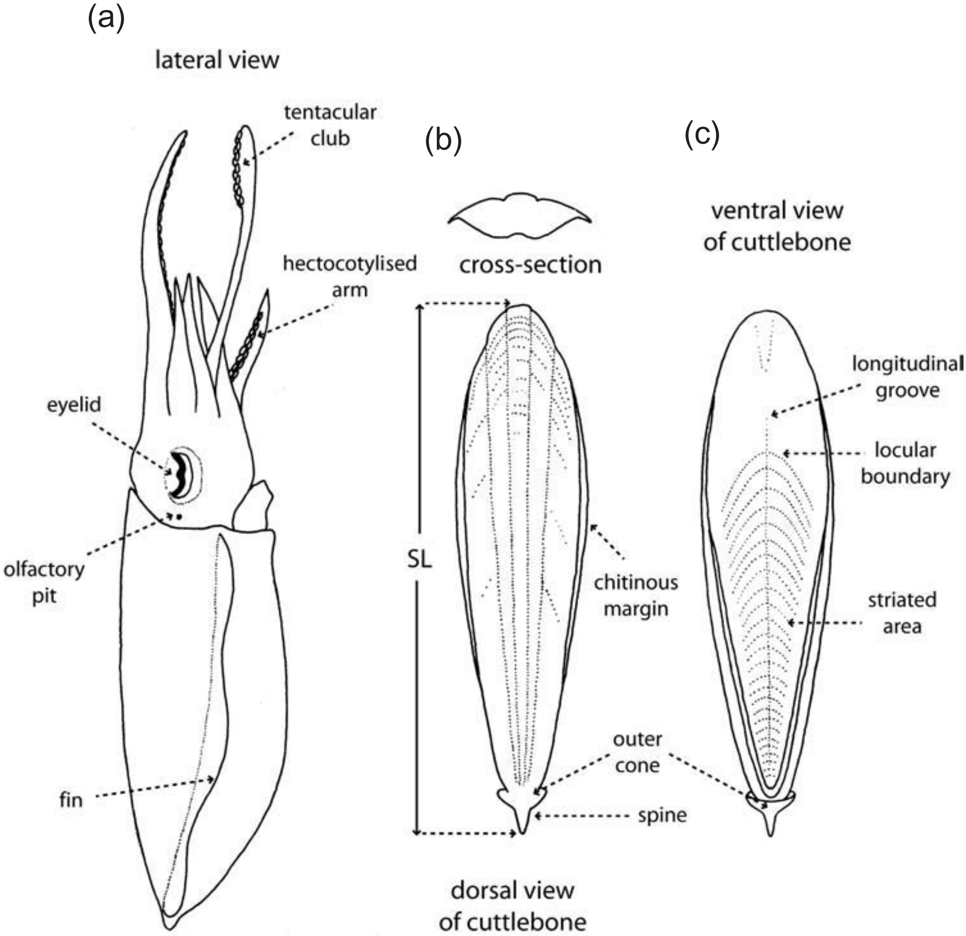

Fig. 5.1 Key morphological characters used for taxonomic analysis of the cuttlefishes (not to scale). (a) Whole animal. (b) Dorsal view of cuttlebone with cross-section. (c) Ventral view of cuttlebone (SL, cuttlebone (shell) length). After Okutani *et al.* (1987).

5.3 Systematics

The molluscan class Cephalopoda contains two sub-classes of living cephalopods. The Nautiloidea contains two genera, one of which was only recognised recently (Ward & Saunders, 1997), and these are the so-called living fossils with chambered external shells that are thought to originate in the Cretaceous. The Coleoidea, which includes all other living families, is sometimes sub-divided further into the Neocoleoidea to exclude the extinct belemnites, which were also coleoids. It has been proposed that the terms dibranchiate and tetrabranchiate, as characters distinguishing the coleoids from the nautiloids and other ectocochleates, should be abandoned as taxonomic divisions because, in the fossil forms, little or no soft tissue is preserved so there is no way of telling how many gills they had (Clarke 1988a).

The living Coleoidea (Neocoleoidea) all have an internal shell (which in some groups is much reduced or vestigial), a single pair of gills (i.e. they are dibranchiate), a

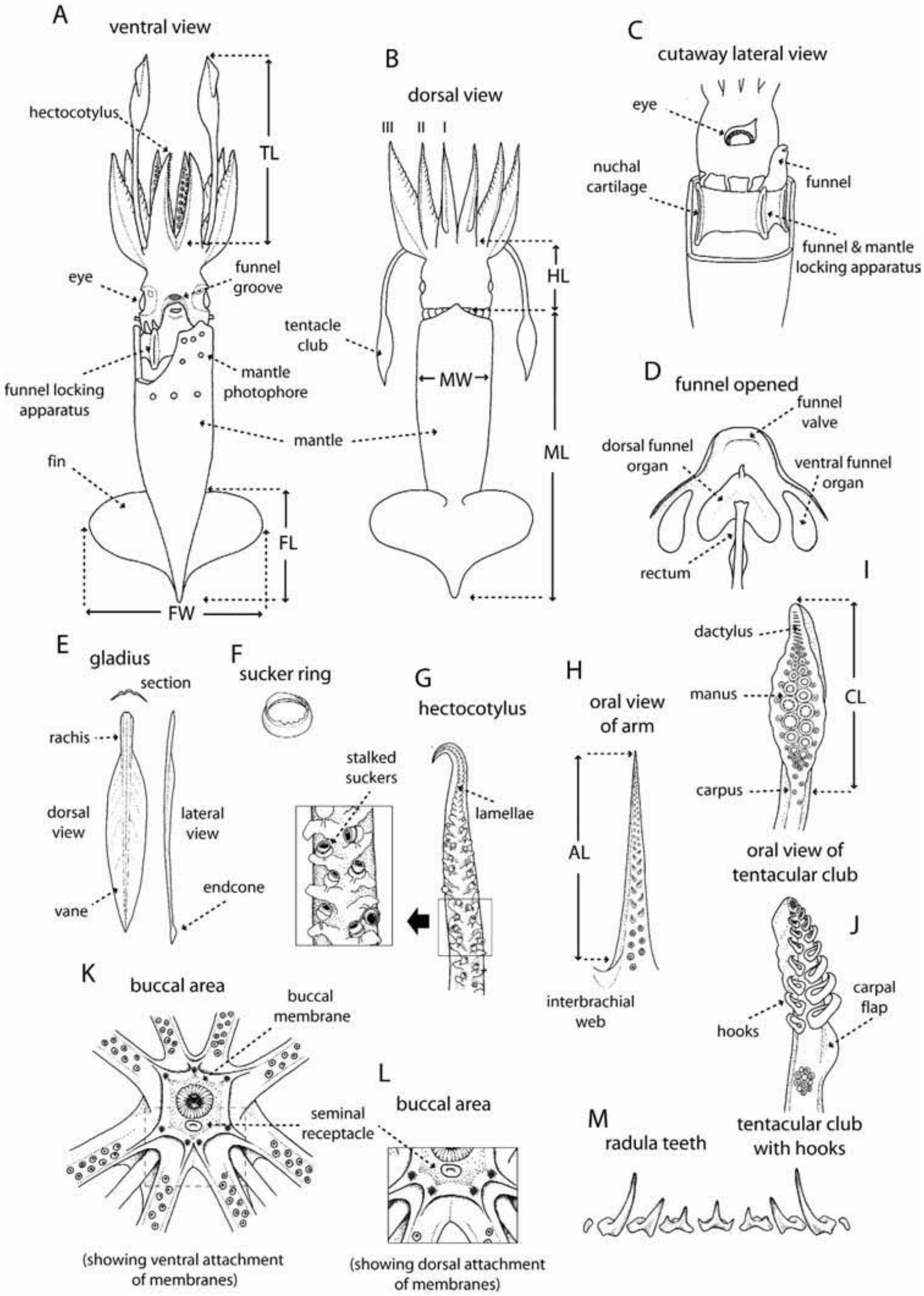

Fig. 5.2 Key morphological characters used for identification and taxonomic analysis of the squids (not to scale). A Ventral view of an oegopsid squid with funnel exposed. B Dorsal view showing standard measurements. C Right side of the head of an oegopsid squid. D Funnel laid open. E Gladius, dorsal and lateral views. F Toothed sucker ring. G Hectocotylised male arm. H Oral view of arm. I Oral view of tentacular club with suckers. J Tentacular club with suckers modified into hooks. K Buccal area. L Buccal area. M Row of radula teeth (AL, arm length; CL, club length; FL, fin length; FW, fin width; HL, head length; ML, mantle length; MW, mantle width; TL, tentacle length). After Roper *et al.* (1984) and Okutani *et al*. (1987).

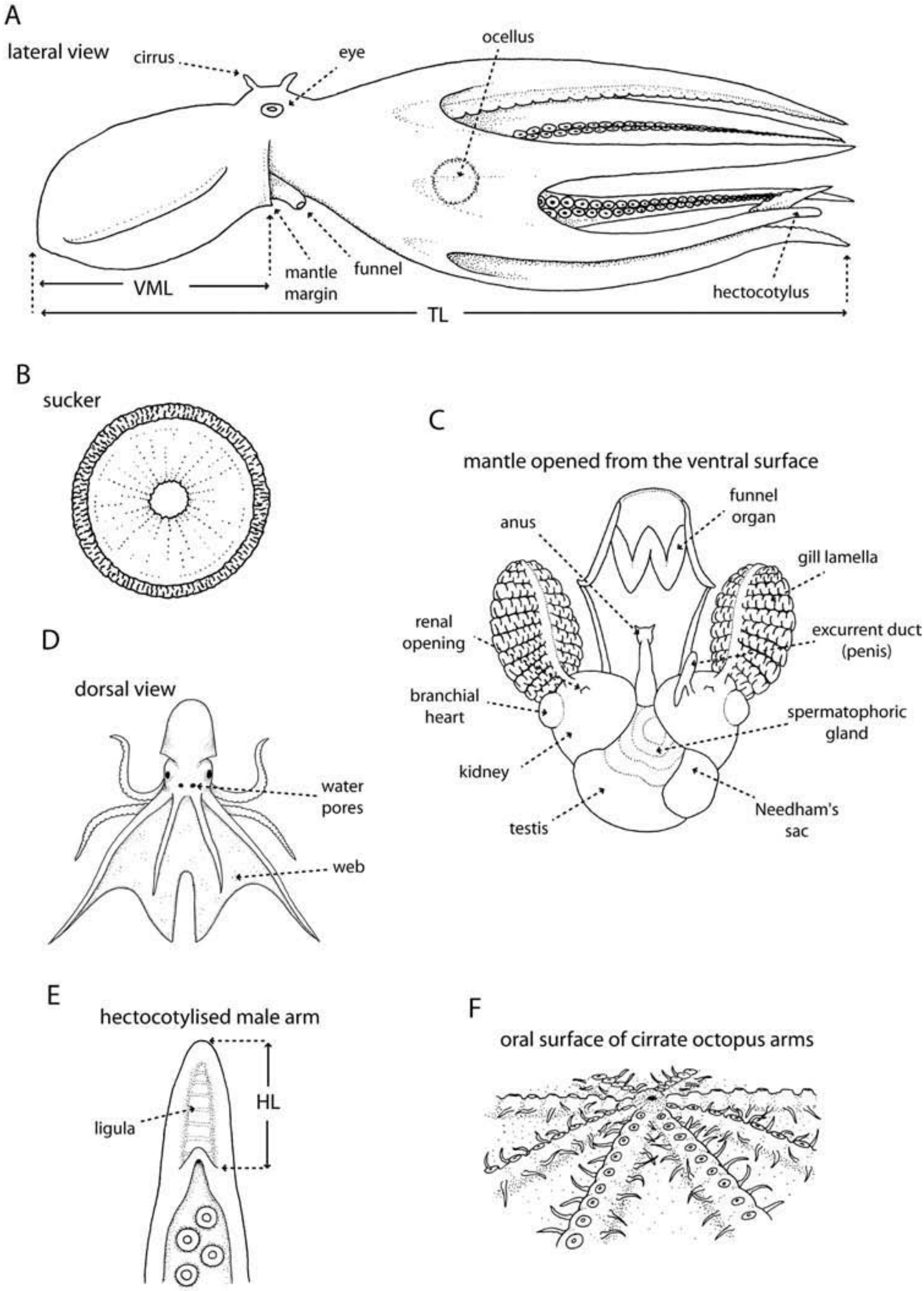

Fig. 5.3 Key morphological characters used for identification and taxonomic analysis of the octopuses (not to scale). A Lateral view showing standard measurements (TL, total length; VML, ventral mantle length). B Sucker. C Mantle and funnel laid open showing some viscera and male reproductive organs. D Whole octopus showing web and water pores. E Hectocotylised male arm (HL, hectocotylus length). F Cirri on the oral surface of the arms in cirrate octopuses. After Roper *et al.* (1984) and Okutani *et al.* (1987).

Table 5.2 Examples of recent schemes for classifying the orders of the subclass Coleoidea.

Voss 1977b	Fioroni 1981	Clarke 1988b	Young 1989	Guerra 1992	Doyle *et al.* 1994	Young *et al.* 1998
Sepioidea	Sepioidea Sepiolidea	Sepiida Sepiolida	Sepiida Sepiolida Spirulida	Sepiida Sepiolida Idiosepioidea	Sepiida Sepiolida Spirulida	Sepiidae Sepiolidae Spirulidae
Teuthoidea	Teuthoidea	Teuthida	Teuthida	Teuthoidea	Teuthida	Myopsida Oegopsida
Octopoda	Octopoda	Octopoda	Octopoda Cirroctopoda	Octopoda Cirroctopoda	Octopoda Cirroctopoda	Incirrata Cirrata
Vampyromorpha	Vampyromorpha	Vampyromorpha		Vampyromorpha	Vampyromorpha	Vampyromorpha

tube-shaped funnel for jet propulsion, and either eight arms or ten circumoral appendages (eight arms and two tentacle filaments). In the modern literature, several schemes have been proposed for the division of the Neocoleoidea. A simple classification was proposed by Voss (1977b) and this was widely adopted, including by the FAO for fishery purposes (Roper *et al.* 1984). More recently, Sweeney & Roper (1998) have presented a new classification which ranks the currently accepted taxa of recent cephalopods, and it is this system that has been adopted for the synopsis of families in Appendix B. The other classifications differ largely in the way the cuttlefish and their relations, and octopuses are sub-divided (Table 5.2). There have also been differences in the endings used for the names of the orders, for example the Teuthoidea of Voss (1977b) is the Teuthida of Clarke & Trueman (1988); the latter being in accordance with the International Code of Zoological nomenclature which recommends that the zoological suffix '-oidea' should only be used to designate super-families (Quicke 1993).

An alternative approach to classifying the Coleoidea has been taken by Young *et al.* (1998), who focus their discussion on monophyletic clades, rather than taxonomic ranks, in an analysis of the evolution of the coleoids and their present biodiversity. This approach avoids the use of unstable taxonomic ranks and provides a powerful approach to understanding coleoid evolution.

Although Sweeney & Roper (1998) include several new divisions at the level of Order, given the fluid state of cephalopod systematics and the variety of alternative names for higher groupings, the following descriptions of the cephalopod Orders uses the four divisions of Voss (1977b). These are in widespread and common use, and are the sub-divisions which have been adopted world-wide for fisheries purposes (Roper *et al.* 1984).

5.3.1 Order Sepioidea Naef, 1916 (ram's horn squid, cuttlefish, bobtailed squid, bottletail squid and pygmy squid)

The sepioids (grouped within the Decapodiformes (see Fig. 3.4) or Decabrachia (see Fig. 3.5)) are mostly a coastal/neritic group which occur in temperate and tropical seas.

All have five pairs of circumoral appendages, the fourth pair of which are tentacles which can partially or fully retract into pockets. Suckers on the arms and tentacles possess chitinous rings. The eyes are protected by a corneal membrane except in the Spirulidae.

The Sepioidea are divided into two groups of families depending on whether they have an internal calcareous shell or an internal chitinous shell, which may be reduced or entirely absent. Two families have a calcified shell: in the ram's horn squid (Spirulidae) this is coiled and contains gas-filled chambers for buoyancy, and in the cuttlefish (Sepiidae) it is a nearly straight and finely laminated structure – the cuttlebone. The other three families lack calcification of the shell. In the bobtail squid (Sepiolidae), the chitinous gladius is rudimentary or absent, and in the bottletail squids (Sepiadariidae) there is no shell at all. Hylleberg & Nateewathana (1991) show that *Idiosepius pygmaeus* (family Idiosepiidae) has a thin, clear gladius and is possibly more closely related to squid.

5.3.2 Order Teuthida Naef, 1916 (Teuthoidea, true squid)

The teuthoids (grouped within the Decapodiformes (see Fig. 3.4) or Decabrachia (see Fig. 3.5)), the neritic and pelagic squid, are found throughout the world oceans from shallow coastal waters to the deep oceans, and from the polar seas to the tropics. The ancestral shell of the squids has become much reduced during evolution to become an internal stiffening structure in the mantle. This is the gladius, or pen, and it lies internally along the length of the dorsal surface of the mantle, inserted into a pocket in the muscle. In common with the cuttlefishes, squid have five pairs of circumoral appendages, the fourth pair of which are contractile tentacles which do not retract into pockets. In some groups, e.g. the Octopoteuthidae, the tentacles have become secondarily lost in the adult in the course of evolution, leaving just four pairs of arms.

The squid are currently divided into two sub-orders, the Oegopsina which have eyes that are open to the water, and the Myopsina which have a membrane (cornea) covering the eye (Appendix A). The oegopsids have paired gonoducts in the female, and in several groups some of the suckers on the arms and/or tentacles have become modified into hooks that are used for capturing and gripping slippery prey such as fish (Engeser & Clarke 1988). The myopsid squid have single gonoducts and, unlike most oegopsids, generally have suckers on the buccal lappets around the mouth.

There are four key external characters that are used for classification of adult squid to family level (Roper *et al.* 1969). First the funnel locking apparatus, i.e. paired cartilaginous structures which lock the funnel to the mantle, and which fall into five basic types that to some extent reflect the lifestyle of the different species. Of less obvious functional importance are the lower buccal connectives, which attach either to the dorsal or ventral side of the fourth arm. This has been found to be a consistent feature within squid families. The third character is the form of the armature of the arms, i.e. whether the suckers are arranged in two, four or more rows, and whether hooks are present. The fourth and last major character in the squids is the tentacular club, in which the armature may be arranged in four or more rows and may consist of either suckers or a combination of suckers and hooks. In three families the tentacles are absent in the adult form.

The Teuthida is by far the most diverse order in terms of number of families. Nesis (1982, later published in English in 1987) recognised 26 families, 24 of which are oegopsids. Since then new families, the Walvisteuthidae (Nesis & Nikitina 1986), Magnapinnidae (Vecchione & Young 1998), Pyroteuthidae and Ancistrocheiridae (Clarke 1988b) have been added. Conversely, it has been proposed that the myopsin family Pickfordiateuthidae should be integrated into the Loliginidae (Brachoniecki 1996), although this has not been generally accepted (Voss *et al.* 1998a, b). Inclusion of new families is always a matter of debate among specialists. More information about the cephalopod families is included in the synopsis in Appendix B.

The diversity of the squid families reflects the wide range of habitats that they have successfully invaded. The muscular loliginids in coastal and shelf waters and the ommastrephids over continental shelves and in the epipelagic of the open ocean are adapted for rapid swimming as they are active predators, but must also avoid superior predators including large fish and cetaceans. These squid show obvious convergent evolution with the demersal and pelagic fishes (Packard 1972). Other families, including the deep sea Mastigoteuthidae, Chiroteuthidae and Cranchiidae, are weak swimmers which are neutrally buoyant by virtue of ammonium chloride stored in gelatinous muscles or coelomic fluids (see Chapters 2 and 12, and Fig. 12.3). They probably float passively in the water column, occupying ecological niches more akin to those of the cnidarians and siphonophores. The mesopelagic Histioteuthidae, Lycoteuthidae and Enoploteuthidae have numerous photophores in the skin that are adaptations for counter-illumination and signalling (Young 1977). In the dim midwater layers of the ocean, these luminescent squid undoubtedly fill an ecological niche close to that of the myctophids (lanternfishes) of the deep scattering layer. The special characters of other families, such as the cartilaginous ‘scales’ on the mantle of the Lepidoteuthidae and the extraordinary long tail of the Joubinoteuthidae, further exemplify the extent of diversification in the squids.

The squid also present the greatest size range among the cephalopods, ranging from the small myopsids such as *Pickfordiateuthis pulchella*, with a mantle length of around 15 mm, to the giant squid, *Architeuthis dux*, which grows to a mantle length of several metres.

5.3.3 Order Vampyromorphida Pickford, 1939 (Vampyromorpha, vampire squid)

The vampire squids are distributed world-wide in the deep ocean. There is only one known family in the Order and this is represented by a single species, *Vampyroteuthis infernalis*, which has dense black or deep purple skin. There are eight circumoral arms with stalked suckers, and no tentacles, but it possesses a pair of long extensible filaments that arise from pouches between the first and second arms. *Vampyroteuthis infernalis* has a chitinous internal shell which has become reduced to a thin, broad plate. There are two types of light organs, a pair of large and complex organs just behind the fins, and a scattering of many small simple organs on the dorsal surface of the mantle. There are two organs situated on the dorsal surface between the eyes which are believed to be photoreceptors (Herring *et al.* 1994).

5.3.4 Order Octopodida Leach, 1818 (Octopoda, all octopuses)

The octopuses are widespread in the world oceans from the poles to the tropics. Although the typical octopus is benthic, occurring from the inter-tidal to the deep ocean, there are also several wholly pelagic families (Argonautidae, Bolitaenidae, Ocythoidae, Tremoctopodidae and Vitreledonellidae; Appendix B). They all have eight arms, which can be derived from the basic ten-armed pattern of the coleoids by suppression of one pair (see Fig. 3.5). This is probably the pair differentiated as filaments in the vampyromorphs. The suckers are attached directly to the arm without obvious stalks, and never have the horny rings found in the squid and cuttlefishes. The internal shell is usually reduced to small vestigial cartilaginous-like rods or a simple U-shaped supporting structure for fins (suborder Cirrina). With the exception of the pelagic Bolitaenidae, no octopuses are known to possess light organs, although *Stauroteuthis* suckers have been shown to emit light on mechanical stimulation (Johnsen *et al.* 1999). In octopuses that have fins (Cirrina), these are widely separated on either side of the mantle. The eyes are open to the sea with no fixed corneal membrane, but they do have two concentric eyelids which can be closed over the eye.

There are two very distinct groups within the order Octopoda, the Cirrina and Incirrina, each of which is generally considered to be a sub-order. The Cirrina have conspicuous cirri along the length of the arms and they all possess paddle-shaped fins that are adapted for slow swimming in their deep-ocean pelagic or epibenthic habitat. They also move by making medusa-like contractions of the arms and web (Vecchione & Young 1997; Villanueva *et al.* 1997), and jet propulsion using the mantle has virtually been lost. As a group, the cirrates are characterised by extreme compaction of the viscera and much reduced mantle cavities. The Cirrate octopus families Opisthoteuthidae and Cirroteuthidae are distinguished by the presence or absence of a secondary web between the arms.

The Incirrina include the common benthic octopuses of shallow water, but they also extend into deeper water and there are both benthic and pelagic forms. There are no cirri on the arms and none have fins, but four families (Alloposidae, Tremoctopodidae, Ocythoidae and Argonautidae) are distinguished by having a detachable hectocotylus in the males. These may be grouped together in an argonaut clade.

Among the incirrates there are three gelatinous families which differ in the number of sucker rows on the arms, the position of the stomach relative to the digestive gland and the form of the mantle opening. These families are the Amphitretidae Hoyle, 1886, the Bolitaenidae and the Vitreledonellidae. Of the argonaut clade, the Alloposidae are gelatinous and the families Tremoctopodidae and the Ocythoidae possess characteristic water pores at the base of the web; the latter are distinguished by differences in the distribution of the water pores. To brood their eggs, the pelagic argonauts (Argonautidae) secrete a thin external egg case with a strong superficial resemblance to that of the fossil ammonites. An interesting evolutionary suggestion was put forward by Naef (1921–1923) that the early argonauts might have occupied empty ammonoid shells and used the secretory properties of glandular structures on their arms firstly to repair, and then to secrete, a flimsy new structure on the mould of the original. Young *et al.* (1998) point out that a gap of about 40 million years exists between the extinction of the ammonites and the first appearance of the fossil argonauts, so Naef's suggestion perhaps stretches credibility. The evolution of the argonaut shell, or pseudoconch, remains an interesting question.

The Octopodidae, which is by far the most diverse family of octopuses, is separated from the other families largely by benthic habit and by the special features of the hectocotylus of the males. The family contains 90% of incirrate species. Up to five subfamilies have been recognised, but they are distinguished by relatively minor characters and are best ignored until they are better defined. Of all the cephalopod families, the state of knowledge of the systematics of the octopodids is probably in the least satisfactory state, largely because of the relatively few reliable taxonomic characters possessed by the group. The apparently universal geographic distribution of the species *Octopus vulgaris* is probably incorrect, and will be resolved by careful attention to the original type description and its separation from other, possibly new, species (Mangold & Hochberg 1991). Advances have been made on details of the octopod fauna of specific regions (Lu & Stranks 1994; Norman & Hochberg 1992; Norman & Sweeney 1997; Norman *et al.* 1997; Voight 2000b), and there are major reviews of the regional systematics of octopodids by Mangold, Stranks, Toll, Voight and Voss in Voss *et al.* (1998a) but much more research is needed for a fuller understanding of the evolution of this family.

5.4 New tools for taxonomy: molecular genetic markers

J.B.S. Haldane wrote in an essay (Maynard Smith 1985) that one aim of the evolutionary biologist is to establish a family tree of plants and animals that identifies when, in the past, the common ancestors of extant species lived. He predicted that eventually, in thousands of years, it would be possible to reconstruct phylogenies using chemical methods. Haldane's predictions are now being realised owing to advances in the rapidly developing field of molecular genetics.

This is a relatively young science, particularly in relation to the cephalopods, but sequence analyses of a small fragment of the genome, the 3′ end of the 16S rDNA mitochondrial gene, has shown promise for determining taxonomic relationships at the infra-family level (Bonnaud *et al.* 1994, 1997). The same gene region has been used by Piertney *et al.* (2003) and Allcock & Piertney 2002 to revise phylogenetic relationships among the cirrate octopods. Sequence analysis of another mitochondrial gene (cytochrome oxidase III, COIII) has also been used (Bonnaud *et al.* 1996) to show that the southern African loliginid *Loligo reynaudi* D'Orbigny 1839–1841 in Férrusac & D'Orbigny (1834–1848) is more closely related to the Atlantic species *L. vulgaris* Lamarck 1798 than had previously been thought (Augustyn & Grant 1988), and to suggest that the families Sepiidae, Spirulidae and Sepiolidae are not particularly closely related. The same gene has also been used to ascertain the phylogenetic relationships between several species of Pacific octopuses (Barriga Sosa *et al.* 1995). Mitochondrial and nuclear DNA sequences, combined with morphological characters, have been used to examine the phylogenetic relationships among the living *Nautilus* spp. (Wray *et al.* 1995), providing evidence that diversification is taking place within the genus along lines dictated by geographic boundaries, and that species erected on the basis of morphological characteristics are not fully supported by the molecular data. Warnke *et al.* (2000) used DNA sequences to demonstrate rapid differentiation between *Octopus vulgaris* and *O. mimus*.

Ground-breaking studies using mtDNA sequences from the cytochrome *c* oxidase I gene (COI) from 48 cephalopod species from a broad spectrum of coleoid diversity have been used to examine the higher-level phylogenetic relationships within the group (Carlini & Graves 1999). The conclusions were that the Coleoidea, Octopodida, Vampyromorphida and Decabrachia are monophyletic groups, that the Vampyromorphida and Octopodida are sister groups (consistent with Boletzky 1999, shown in Fig. 3.5), that the Sepioidea (five families) is polyphyletic, that *Spirula* is more closely related to the Teuthida than it is to the remaining members of the Sepioidea, and that the assemblage of families in the sub-order Oegopsina is polyphyletic. Sequences extracted from nuclear DNA from the actin gene family of 44 cephalopod species were used for a new phylogenetic analysis by Carlini *et al.* (2000). The results supported some of the conclusions from the previous COI analysis (Carlini & Graves 1999), the monophyly of both the Decabrachia and Octobrachia (terminology as in Fig. 3.4) were confirmed, but results for the Sepioidea did not fully concur. The phylogenetic inferences obtained from molecular approaches are beginning to be evaluated in the context of morphological approaches (Carlini *et al.* 2001). It is clear that the molecular data are beginning to make an impact, but cannot yet be fully reconciled with traditional methods.

The study of cephalopod phylogeny is entering a new era. The review by Shaw (2002) is the first collation of molecular genetics approaches to cephalopod phylogeny and population biology, and includes a full bibliography. Undoubtedly in the future some of the currently held views presented in this chapter and throughout this book may need to be reassessed in the light of new information.

5.5 Phylogeny of the recent cephalopods

The first comprehensive analysis of the phylogenetic relationships among the extant cephalopods was undertaken by Naef (1921–1923) on the basis of general morphology, and embryological and palaeontological data. At that time there was little or no information on anatomical and functional characters such as the brain, buoyancy, statocysts, statoliths, suckers and hooks, and there was little detailed information on gladii or beaks. Using information on these characters gathered since Naef's work, Clarke (1988b) re-assessed the phylogeny of the coleoids. More recently, Young *et al.* (1998) reviewed cephalopod phylogenetics on the basis of a cladistic analysis of fossil and morphological characters (Fig. 5.4) differing principally in the relationships of the families of the order Sepioidea.

As we have seen already in this chapter and in Chapter 3, the phylogenetic relationships of the coleoid families and the terminology of the higher-order groupings are in a state of flux, involving detailed argument largely beyond the scope of this book. The following discussion is intended only as an introduction and not a definitive version.

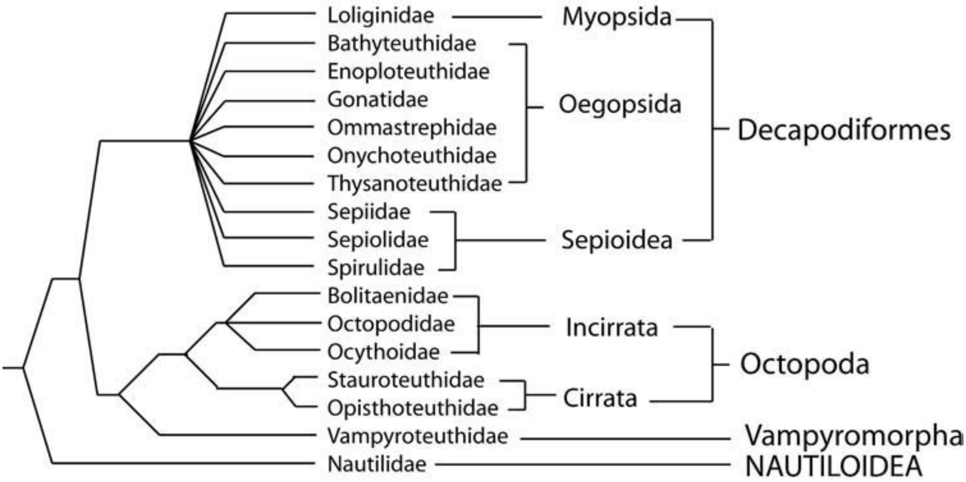

Fig. 5.4 Cladistic analysis of the Coleoidea for a number of representative families (nodes to the left indicate groups with shared characteristics) and their classification (after Young R.E. *et al.* 1998).

The octopuses are clearly separated from the squids and cuttlefishes on the basis of the number of arms, the lack of chitinous sucker rings and sucker stalks, and this is supported by the molecular evidence (Carlini & Graves 1999). The Vampyromorphida are superficially similar to the cirrate octopods, but there are substantial differences such as the possession of a gladius, the presence of photophores, simple radula teeth and small filaments that are clearly homologous with a fifth pair of arms, so Clarke (1988b) placed them as a sister group to the Octopodida. The Vampyromorphida resemble octopuses in having the mantle fused with the head, but in the embryo the mantle margin is free from the head so this feature is convergent with the octopuses (Young *et al.* 1998). Nevertheless, the molecular evidence shows that the Octopodida and Vampyromorphida are sister groups and more closely related to each other than the Vampyromorphida and the Decabrachia (Carlini *et al.* 2001).

Young *et al.* (1998) conclude that the octopuses probably arose from a squid-like ancestor via one of two routes, either a benthic route through an intermediate *Sepia*-like form, or a pelagic route through something like *Vampyroteuthis*. The weight of evidence is that the pelagic route is more likely. For instance, *Vampyroteuthis*, in common with the octopuses, has no buccal membranes and, perhaps more importantly, the inferior frontal system in the brain of *Vampyroteuthis* is better developed than in the decapods (J.Z. Young 1988). This system is concerned with memorising objects that have been touched by the arms, and is well developed in the benthic octopuses which search for food with the arms.

The squid families fall into several groupings according to Clarke (1988b). The Cranchiidae are a highly evolved family and are closest to the group including the Chiroteuthidae, Mastigoteuthidae and Joubiniteuthidae, possessing ventral buccal connectives that attach to the fourth arm and having funnel connectives with similar morphology, but they are distinct from this group in possessing a coelomic buoyancy chamber and a mantle cavity divided by a septum. The grouping of families with the

Chiroteuthidae is apparently also justified on the basis of ammoniacal buoyancy, a secondary conus on the gladius, ventral buccal connectives that attach to the fourth arm and similar shaped beaks. The Octopoteuthidae and Lepidoteuthidae store ammonia in the tissues for buoyancy, lose the tentacles during growth and have very similar beaks. The Histioteuthidae have ammoniacal tissues for buoyancy, a broad, small body, a large head with asymmetric eyes, and small fins, and some of these these characters are shared by the Bathyteuthidae, which also have a similar statolith. There are some common features of the beaks of the Onychoteuthidae and Enoploteuthidae which, together with the presence of similar tentacular hooks, statoliths, fin shape and body form, indicate a relationship. The Ommastrephidae appear quite distinct from other families, and the position of several other teuthoid families, including the Thysanoteuthidae, Brachioteuthidae, Chtenopterygidae and Batoteuthidae, is not clear on the basis of the evidence available.

The Spirulidae and Sepiidae are placed by Clarke (1988b) into the Sepioidea, a group characterised by their chambered phragmocones as well as similarities between their statoliths, statocysts, beaks and simple radula teeth. However, molecular data (Carlini & Graves 1999) show that the Spirulidae are probably more closely related to the Teuthida than the Sepioidea. The Sepiolidae were placed by Clarke (1988b) in a separate sub-order, the Sepiolida (or Sepiolina).

Within-family phylogenetic analyses of the living cephalopods have not generally been attempted because of uncertainty about the taxonomy of many groups and the absence of enough anatomical data for the analysis of evolutionary relationships. Exceptions are the Cranchiidae and the Ommastrephidae. Voss & Voss (1983) used formal cladistics methods to construct a phylogeny for the Cranchiidae, and found that their reconstructions agreed well with some of the groupings proposed by Voss (1980) on the basis of phenotypic similarities. A preliminary cladistic analysis of the ommastrephids by Roeleveld (1988), who emphasised the use of morphological characters rather than meristics, yielded a phylogeny that was later broadly supported by an allozyme survey of the family (Yokawa 1994).

5.6 Patterns in biodiversity

Some 206 genera and 983 species of cephalopods had been described by the mid-1970s when Voss (1977a) reviewed the subject, but at that time the total actual numbers known were probably about 144–150 genera and 650 species. The difference between the total list of names and the number of species that could be confirmed was due to the number of generic and species names that had been synonymised. Since then, new species, as well as genera and even families have been added so the total confirmed number continues to grow.

In Appendix B, estimates are given of the numbers of genera and species for the cephalopod families. A surprisingly large number of families include only a single genus, while many genera contain very few species. About 50% of known genera are monotypic, i.e. justified by a single species. The low diversity of these genera is balanced by cuttlefishes and octopuses from two genera, *Sepia* and *Octopus*, each of which include over 100 species. The pattern emerging is that the monotypic genera are mostly the mesopelagic squid of the deep oceans, while the more diverse genera are either from shallow coastal waters or deep-sea benthic habitats, suggesting that these areas are perhaps more conducive to the evolution of new species.

Few subgenera or subspecies of cephalopod have been described, and those that do exist in the literature are dubious (Voss 1977a). While this characteristic may reflect an evolutionary feature of the class, it is certainly also due to the lack of museum material in good condition on which to distinguish even species. Clearly the introduction of molecular methods will have a major impact with its potential power to recognise separate populations with varying degrees of genetic exchange, and may lead to a redefinition of the meaning of species. Analysis of molecular genetic markers (allozymes) in squid species of fisheries interest has revealed the presence of cryptic species that had not previously been recognised by the analysis of conventional taxonomic characters (Smith *et al.* 1981; Brierley *et al.* 1993a; Yeatman & Benzie 1993), the separation of closely related species (Guerra *et al.* 2001a), and the transfer of species between genera (Brierley & Thorpe 1994; Brierley *et al.* 1996a). On the other hand, allozyme analysis of two nominal species from the north and south Atlantic, *Loligo vulgaris* and *L. reynaudi*, suggested that the genetic distance between them was only sufficient to justify their separation into sub-species (Augustyn & Grant 1988), and subsequent gene sequencing work has revealed that the two species should perhaps be merged (Bonnaud *et al.* 1996). The future use of genetic markers has considerable potential for resolving species problems and analysing evolutionary relationships of closely related taxa.

5.7 Zoogeography

The cephalopods are exclusively marine, they occur in all the world oceans from the Arctic to the Antarctic, and are present in virtually all habitats. There are forms that are benthic, epibenthic, cryptic, burrowing (in sand, mud, rocks, seagrass flats and coral reefs) and pelagic. They are found from coastal seas to the open ocean, and from the surface layer to depths of up to 5000 m. Perhaps because of the unsettled state of the taxonomy, there has been relatively little work on broad biogeographic patterns in the cephalopods (but see regional or taxonomic examples: Clarke 1966; Collins *et al.* 2001; Nesis 1997; Voss 1969, 1985; Voss *et al.* 1998a). Of interest is the short review of the Mediterranean cephalopod fauna by Mangold & Boletzky (1988), which proposes that, apart from some endemic sepiolids, the fauna is composed entirely of species that have invaded from the Atlantic.

5.7.1 Coastal and shelf cuttlefish and squid

The cuttlefishes are primarily demersal in habit. They occur in tropical and temperate seas, but are absent from the polar regions. Most true cuttlefish belong to the genus *Sepia* (family Sepiidae), which is the most diverse among all the cephalopods and over 100 species are reported (Khromov *et al.* 1998). Some species, such as *S. officinalis* and

S. pharaonis, are widespread in the eastern Atlantic/western Indian Ocean and Indo-Pacific, respectively, whilst others, such as *S. incerta*, which are found only on the east coast of Cape Province and Natal, have very limited distributions. The family Sepiidae are entirely absent from the seas of the New World and this, together with the fossil record, evidence from palaeoceanography and present biogeography, suggests a very recent origin of the family. There is evidence that there have been two separate radiations of the 'cuttleboned cephalopods' (Young *et al.* 1998).

The most diverse group of squid on the continental shelves is the Loliginidae (see Chapter 11 and Appendix B). Loliginids are found on all temperate and tropical shelves of the world's oceans. Although one species, *Loligo gahi*, is abundant on the Patagonian Shelf very close to the sub-Antarctic Front, no loliginids extend into the polar regions.

The ommastrephid squids probably make the greatest contribution to squid biomass on the continental shelves and they make large-scale migrations over the course of their lifespan, often spawning in the tropics or sub-tropics and migrating to high-latitude feeding grounds during the major period of growth and maturation (O'Dor & Coelho 1993). Species are often divided into populations which spawn in different seasons and have different migratory behaviour (Okutani 1977; Haimovici *et al.* 1998). The greatest concentrations of ommastrephids are associated with the major western boundary currents or the high-productivity upwelling systems over the shelves on the eastern side of the continents (see Fig. 18.1), but other species, e.g. *Sthenoteuthis oualaniensis* and *Ommastrephes bartrami*, inhabit the great sub-tropical ocean gyres.

5.7.2 Oceanic squid

The zoogeography of the epi-, meso- and bathypelagic squids seems to be similar to that of the pelagic fishes, crustaceans and other organisms (Voss, N.A. 1988b). As for most pelagic organisms, there are warm-water, cold-water and widespread groups, and the deeper-living species probably have wider geographic distributions than those inhabiting the surface layers. For instance, the deep-living mesopelagic squid *Chiroteuthis veranyi* apparently extends from the Mediterranean to the Antarctic (Rodhouse & Lu 1998). The bathyteuthids, cranchiids, histioteuthids and gonatids are the best known families in the epi- and mesopelagic layers from an analysis of broad patterns of distribution, and they have different biogeographic characteristics (see Chapter 12 and Appendix B).

Bathyteuthis abyssicola, a representative of a family of one genus with three species, is a bathypelagic animal, commonest between 700 and 2000 m (Roper 1969). It has a world-wide distribution and its abundance is determined largely by productivity or limited by low oxygen concentration. It is most abundant in the productive regions of the Southern Ocean, the eastern Pacific, and the Atlantic and Indian Oceans. The Cranchiidae are neutrally buoyant species occurring from the surface to 2000 m in all oceans except the Arctic, and many species are widely distributed. Although they make diel vertical migrations they do not migrate horizontally. Typically, there is contiguous distribution of closely related species from the same genus, but between some genera there is considerable overlap in geographical range. Histioteuthidae have the same vertical range as the cranchiids and extend from the sub-Arctic to the sub-Antarctic. They migrate vertically, but it is not known to what extent they migrate horizontally. Species in the Southern Ocean probably have circum-global distributions, but only one warm-water species, *Histioteuthis meleagroteuthis*, appears to be circum-global. Species ranges appear to be composed of a number of localised breeding populations.

The muscular Gonatidae are medium/large squid that migrate vertically and horizontally and can occur in large numbers between the surface and 1200 m. They are only distributed in the cooler oceanic regions in the northern and southern hemispheres. Of the three genera in the family only one, *Gonatus*, is present in the Atlantic and Pacific oceans in both hemispheres; the other two genera are found only in the north Pacific. The geographical range of the two north Atlantic species, *G. steenstrupi* and *G. fabricii*, do not appear to overlap and are separated by oceanographic fronts, whereas the Pacific species are sympatric.

5.7.3 Benthic octopuses of the continental shelves

Distribution patterns in benthic octopuses are primarily determined by four factors: egg size and the resulting behaviour of hatchlings, habitat continuity, temperature tolerance, and phylogenetic history. Species with small eggs produce planktonic juveniles with more potential for dispersal than the benthic juveniles that hatch from large eggs, but all species are limited by habitat and temperature-range limits. The contingencies of phylogenetic history have determined their distribution by providing opportunities for colonisation of regions during particular climatic, geological or evolutionary events.

Older clades of octopuses are distributed across the world's oceans as remnants of the fauna of the former circum-equatorial Tethys Sea. More recent lines are restricted to particular areas, e.g. the blue-ringed octopuses of the genus *Hapalochlaena*, which only occur in the tropical Indo-Malayan Archipelago.

5.7.4 Deep-sea octopuses

Both cirrate and incirrate octopuses are found in the deep ocean on or close to the sea bed (Vecchione 1987b; Voss, G.L. 1988b). There are also some incirrates that are pelagic in the deep sea, but there is very little information about them. The majority of deep-water octopuses are found in high latitude seas (25% of species in the Antarctic and 22% in the sub-Arctic) and most of the rest inhabit cold deep or intermediate water of Antarctic or Arctic origin at lower latitudes. Only 10% of the known species are found at moderate depths in the warm oceans. The distribution of the deep-sea octopuses seems to be related to high productivity at the surface, and this is probably the most important factor behind their absence from the high Arctic.

Chapter 6

Life cycle

Summary: The living coleoid cephalopods are monocyclic, single-season breeders. They may produce their eggs in successive batches within one season, but there are no known cases of individuals breeding repeatedly in successive seasons. They have short lives, <1–2 years in most cases, with only some exceptionally large or cold-water species living longer. This pattern holds for coastal octopuses, cuttlefish and squid, but the generalisations are based on knowledge of a few species from selected families. Within a species there may be several breeding groups, and there is evidence for the alternation of long- and short-generation life cycles. In such species, the early part of the breeding population in one year gives rise to offspring breeding in the following year; offspring from those breeding late in the season may not be mature by the next breeding season, but contribute to the early breeders of the following year. Plasticity in life cycles in response to environmental conditions arises from variations in development time, growth rate, timing of breeding and mode of spawning. Commonly, there are annual migrations between breeding and feeding grounds, but information on the presumed return migrations is limited.

The life cycle characteristics of cephalopods are central to the interpretation of much of their ecology and of key relevance to fisheries assessment. There is a large body of information from field and laboratory studies on which to base generalisations about the cephalopod life cycle. Reviews of the life cycle characteristics of a series of cephalopod types, and reviews of the stages and processes in the life cycle are contained in Boyle (1983a, 1987a). Here, we summarise and update that information, with particular attention to the general patterns of life cycle biology and evidence for variation in selected examples.

There appears to be a universal pattern within the living Coleoidea of a single breeding season and a short life span. Immediately, however, we must make the *caveat* that our current knowledge of life cycle characteristics is based on a relatively small number of species; typically those occurring over the shelf and accessible to coastally based scientific study, or those of fisheries significance. Exceptions to these generalisations may well arise in oceanic and deepwater species which are less accessible and less well studied. This account is based on the best known species, and the exceptional cases receive a shallower treatment. The justification for making generalisations lies in the similarities between life cycle patterns found in representatives of each of the three main extant groups (octopuses, cuttlefish and squid), and the relevance of these models to the interpretation of their population biology and exploitation characteristics.

6.1 Single breeding

With the exclusion of the nautiluses, all cephalopods whose life cycles are known undergo only one breeding cycle (monocycly). Unlike most of their molluscan relatives, there is no alternation of reproductive condition from reproductively fully mature and spawning to post-spawning, spent or dormant, then returning to reproductive maturity and shedding of gametes in a subsequent season. In this fundamental sense, all the modern cephalopods (Neocoleoidea) are single-season breeders, or semelparous in the strict sense.

There has been confusion and controversy in the cephalopod literature over the use of the terms semelparity, to mean single breeding, and its alternative of iteroparity, or repeated breeding. These terms were first coined by Cole (1954) to describe breeding patterns in widely diverse organisms, and they have subsequently been used extensively in writings on life-history theory (e.g. Kirkendall & Stenseth 1985; Stearns 1992; see Box 6.1). The real confusion arises because the issue of whether an organism concentrates all its breeding potential into a single event has important consequences for life-history theory. As will be seen in Chapter 9, coleoid cephalopods show a range of spawning strategies from species with a very clear single spawning event followed by death, through a range of examples which produce a series of spawns, to the cirrate octopods which apparently produce single eggs continuously over a wide range of adult body size. There is little consistency in the terminology which has been used to describe these events, the word iteroparity often being used for serial spawners. Unfortunately, this usage maintains the confusion between cephalopods and those animals which breed seasonally in successive years, undergoing annual cycles of gonad development (like most other molluscs). Despite efforts to regularise the terminology (Rocha *et al.* 2001), the use of these terms for cephalopods potentially distracts from the important and, as far as we are aware, consistent generalisation of a single terminal breeding season for all coleoid cephalopods. In their application to cephalopods, we use the terms semelparity and iteroparity only to distinguish between single annual breeders (Coleoidea) and multi-annual breeders (Nautiloidea).

The ubiquitous generalisation of a single breeding season is rather surprising and apparently runs counter to accepted theory (MacArthur & Wilson 1967), which suggests that animals of large body size would tend to have a relatively long lifespan, and breed for many years after maturity. The types of evidence available to support the contention that cephalopods complete their lifetime breeding activity in one reproductive cycle are quite diverse (Table 6.1). Boletzky (1981) points out that only a few cephalopod groups, such as the benthic sepiolids, show consistent features of either *r*-selected or *K*-selected life cycle strategies, and in view of doubts expressed by Stearns (1992) of the value of the concepts of *r*- and *K*-selection to the interpretation of life histories, a theoretical framework for the cephalopod life cycle is perhaps premature (Boyle & Boletzky 1996; Wood & O'Dor 2000).

If the simple single-breeding (semelparous) model of the coleoid life cycle is accepted, it is possible to accommodate most of the known variability in timing and frequency of breeding and spawning. Arguably, the continuously egg-laying deep-sea cirrate octopods (Villanueva 1992a), and the repeated spawning of the small tropical octopus (*Octopus chierchiae*, Rodaniche 1984) and the pygmy squid (*Idiosepius pygmaeus*, Lewis & Choat 1993; Jackson 1993) can both be accommodated within that range. At the time of writing, no one has demonstrated that gametogenesis in cephalopods can normally be restarted after spawning has finished, although there is increasing evidence for flexibility in the timing and frequency of spawning activity during the breeding season (Boyle *et al.* 1995) and for the atresia of unspawned eggs (Melo & Sauer 1999).

Box 6.1 On defining 'breeding once'

(L.R. Kirkendall & N.C. Stenseth 1985. *The American Naturalist* 125:189–204)

The life cycles of organisms are of central interest to ecological and evolutionary theory as well as being critical to an understanding of biological interactions with the environment. The term *semelparity*[1] was first proposed by L.C. Cole (1954) to 'describe the condition of multiplying only once in a lifetime', as distinct from *iteroparity* meaning 'those which reproduce more than once in a lifetime'.

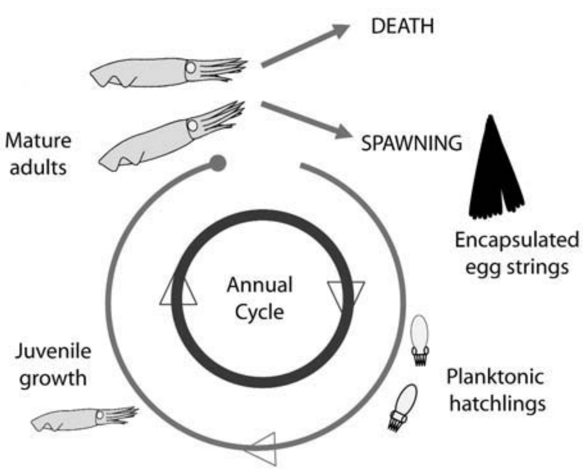

Fig. 6.1.1 The annual life cycle of *Loligo forbesi*.

The classic paper by Kirkendall & Stenseth explores the range of breeding strategies of animals and plants and the application of these terms to the differing time-scales of breeding involved, and in particular how to deal with the basic difficulty of distinguishing between within-season and between-season patterns of reproduction. Throughout the wide range of reproductive strategies of invertebrates (Strathmann & Strathmann 1982; Giangrande *et al.* 1994), the diversity available within the cephalopods (Rocha *et al.* 2001) is relatively narrow.

On the basis that the majority of cephalopods have a clearly defined breeding event, followed by death, that there is no evidence for repeated cycles of gametogenesis, but that plasticity in the life cycle allows for the release of gametes to take place over a period of weeks or months and in distinct batches, we regard the coleoids as essentially semelparous, or monocyclic.

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[1] In Greek legend, *Semele* was one of the human lovers of the god Zeus. On her death during pregnancy caused by the impact of seeing him appear in full celestial splendour, their child was saved from her womb by Zeus and borne on his own thigh until his birth. Her name now associates reproduction with death.

Table 6.1 life cycle characteristics associated with the single breeding season (semelparity) and short life-span of coleoid cephalopods, with examples of selected species.

	Example	Reference
Field conditions		
Mass mortality at squid breeding aggregations	*Loligo opalescens*	Fields 1965
Infrequency and degenerate condition of 'spent' individuals	*Moroteuthis ingens* *Todarodes pacificus*	Jackson & Mladenov 1994 Hayashi 1971; Hamabe & Shimizu 1966
Loss of adult (mature) size mode after breeding	*Loligo forbesi* *Loligo vulgaris*	Guerra & Rocha 1994
Single size mode in exploited fished populations	*Illex argentinus* *Dosidicus gigas*	Rodhouse & Hatfield 1990a Taipe *et al.* 2001
Low age estimates (≤1 year) of breeding animals (maximum age estimates normally <450 days)	*Loligo forbesi* *Alloteuthis* (*Loligo*) *africana* *Alloteuthis* (*Loligo*) *subulata*	Collins *et al.* 1995a, b Arkhipkin & Nekludova 1993 Arkhipkin 1994
Death after brooding by octopus in the field	*Octopus bimaculatus* *Octopus dofleini*	Ambrose 1988a Cosgrove 1993
Culture conditions		
Death after spawning in aquarium conditions	*Octopus maya* *Illex illecebrosus*	Van Heukelem 1977 O'Dor *et al.* 1980
Endogenous control of maturation and death?	*Octopus hummelincki*	Wodinsky 1977

6.2 Short life

The spawning aggregations of the squid *Loligo opalescens* at specific localities on the California coast are followed by immediate and dramatic post-spawning mass mortality (Fields 1965), which is readily witnessed by fishermen and divers, and from the accumulations of predators (Cousteau & Diolé 1973). More than any others, these annual events have shaped thinking that death follows reproduction in squid. Other similar squid, such as *L. vulgaris reynaudi*, do not necessarily show such obvious post-spawning mortality in the population (Sauer & Smale 1993), and these authors have argued that *L. opalescens* is an exceptional species and these events should not be extrapolated. It can also be argued that in *L. vulgaris reynaudi*, mortality of the post-breeding adults is occurring continuously throughout the spawning season, but that an accumulation of corpses is less evident owing to emigration from the spawning ground and consumption by predators (Sauer & Smale 1991, 1993). At this point, however, we should note that these events are not universally expressed in all cephalopods. Some, like *Octopus chierchiae*, continue to grow between spawning events (Rodaniche 1984), or steadily release single eggs over a lengthy period of time (*Opisthoteuthis agassizii*, Villanueva 1992a).

In the laboratory, it has been widely observed that the female octopus will brood its eggs until hatching occurs and will then die, apparently of endogenous causes (O'Dor & Wells 1978), an effect also observed in the field (Cosgrove 1993). Numerous experiments have suggested that the optic gland of *Octopus* is the source of hormone(s) controlling the onset of maturity and the progress of vitellogenesis (Wells & Wells 1975, 1977a). An experiment by Wodinsky (1977) showed that excision of the optic glands from maturing octopuses would cause the gonad to regress and stimulate accelerated growth, thus strengthening the view that post-spawning mortality in all cephalopods is due to endogenous causes and applies to both males and females.

Further evidence for the short life of most of the species caught by fishing comes from the use of statoliths for the ageing of squid and application of the technique to population biology. The hypothesis that one increment of the statolith is formed daily has been tested experimentally in a few species (Jackson 1994b). Although strictly requiring species-specific validation, ageing studies on many squid populations have been conducted on the basis that 1 increment = 1 day. In this way, it should be possible to gather direct information on the lifespan of many species. These studies mostly suggest that the maximum lifespan of the commonly known species is 1–2 years (see Table 6.1). Large-scale studies on size frequency in cephalopod populations also found that the large size mode disappears suddenly from the population, although small numbers of large individuals sometimes remain (Boyle & Pierce 1994). Consistent with the low estimates for maximum age obtained from statoliths, evidence from field and laboratory studies coincides to support the semelparous short lifespan of the coleoids.

For many of the small to medium-sized temperate, sub-tropical and tropical cephalopods, the hatching–spawning interval and the maximum lifespan coincide to give a more or less consistent annual life cycle. Individuals of particularly large species, and those from cold water habitats, may take longer to reach maturity and breed. This results in species in which the population breeds annually, but individuals may have 2–3-year lifespans culminating in terminal breeding. Squid falling into this pattern are the Antarctic *Kondakovia longimana* (Jarre *et al.* 1991), *Psychroteuthis glacialis* (Groger *et al.* 2000) and the large (2.5 m mantle length) *Mesonychoteuthis hamiltoni* (Clarke & Prince 1981).

The very large octopus, *Octopus dofleini*, which grows regularly up to 60–70 kg body weight, is known to take 2–3 years to reach maturity, and is estimated to live 3–5 years unless breeding intervenes (Hartwick *et al.* 1981; Hartwick 1983). Age estimates for the giant squid A*rchiteuthis* sp. ranged between 290 and 420 days for animals of about 1 m mantle length (Lordan *et al.* 1998a). By extrapolation, even at very high growth rates, the very large specimens of this genus (Roper & Boss 1982) can be expected to take several years to reach their 2–3-m mantle lengths.

With typically maximum lifespans of less than 450 days, the most important consequence for cephalopod population biology is that in seasonally breeding species there is little overlap of generations. Apart from short and variable periods of overlap due to extended periods of breeding activity, the population size at any time in the cycle is determined entirely by the success of the annual recruitment. Marine organisms are notoriously vulnerable to year-on-year fluctuations in the strength of recruitment. The imposed effects of environmental factors such as temperature, food supplies and predation levels are the main factors controlling the numbers surviving to maturity. When there is no stabilising component of older animals in the population the effect of these fluctuations is extreme, and is the main factor driving inter-annual variability in cephalopod numbers and biomass (Boyle & Boletzky 1996). Among molluscs, parallels to this situation can be found, for example, among the nudibranchs (Boyle 1987b), and among fish, only among the smaller tropical species (Pauly 1985).

A series of mechanisms operate on the phasing of reproduction and growth to reduce the acute dependence of the population on the recruitment strength of a single generation. Extension of the length of the breeding season, single or multiple spawns, and episodic (batch) spawning, two spawning populations (Holme 1974), alternating life cycle length (the half-year model) (Mesnil 1977), and the intrinsic variability of development times and growth rates all operate to mitigate the consequences of this vulnerable life cycle pattern (Boyle & Boletzky 1996).

The brief life cycle accounts which follow are used as representative examples to illustrate the rather consistent pattern of cephalopod life cycles and introduce the main variable features. The species selected are each the subject of significant fisheries. Some of them are relatively localised in distribution (*Loligo opalescens*), while others cover very wide geographical areas (*Sepia officinalis*), and the summary given may apply only to a restricted portion of the population range.

In many respects cephalopods in similar habitats show similar life cycle characteristics. The differences between those groups which lay their egg masses attached to the bottom (octopodids, sepiids and myopsid squid) and those with entirely pelagic life styles (oegopsid squid) are particularly clear. The influences of environment on the oceanic species (Nesis 2002), particularly the hydrographic conditions, are especially important (see Chapter 18). The following brief summary is based on a few key sources which will serve as an access to the wider literature, but omits many details of regional variation.

6.3 Case histories

6.3.1 Sepioidea

6.3.1.1 Sepia officinalis (Boletzky 1983; Boucaud-Camou 1991; Boucaud-Camou & Boismery 1991; Boucaud-Camou et al. *1991; Mangold-Wirz 1963; Nixon & Mangold 1998)*

This is the cuttlefish of the Mediterranean Sea, which has been eaten and studied since classical times. It is also widespread on the coasts of the eastern Atlantic from the North Sea to west Africa. Over most of its range it is a valuable resource species to both artisanal and commercial fisheries. Cuttlefish from the southern part of the established range are now recognised as a distinct species *S. hierredda* (Khromov *et al.* 1998), with the southerly extent of *S. officinalis* reaching to North Senegal.

In the English Channel, adult animals migrate coastally on to localised spawning grounds along the coast of France during April. Mature males arrive before the females, mating takes place, and the clusters of large lozenge-shaped black eggs (25–30 mm long) are attached to seaweed and algae on rocky and pebbly bottoms. Large-scale hatching occurs from the beginning of August, and smaller, immature cuttlefish appear along the coast about 1 month after the adults.

Two size classes of cuttlefish, estimated at age 2–3 months (the new recruits, or ‘0’ group) and 13–14 months (remains of the breeding population, or ‘1’ group) are

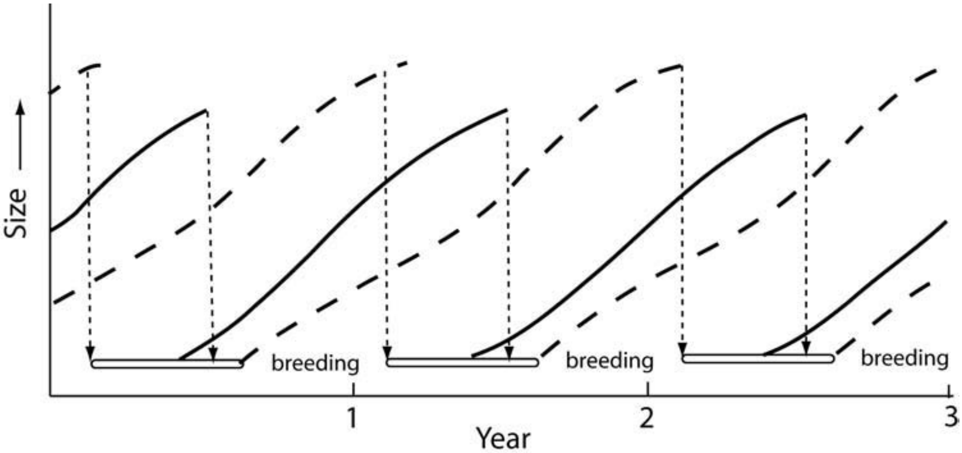


Fig. 6.1 Schematic representation of the life cycle of *Sepia officinalis* (after Boletzky 1983). Solid lines indicate the growth of animals hatched early in one year that reach breeding condition towards the end of the spawning season of the next year. Broken lines indicate the slower growth of animals hatched at the end of the spawning period, too late to breed in the next year, but contributing to the early breeding population of the second year.

present in October and the beginning of November. Both groups leave inshore waters and move progressively offshore into central areas of the Channel, from where there is a gradual westwards spread during the winter (January–March), and they then remain in deeper, warmer and food-rich waters. The spring return migration from the Atlantic water of the Channel approaches on to the Normandy coast apparently occurs over only about 2 weeks. This pattern is typical of many seasonal breeding/feeding migratory cycles, but direct evidence for the presumed rapid return migration is lacking.

The lifespan of individual *Sepia officinalis* appears to be 18 months to 2 years. In some areas (Atlantic coasts) mass post-spawning mortalities are recorded, but this is not normal in the Mediterranean. In the Mediterranean, whether an individual becomes sexually mature during its first winter depends on the time spent as a juvenile in optimal growth conditions the previous summer. At breeding, large mature males and females, estimated to be about 18 months old, are the first to appear in shallow inshore water. Females arriving later, in the early summer, are only 14–16 months old and are apparently the progeny of the early spawners of the previous year. For the females, at least, there appears to be alternating long- and short-generation cycles (Fig. 6.1).

6.3.1.2 Sepiella japonica (Choe 1966; Hayashi & Tako 1983; Natsukari & Tashiro 1991)

This is a cuttlefish which is distributed in the western Pacific and is of fishery importance along the coasts of Japan and China. It has also been used successfully in experimental aquaculture.

In Japanese waters, this is one of three cuttlefish species (*Sepia esculenta*, *S. lycidas* and *Sepiella japonica*) which comprise important fisheries. The main spawning season

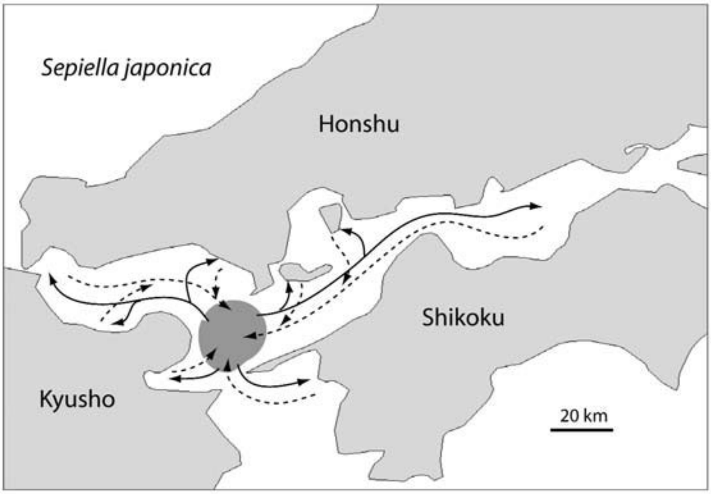


Fig. 6.2 Migration routes of *Sepiella japonica* in the Inland Sea of Japan from dense wintering aggregations (December–February) to coastal spawning and growing areas (April–September). After Ueda & Ishioka 1982 in Natsukari & Tashiro 1991.

for *Sepiella japonica* in Tokyo Bay and along the inland sea coast is from early April, when schools of migrating adults move onshore, until late July (Fig. 6.2). Warmer temperatures (14–15°C) are the cue for spawning in the inner parts of enclosed sheltered bays. Egg-laying is diurnal (sunrise to sunset) in this species, with the female depositing some hundreds of eggs per day for 3–4 days, followed by a resting period of 1–2 days. This pattern of spawning behaviour may continue for weeks until exhaustion and death.

Hatching occurs after 35–55 days (depending on temperature), resulting in shoals of juveniles feeding and growing rapidly in shallow water from June/July to October. Beginning in September, at a mantle length of about 55 mm, they start to move into water over 10 m deep and are recruited into by-catch fisheries. From October to December they continue to move offshore into water >20 m, and are the target of small beam trawlers. Migration continues southwards and offshore, while they grow almost linearly to a mean mantle length of about 117 mm in December, and then slow to reach about 130 mm in the following March. In the closely similar *Sepia esculenta*, the mean size (mantle length) of the spawning stock decreases throughout the spawning season, and the spawners are increasingly joined by poorly grown, late-hatched specimens.

Like the other commercial cuttlefish in this area (*Sepia esculenta*, *S. lycidas*), the estimated lifespan of *Sepiella japonica* is 1 year.

6.3.2 Teuthoidea (Teuthida) – Loliginidae

All of the loliginid squids spawn egg masses attached to firm surfaces or algal fronds. Mostly these are rocky or stony gravel bottoms, but some, like *Loligo vulgaris reynaudi* (Sauer & Smale 1993), insert their egg strings into coarse shifting sand. This preference for shallow coastal water results in the frequent appearance of loliginid spawn deposits on fixed fishing gear such as nets and lobster traps (Lum-Kong *et al.* 1992). Their universal dependence on surfaces for egg laying at the breeding season clearly associates the loliginids with the shallow coastal habitat. There are a few exceptions, such as *Loligo forbesi*, which may occur seasonally over deep water around oceanic islands (Martins & Porteiro 1988), with some evidence for offshore breeding in this species (Porteiro & Martins 1992).

6.3.2.1 Loligo pealei (see Brodziak & Macy 1996; Brodziak & Hendrickson 1998; Dawe et al. *1990; Hatfield* et al. *2001; Hatfield & Cadrin 2002; Mesnil 1977; Summers 1971, 1983; Vecchione 1981)*

This is the long-finned inshore squid of western Atlantic coastal waters, which is distributed from just north of the equator, throughout the Gulf of Mexico and the Caribbean Sea and along the US coastline, into Canada and the coasts of Newfoundland. Formerly only taken as a by-catch, it is now a valued and well-studied fishery.

The work of Mesnil (1977) on the life cycle of *Loligo pealei* on the Scotian Shelf and Georges Bank off Newfoundland, Canada, has provided one of the key models of a cephalopod life cycle. He reconciled the population size frequency modes in the population with the finding that there were both spring (April–May) and summer (July–August) spawning groups by proposing that two reproductive cycles co-existed (Fig. 6.3). Squid hatching from the early brood (May–June) grow rapidly during the summer of their natal year (year of hatching), become mature over the subsequent winter, and breed in the summer of the next year at about 14 months of age. Squid hatching from this summer brood are too small to mature in their first winter and remain immature throughout the following summer. The shortened day-length of their second winter induces maturation (implied as a causal factor stimulating vitellogenesis in females from the work of Richard (1967) on *Sepia officinalis*), resulting in the spring-spawning group of the subsequent year.

Mesnil (1977) refers to these two reproductive cycles as the short (one winter) and long (two winters) cycles, and credits his ideas to the work of earlier European authors working on *Sepia officinalis* and *Loligo vulgaris* (Tinbergen & Verwey 1945; Mangold 1963). For any lineage of squid, the proposal suggests that the two life cycles alternate between the ‘short’ and ‘long’ formats, with successive generations breeding at about 14 months, followed by 18 months. This alternating 1- or 2-year (winter) model has been usefully applied for several other species (Boyle *et al.* 1995). It means that the two annual spawning periods observed in this species and many others are consistent with semelparity, since each arises from a separate breeding group. Although no evidence has yet been produced to show any degree of genetic separation between the spring- and summer-spawners in this or other species (Carvalho & Loney 1989), it would be expected that selective pressures could operate differently on the two groups but this would be offset by interbreeding.

It should be recognised that although this alternating generation model fits the observed data, there is no direct evidence to show that the separate breeding groups give rise to different lineages, or that there is any degree of genetic difference between

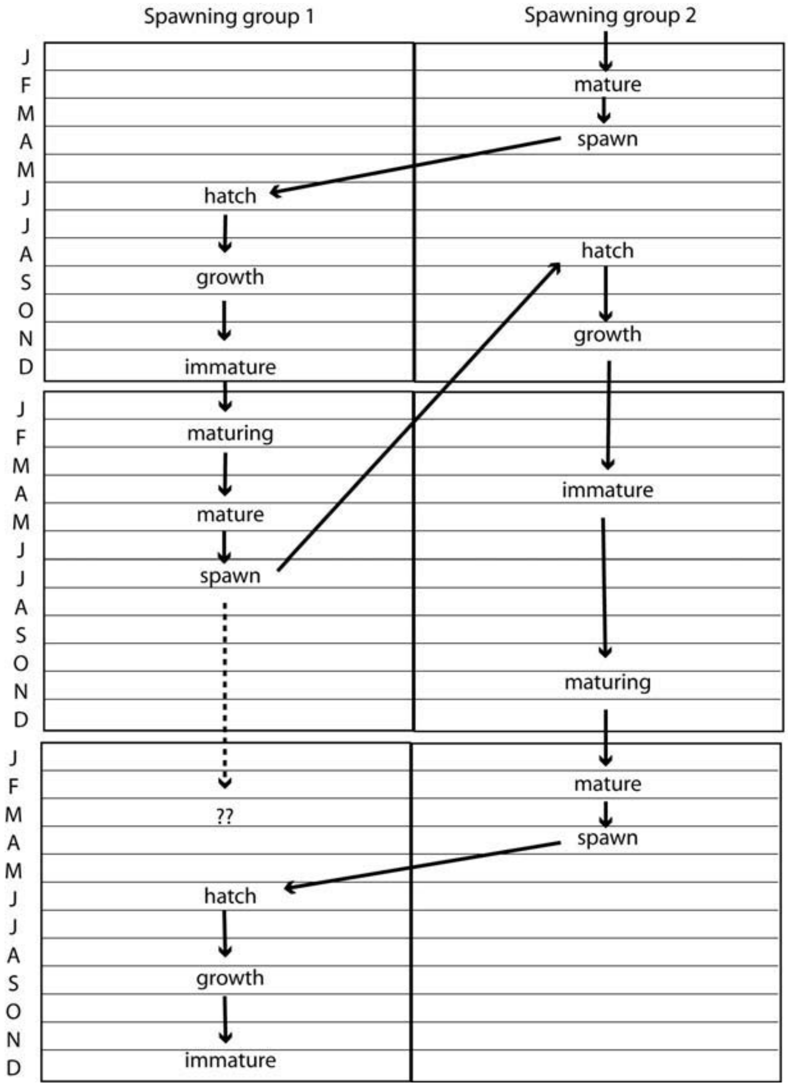


Fig. 6.3 Life cycle summary of *Loligo pealei* (after Mesnil 1977) to show how two annual spawning groups might co-exist in a semelparous species and account for multiple size modes in the population. The proposed persistence of large post-spawning animals up the age of 21 months was not supported by subsequent ageing studies (Brodziak & Macy 1996).

them. Indeed, ageing of *L. pealei* by statolith readings fails to provide evidence for animals over 1 year old (Brodziak & Macy 1996). Other models could be applied to this species which would simply propose that fast- or slow-growing cohorts arising from any one spawning season reach their own breeding season at different times. The relative success of the two groups then determines the balance of their contribution to the succeeding population (see discussions of *Loligo gahi*, *Octopus bimaculatus* and *Eledone cirrhosa*).

6.3.2.2 Loligo forbesi (see Boyle & Ngoile 1993; Boyle & Pierce 1994; Boyle et al. *1995; Collins* et al. *1995a, b; Forsythe & Hanlon 1989; Guerra & Rocha 1994; Hanlon* et al. *1989; Holme 1974; Moreno* et al. *1994; Pierce* et al. *1994a, b, c, d, e)*

Two species of loliginid squid, *Loligo forbesi* and *L. vulgaris*, comprise significant commercial fisheries in the eastern North Atlantic. Although overlapping throughout most of their ranges, *L. forbesi* has the slightly more northerly and offshore distribution of the two. In the Atlantic, it extends from the coasts of southern Norway and the Faeroes (60°N) southwards to about 20°N on the coast of Africa, and occurs throughout the Mediterranean Sea.

Spawning takes place predominantly in winter over a fairly extended period during November–April, but with the bulk of the population breeding in December–January. The large egg mops are laid on the bottom or attached to other objects in the water such as ropes or fishing gear. There is no definite evidence for major spawning aggregations in this species. Instead, the egg masses seem to be widely distributed in coastal waters at depths 10–300 m, with deposits down to 500 m reported by Lordan & Casey (1999) and 730 m in the Aegean Sea (Salman & Laptikovsky 2002).

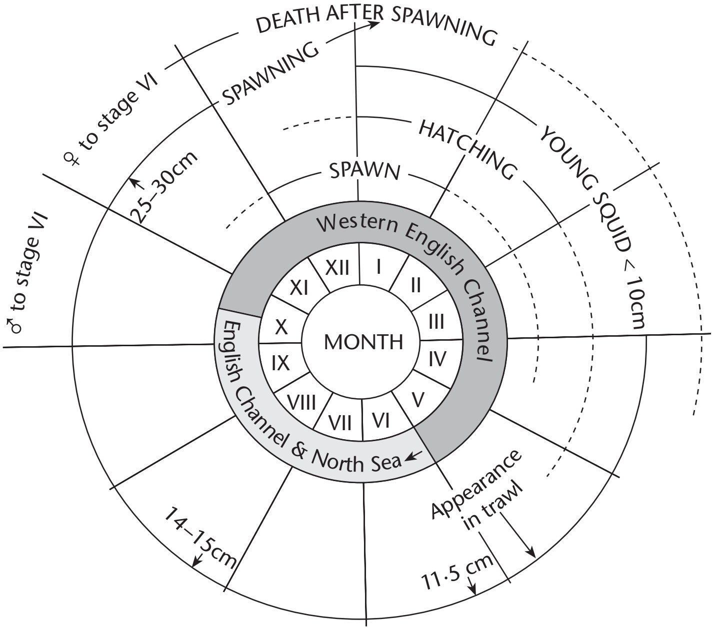
As depicted by Holme (1974), the life cycle of this species in the English Channel fits the annual pattern (Fig. 6.4). After an incubation period of about 50 days, followed by a planktonic phase during which the paralarvae are rarely caught, young squid (≥100 mm mantle length) appear in trawls during May as the recruits of that year. Growth is rapid (20–30 mm mantle length per month), and the bulk of the recruits appear capable of reaching adult size and maturity as part of the winter spawning population. The bulk of the fisheries for this species occur in the autumn–winter season (October–December) and take place on the maturing/breeding population. The small numbers of large animals present in the early part of the year suggests that some fraction of the population survives the winter, probably without breeding, and is present when the new recruits appear.

Although this picture of a simple annual life cycle, which is typical of most Loliginidae, appears to hold throughout the geographical range, it does not fully account for all of the features of the population. Some animals can be mature at almost any season of the year: typically at least two pulses of juvenile recruitment are present even if there is only one principal breeding season; two size-modes may be distinct at breeding (especially evident in males); females may mature the eggs in several batches; and the time between spawning and hatching may vary by at least 35–125 days depending on temperature (Boyle *et al.* 2001). These departures from a simple, seasonally breeding model of the annual cycle contribute plasticity to the life cycle and reduce the risk of local extinctions due to unfavourable conditions in any one year (Boyle *et al.* 1995; Pecl 2001; Pecl *et al.* 2004).

6.3.2.3 Loligo gahi (see Arkhipkin 1993a; Baron & Re 2002; Carvalho & Pitcher 1989; Hatfield 1991; Hatfield & Rodhouse 1991, 1994b; Guerra & Castro 1994; Patterson 1988; Vega et al. *2002)*

This southern hemisphere species is distributed from Peru on the Pacific coast of South America to the southern tip of Chile, and northwards on the Atlantic coast at least

(a) *Loligo forbesi* – life cycle summary



(b) *Loligo forbesi* – reproductive strategies

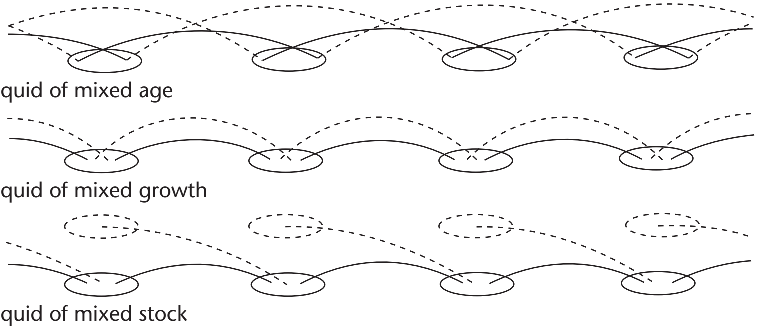


Fig. 6.4 (a) Annual life cycle of *Loligo forbesi* in the English Channel (after Holme 1974). (b) Representation of alternative explanations for the occurrence of distinct size modes in the population at breeding based on the co-occurrence of cohorts of different age or growth rate, or from different stocks (Boyle *et al.* 1995).

along the entire coast of Argentina. Beginning in the early 1970s, a major fishery developed on the Patagonian Shelf in waters off the Falkland Islands (Malvinas).

The spawning grounds of *Loligo gahi* are inshore and the young squid first appear in shallow water. They then migrate away from the shore (Fig. 6.5a) into deeper water while feeding and growing. At maturity they make a return migration into shallow water to breed. The species appears to be annual, but since there are two major seasons when squid are available to fishing (February–June, August–October), at least two (possibly three) spawning groups are inferred. In common with other loliginids with

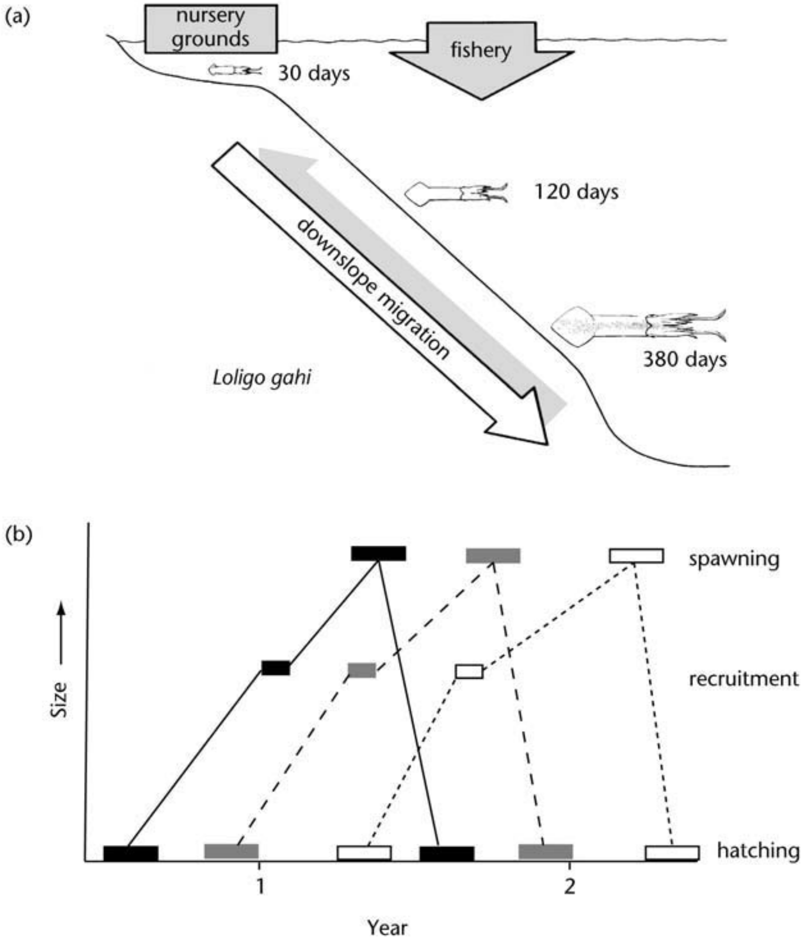


Fig. 6.5 Size frequencies of *Loligo gahi* fished on the Patagonian Shelf clearly showing the growth of recruits (a) as they migrate offshore from spawning grounds (Hatfield & Rodhouse 1994a), but the two or three annual recruitment modes identified in the fished population (b) cannot be clearly linked to evidence for proposed spawning episodes (after Hatfield & Rodhouse 1994b).

several recruitment episodes, models can be proposed to account for the observed population structure (Fig. 6.5b), but evidence linking the recruitment modes to distinct spawning seasons is lacking.

6.3.3 *Teuthoidea (Teuthida) – Ommastrephidae*

Largely because of their significance to major commercial fisheries, much is known about the migrations and population biology of the ommastrephid squid. Characteristically they are of shelf-break and oceanic distribution, but they also make large-scale, seasonal migratory incursions over the continental shelf, apparently in pursuit of prey. Spawning in species of the family Ommastrephidae occurs entirely in the pelagic environment. The masses of spawn produced by the female hydrate and swell to 1 m in diameter (O'Dor & Balch 1985; Bower & Sakurai 1996). Almost neutrally buoyant, these fragile gelatinous masses drift in oceanic currents, probably at considerable depth, at the density interface of stratified water masses. For these reasons the closing stages of the ommastrephid life cycle, breeding and spawning are much less accessible to study, are less well known than those of the Loliginidae, and are more open to surmise. Some comparisons between the life-history strategies of these two families are reviewed by O'Dor (1998a).

6.3.3.1 Illex illecebrosus (see Arkhipkin & Fetisov 2000; Coelho & O'Dor 1993; Coelho et al. *1994; Dawe* et al. *1981, 1990; Dawe & Beck 1985; Hatanaka* et al. *1984, 1985; Mesnil 1977; O'Dor 1983; O'Dor & Coelho 1993; O'Dor & Dawe 1998; Rodhouse* et al. *1995)*

This is the northern shortfin squid of the west Atlantic, ranging from Florida to the cold waters of the Grand Banks and coastal Newfoundland. The northern and eastward extent of the species is not clearly demarcated from the closely similar *Illex coindetii* of the eastern north Atlantic, which has sometimes been recorded as *I. illecebrosus* in fishery statistics.

The life cycle of *I. illecebrosus* is closely linked to the northward movement of the Gulf Stream (Fig. 6.6). Spawning is thought to take place in late winter in deep water off the coast of Florida. The hatchlings ascend into the lighter surface waters to coincide with the spring production associated with the phytoplankton bloom. Feeding and growing on the subsequent increase in zooplankton, the paralarvae and juveniles are carried northwards by the current, gradually moving inshore to contribute to the seasonal fishery for squid off the coasts of Nova Scotia and Newfoundland in the late

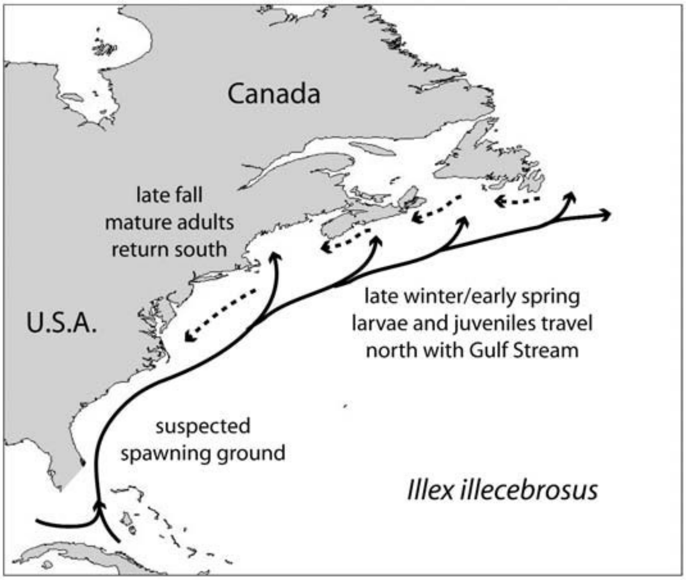


Fig. 6.6 The hypothetical life cycle of *Illex illecebrosus* in the northwest Atlantic (after O'Dor & Coelho 1993, Black *et al.* 1987).

summer and autumn. A deepwater return migration of adults back south to the spawning grounds is hypothesised to take place in late autumn and early winter.

Although a 1-year lifespan is considered to be the basic pattern, there is evidence that a variable component of the population of large squid may remain immature in deep, colder water, overwintering in the north. The balance between these two components of the adult population varies year to year, and may show trends over several years (O'Dor & Coelho 1993). The effect is to offset the instability of an annually migrating semelparous population by providing a 'reserve' stock, normally unavailable to fishing (too deep) and less vulnerable to inter-annual fluctuations in hydrographic conditions.

6.3.3.2 Illex argentinus (see Arkhipkin & Laptikhovsky 1994; Arkhipkin 1999; Coelho & O'Dor 1993; Coelho et al. *1994; Dawe* et al. *1990; Rodhouse* et al. *1995; Dawe & Beck 1985; Hatanaka* et al. *1985; Mesnil 1977; O'Dor 1983; O'Dor & Coelho 1993; Haimovici* et al. *1998)*

The Argentinian shortfin squid has a geographical range from the coast of Brazil at about 22°S latitude, south to the southern Patagonian Shelf and extending eastwards to the whole of the Patagonian Shelf, but concentrated close to the shelf edge (Fig. 6.7).

Recruitment patterns in this species suggest that there are several spawning stocks, although the total biomass is dominated by the winter-spawning stock. The locations of spawning are not clear, but it is thought to take place from early winter to mid-spring (July–October) along the continental shelf edge off northern Argentina, in the northward-moving Falklands Current. Paralarvae and juveniles are found in the confluence of the Falkland and Brazil Currents, and they then migrate southwards, spreading out over the Patagonian Shelf and around the Falkland Islands (Malvinas). Here, the main international fisheries take place on pre-spawning stocks before the presumed northward migration to breed along the shelf edge.

Although the recruitment patterns and spawning groups in this species are complex, there seems little doubt that this is a strictly annual life cycle.

6.3.3.3 Todarodes pacificus (see Hamabe & Shimizu 1966; Hatanaka et al. *1985; Okutani 1983; Murata 1989; Nakata 1993; Takami & Suzu-uchi 1993)*

This oceanic and neritic species is distributed in the western Pacific between 20°N and 60°N and is historically landed by the Japanese fishery in quantities which rank it as the largest single cephalopod resource on record.

Todarodes pacificus spawns in waters off southern Japan (Fig. 6.8) in at least three spawning groups at different seasons (winter, summer and autumn). Moving northwards in branches of the Kuroshio and Tsushima Currents, the juvenile squid feed and grow in rich upwellings around the coast. The different spawning groups contribute populations which penetrate northwards to differing distances, the winter-spawning group having the furthest long-range migration.

Each of the spawning subgroups is presumed to have an annual lifespan and to contribute a return migration of mature adults to spawn in the south.

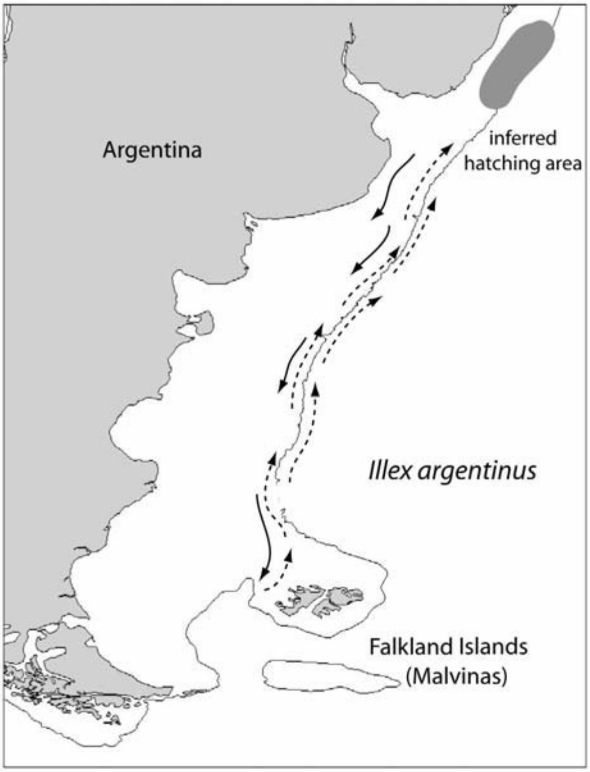


Fig. 6.7 Life cycle of *Illex argentinus* in waters off South America, showing the migration of the winter-spawning stock and and inferred hatching area at the confluence of the Falklands and Brazil Currents (after Arkhipkin 1993b; Haimovici *et al.* 1998; Waluda 2000). The shoals of juvenile and sub-adult squid move southwards over the Patagonian Shelf, where they contribute to major multi-national fisheries, before beginning the northward migration in the Falkland Current along the shelf edge.

6.3.4 Octopoda (Octopodida)

6.3.4.1 Octopus vulgaris (see Buchan & Smale 1981; Guerra 1981; Mangold & Boletzky 1973; Mangold-Wirz 1963; Mangold 1983b; Nixon 1969; O'Dor & Wells 1978; Sánchez & Obarti 1993; Nixon & Mangold 1996; Balguerias et al. *2002; Caverivière* et al. *1999, 2002; Hernández-García* et al. *2002; Smith & Griffiths 2002)*

The 'cosmopolitan' species *Octopus vulgaris*, nominally with global distribution, is probably a species group awaiting full description within which the historically designated species has a distribution centred on the Mediterranean (Mangold & Hochberg 1991). There is no comprehensive study of the life cycle, but there is a large literature of parallel biological and fisheries studies. The largest regional commercial trawl fishery for octopus is that of the Saharan Bank, from where we take this summary of their life cycle characteristics (Caverivière *et al.* 2002).

Found from the shoreline down to about 400 m off the coast of northwest Africa, octopuses are most abundant between 15 and 100 m on all types of seabed. Sub-populations are not recognisable by clear morphometrical characters, but genetic

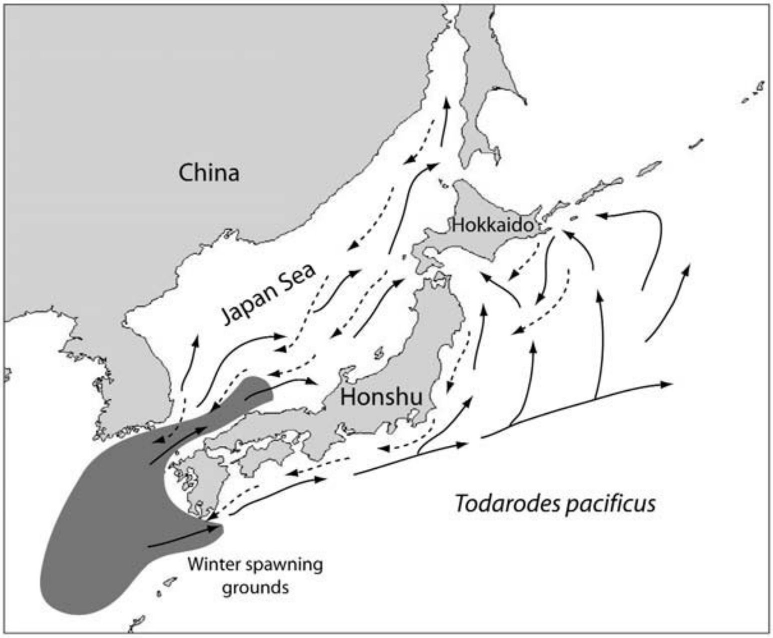


Fig. 6.8 Spawning areas (shaded) and migration routes of the main winter spawning population of *Todarodes pacificus* in Japanese waters (after Hatanake *et al.* 1985, from Kasahara 1982). The spring–summer northward migration occurs into the Japan Sea and along the Pacific coast in the Kuroshio Current. The southward return migration occurs in autumn–winter. Distinct summer and autumn spawning populations that occupy part of the winter spawning area and extend further into the Japan Sea coastal area are also recognised.

structuring of the population may be present based on depth distribution and oceanographic boundaries (Murphy *et al.* 2002). Maturing sexually at a small size (males 260 g, females 500 g), breeding in these waters occurs year-round, with two main periods in late summer and winter. The female lays as many as 200 000 eggs, each about 2 mm × 1 mm, attached in strings and anchored to a hard surface, and frequently under a rock overhang. She then broods the eggs, keeping them clean and ventilating them for the period to hatching, which may last between 15 and 87 days at temperatures between 27 and 17°C. Both females and males lose weight and die shortly after reproducing, at about 1 year of age.

Hatching larvae weigh about 1.4 mg and enter a planktonic phase lasting 33–54 days (27–21°C) or even up to 3 months at low temperatures on the outer limits of distribution. Settlement to the seabed and transfer to a diet of small benthic prey occurs when the juveniles have reached about 200 mg. A combination of captive growth experiments and tag–recapture programmes in artisanal and commercial fisheries gives a wide range of individual rates. Overall, estimates suggest that *O. vulgaris* off the northwest African coast take about 90 days from hatching to reach 50 g in weight, projecting the age of the largest animals (females 5 kg, males 6–8 kg) to be between 12 and 14 months with a strictly annual life cycle.

6.3.4.2 *Octopus bimaculatus (see Ambrose 1988a)*

Water temperature has a profound influence on rates of growth and maturation in all cephalopods, and may cause all or part of the population to switch between 1- and 2-year life cycles. At Catalina Island, off the California coast, a 6-year field study (by diving) of *Octopus bimaculatus* (Ambrose 1988a) showed that most matings occurred in May/June, with egg laying in April–August. Octopuses spawning earlier in the year, at lower water temperatures, were less likely to be reproductively successful.

Octopuses settling in July–September at 5 mm mantle length (ML) grew to 50 mm ML by May–June of the following year. This relatively slow growth is consistent with the 13–18°C ambient temperatures. Combining estimates of 8–10 months from settlement to adult and a further 11–12 months as an adult gives a preliminary overall lifespan estimate of 19–22 months (post-settlement). At maximum growth rates, it would be possible for individuals hatched at the beginning of the season to spawn 13 months after settling, whereas those hatched late in the season would not breed until the following year (17 months after settling). This separation of the early and late hatchlings gives rise to the 'alternating generation' life cycle model (Fig. 6.9).

The study by Ambrose (1988a) provides some of the most convincing evidence that terminal spawning in octopuses normally occurs in the field. The physical condition of the females visibly deteriorated during the brooding period, and the dead body of the female was found shortly after the eggs had hatched still within the protective barricades of stones and shells in which the eggs were brooded.

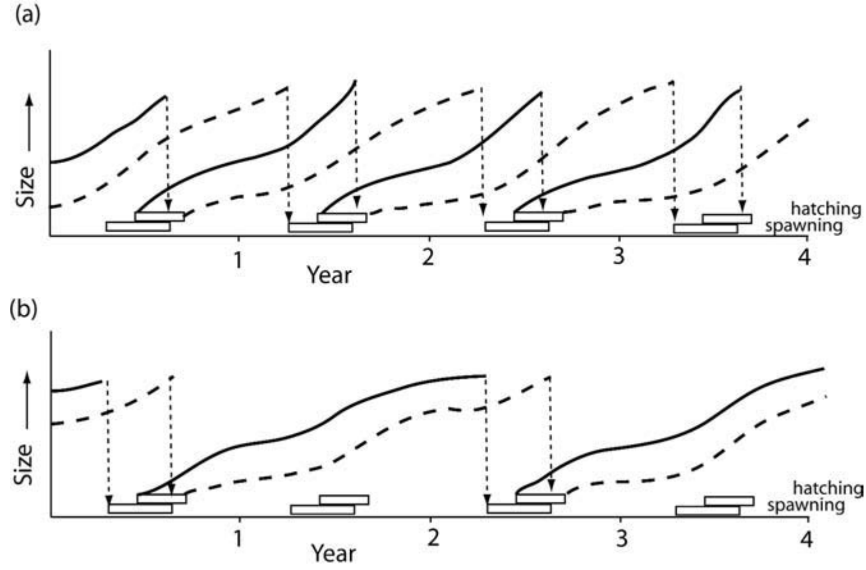


Fig. 6.9 Life history models for *Octopus bimaculatus* (after Ambrose 1988a). (a) 'Alternating generation' in each cohort. Octopuses hatching early (June) spawn 13 months after settling, while those hatching late (September) have a longer planktonic phase and spawn 17 months after settling. (b) Lower temperatures overall give rise to the 'alternating years' model in which each cohort, early or late, breeds within the second year after hatching.

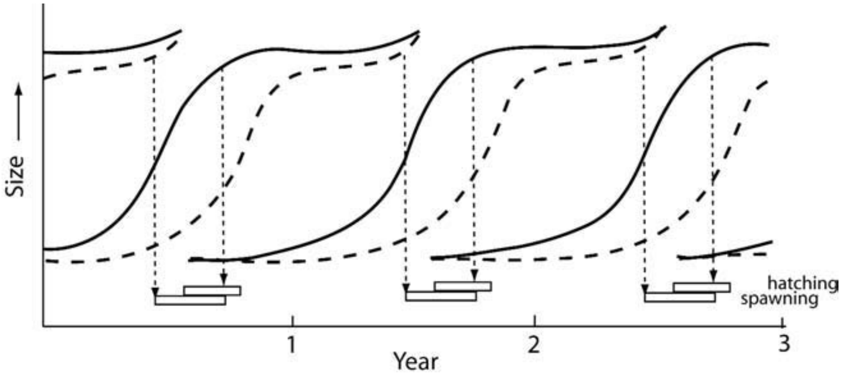


Fig. 6.10 Composite model of the life cycle of *Eledone cirrhosa* (after Boyle 1983b). The estimated period of peak spawning activity and hatching is shown on the lower line. Growth can proceed at widely differing rates after settlement. Rapid growth (upper margin of the growth curve, solid line) and early maturity allows individuals to contribute to the spawning population of the first year, after which they die at about 12–15 months old. Slow growth (lower margin of the growth curve, dashed line) leads to a 2-year cycle in which the over-wintering population matures and contributes to the early part of the spawning peak of its second season and dies at 18–21 months.

6.3.4.3 Eledone cirrhosa (see Boyle 1983b, 1986c; Boyle & Knobloch 1982a, b, 1983, 1984a, b; Mangold-Wirz 1963; Tursi et al. *1995; Wurtz & Repetto 1983)*

In the colder waters inhabited by *Eledone cirrhosa*, an alternating 1- or 2-year life cycle was proposed by Boyle (1983b). This allowed a reconciliation of population characteristics such as the wide differences in individual growth rate within the population, its long breeding season, the over-wintering cohort of immature animals, and the possible occurrence of two size (age?) classes at the beginning of the year, and it could fit both the northerly distribution in cold coastal waters off Scotland, and the southern cold deep-water animals of the Mediterranean.

The inclusion of both high- and low-growth-rate animals (1st and 2nd year breeders) within the same generational cohort allows the model considerable flexibility in explaining the inter-annual variations in life cycle. For example, in a bad year for growth (represented by the lower margin of the growth curve in Fig. 6.10), maturation is delayed until the following year. This condition gives the bulk of the population a 2-year cycle and probably an increased risk of individual mortality before breeding. In a good year, growth is rapid and the bulk of the population becomes mature in the first year (year of settlement), presumably allowing a higher proportion of the cohort to breed successfully.

6.4 Consequences

In life-history theory, the pattern of reproduction in the modern cephalopods presents several enigmas. The minimal (if any) evidence for iteroparous species poses the fundamental evolutionary question of why the coleoids invariably breed once and then die?

Calow (1987), derives three predictions from this apparently universal monocyclic condition:

- that the level of investment in reproduction by semelparous organisms (reproductive effort) should be high;
- that if high levels of investment in reproduction shorten the lives of parents then reduced levels should extend life;
- that the survival of the juveniles should be relatively high.

The total reproductive investment by female cephalopods has been estimated from the relative size (energy content) of the gonad and eggs at the point of egg-laying. Estimates for different species suggest that the total reproductive output by the female cephalopod accounts for up to 30% of body weight. The upper estimates are greatest for the more obviously terminally spawning species, but not at all high in comparison with such classically semelparous types as insects. There are no available estimates for cephalopod species such as *Octopus chierchiae* (Rodaniche 1984) or *Opisthoteuthis* spp (Villanueva 1992a) which obviously extend the period over which eggs are laid, and no instantaneous estimate of fecundity or reproductive investment is possible. Compared with other annual marine species such as nudibranchs or even long-lived fish species which breed each year, the reproductive investment by individual females cannot be particularly high.

High levels of mortality are associated with breeding in almost all animal types, although in relatively few animal forms, e.g. insects and jellyfish, is semelparity and death immediately after breeding the normal pattern. Cephalopods present a puzzling combination of large body size (the largest of all invertebrates) and complex behaviour with a high learned component, which is usually associated with long-lived animals, coupled with universal death shortly after breeding. The ultimate (evolutionary) reason for this condition is sometimes presented as the avoidance of competition between parents and offspring, or between one generation and the next. It is clear from the body size and habitat differences between adult and offspring that competition is avoided during the early life history except where the cannibalism prevalent during migratory and later stages of growth in some species occurs between different growth cohorts of the same annual generation.

The proximate (immediate) causes of death after breeding are also not clear. The condition of post-brooding senescent octopus is poor. Skin lesions often develop, and subsequent fungal infections lead to early death. Breeding concentrations of squid do not conspicuously attract predators, but there are reports of post-spawning and dying squid being fed upon by scavenging fish and mammals. Arising from work on the control of maturity and reproduction is the suggestion that the hormonal and physiological processes leading to vitellogenesis and egg-laying are irreversible, and that once maturation is initiated the cephalopod cannot physiologically return to the pre-breeding state. Wodinsky (1977) showed that excision of the optic glands from maturing octopuses (depriving them of the source of gonadotropic hormone[s]) caused the gonad to regress and feeding and growth to resume. Apart from the work of Tait (1986), these experiments have not been repeated.

The apparently universal, endogenously determined death after spawning is one of the central tenets of cephalopod biology, and one that deserves much greater attention from both theoretical and experimental biologists. Simple physiological control of maturation and spawning, driven through environmental cues such daylength or temperature, is unlikely to provide an overall explanation for the diversity of ecological patterns present in the life cycle and seasonality. The presence of some animals in a mature condition throughout the year, the appearance of distinct cohorts within the population having different reproductive timing, and the alternation of intermittent episodes of spawning with periods of feeding and growth in some species all point to a more complex control of the annual reproductive cycle.

The final prediction, that the survival of offspring should be relatively high, is directly related to the absolute fecundity, the provision of yolk and protection for the eggs, and the levels of predation and starvation in the paralarval and juvenile stages. These indices of survival are highly variable between species. Fecundity estimates range from a few tens of eggs (*Sepiola*, Boletzky 1981) to several millions (*Architeuthis*, Boyle 1986d). Levels of yolk provision are minimal in the family Ommastrephidae and the offspring are entirely planktotrophic, whereas many benthic octopuses not only provide very large yolky eggs but a high degree of parental behavioural care. Paralarval and juvenile stages of all cephalopods are probably highly vulnerable to larger and faster predators, but there are no quantitative estimates of mortality due to predation at different growth stages. Presently, there is no generalisation about the relative level of fecundity or stage-specific mortality that is likely to hold across the cephalopods as a class.

Chapter 7

Growth

Summary: Individual growth rates of living coleoid cephalopods are relatively high in both laboratory and field conditions. The high growth rate is sustained by high feeding rates and an exceptionally efficient conversion of food into somatic growth. Measurements of growth are expressed by mantle length (preferred for squid and fishery studies) or weight. Methods for the ageing of squid from daily incremental lines in the statoliths provide the main tool for the assessment of growth in field populations. The length of the squid gladius is virtually the same as the mantle length, and the measurement of incremental lines on the gladius provides an additional means of reading the growth history of individuals. Such methods are not generally available for cuttlefish and octopus. Age–length keys for cephalopods are unreliable, and demographic methods of estimating the growth of populations in the field are subject to biases of immigration–emigration and of gear selectivity. Growth studies in culture conditions have shown that coleoid cephalopod growth can be modelled as a two-stage process, an exponential phase followed by a logarithmic phase. The size at which the transition takes place, and its timing in the life cycle, is variable and not well defined. With some exceptions, such as the cirromorph octopods, growth is concluded by sexual maturation. Growth rate is strongly influenced by temperature. A consequence of this is that later-hatched broods of paralarvae may grow faster and overtake those already hatched. The interaction between the timing of hatching and the optimum conditions for growth is therefore a critical factor determining recruitment success. Allometric growth relationships between somatic, reproductive and digestive components change during ontogeny owing to relative states of maturity development or nutritional status.

Cephalopods are of large body size. Although some species may reach no more than a few grams weight as adults (*Octopus micropyrsus*), most species of octopus, cuttlefish and squid are among the largest of all invertebrates. The maximal size of cephalopods such as *Octopus dofleini* (<272 kg, Hochberg & Fields 1980) or *Architeuthis* spp (<450 kg, Roper & Boss 1982) is greater than that of any animals except the largest fish and mammals. The large body size in the Coleoidea is sustained by their ability to reach high rates of growth, feeding and food conversion. Many of the fossil Nautiloidea and Ammonoidea were also exceptionally large, although growth is slower and lifespan is longer in modern nautiluses than in the coleoids (see Chapter 4).

High growth rates contribute one of the most important ecological characteristics of cephalopods. Their demand for food during the growth phase determines many aspects of:

- their predatory impact on prey populations;
- the high rate of biomass production by populations;
- the availability of this production to other marine predators and to fishing by man;
- the ability with which cephalopod growth characteristics can be incorporated into population models for assessment purposes.

There are numerous directed studies on individual growth and the size–structure composition of populations. Comprehensive reviews of cephalopod growth characteristics are available (Mangold 1983a; Forsythe & Van Heukelem 1987) and, although there are some insights into the energetics and use of nutrients by cephalopods (O'Dor & Wells 1973; Wells & Clarke 1996), the underlying mechanisms is still the subject of research (Jackson & O'Dor 2001; Moltschaniwskyj 2004).

7.1 Estimation of growth rate

An estimation of growth rates in any animal type requires both measurements of size (dimension or mass) and estimations of age (absolute or relative). Cephalopods present problems in quantifying both parameters.

Linear dimensions are difficult to measure consistently in what are mainly soft-bodied animals, especially when there are differences in the methods of handling and processing material, e.g. freezing or fixation. For squid and cuttlefish, where there is a rigid support within the mantle musculature, mantle length (along the dorsal surface) or total weight are the accepted measures of size. Mantle length is routine for fishery studies because of its greater speed of use on bulk samples and the difficulty of weight measurements on ship. Even these simple measurements are subject to significant error and bias, and their use in morphometrical studies has to be approached with caution (Pierce *et al.* 1994c). With the globular rounded shape of octopuses, and the relative lack of demarkation between their mantle and head, mantle-length measurements are useful only in conventional systematic descriptions. Weight, as the normal measurement of size, is also open to major error owing to the water retained within the mantle cavity, especially by octopuses when weighed alive.

Microscopic analyses of muscle tissue (Martinez & Moltschaniwskyj 1999) has also been of value in assessing the mechanisms of somatic growth (Moltschaniwskyj 1994; Moltschaniwskyj & Jackson 2000; Pecl & Moltschaniwskyj 1997, 1999).

7.1.1 Statolith increments

Accurate estimation of absolute or relative age is possible only for animals reared in captivity. Studies on cephalopod growth in the field have advanced owing to the realisation that the statolith grows incrementally (Clarke 1966), and that the lines seen in prepared statoliths are generally laid down on a daily basis (Spratt 1978; Lipinski 1978, 1980, 1986; Kristensen 1980). Dark lines are separated by light spaces, the two together forming a growth increment that in the curved areas of the statolith dome are often referred to as growth 'rings' (Box 7.1). Techniques for the visualisation of the increments have progressed to the use of automated image analysis systems (González *et al.* 1998a, 2000), and detailed accounts of the methodology and variations in technique are summarised in workshop reports (Jereb *et al.* 1991) and reviews (Rodhouse & Hatfield 1990b; Lipinski & Durholtz 1994). Comprehensive bibliographies of the use of statoliths for age estimation can be found in Jackson (1994b) and Jackson & O'Dor (2001). Readings of statolith microstructure are commonly used to identify cohorts of differing age (recruitment times) within fished populations where they might not be recognised by length–frequency analysis (e.g. Dimmlich & Hoedt 1998; Rocha & Guerra 1999). The clarity of the increments and their persistence along the growth

Box 7.1 Age estimation from statolith rings

Laterally within the cartilaginous cranium of the cephalopod is a pair of fluid-filled cavities, the statocysts. Within each statocyst is an irregularly shaped calcareous stone, the statolith. In response to acceleration, the statolith moves within the cavity and stimulates hair cells projecting inwards from the walls of the statocyst. The hair cells are orientated in several planes, so that the number and position of those excited by the movement convey precise information to the brain about the movement of the animal in three dimensions. The statocyst is thus the main organ for the detection of gravity and movement. It has a critically important role in feedback control of locomotion, and is analogous in function to the semicircular canal system of the vertebrates.

When the statolith is removed, cleaned, glued onto a glass slide and gently ground to a thin section with fine carborundum paper and jeweller's polish,

Fig. 7.1.1 Ground section of the dome of a statolith of *Loligo forbesi*.

concentric rings are revealed surrounding a central, amorphous focus. These incremental steps in the statolith structure are widely recognised as 'growth lines' or 'growth rings' concentrically surrounding the focus, or sometimes round a recognisable initial or 'natal' ring.

Despite the variation in their appearance (some rings are darker in appearance or are composed of sub-rings), the finest lines visible with the light microscope are generally believed to represent daily increments of statolith growth. Validation of their daily deposition, using tetracycline or radioactive strontium markers fed to captive squid at a known time, is available for some species. Age estimates of samples from wild populations using this method are generally consistent with estimates of age from modal size–frequency methods. The rings are visible in most squid; they are clearest and most regular in ommastrephids, and are usually indistinct and irregular in cuttlefish and octopus. Increment deposition is likely to relate to diurnal feeding patterns, and to be most definite in those animals with a strong feeding rhythm.

The 1 ring = 1 day hypothesis has become generally accepted, but requires further evaluation and may not apply universally. The mechanisms of ring formation also have not been clearly established. Despite these uncertainties, the application of age estimation by statolith rings has become a useful ecological tool.

axis of the statolith is very variable, but with a degree of interpolation it is frequently possible to identify the natal ring, and estimate the hatching date and absolute age of the individual. Of the exploited squid, the increments are generally clearer and easier to interpret in the ommastrephids.

The increments observed in many species are not all of the same strength, leading early studies (Spratt 1978) to suggest that there were both daily and monthly increments. Direct validation of the one increment per day hypothesis received support from laboratory culture of *Loligo opalescens* (Yang *et al*. 1983; Hixon & Villoch 1984; Jackson 1994b) where squid of known age were available. It has also been possible to use tetracycline or strontium fed to live squid in captivity to leave a mark at the growing edge of the statolith and, after a further period of rearing and subsequent examination of the prepared statolith, to relate the number of added increments to the number of days elapsed. Although there may not be perfect correlation between increments added and days elapsed, such studies have generally supported the relationship 1 increment = 1 day for a range of species from several families.

Ommastrephidae: *Illex illecebrosus* (Dawe *et al*. 1985; Hurley *et al*. 1985; Balch *et al*. 1988); *Todarodes pacificus* (Nakamura & Sakurai 1990, 1991).
Loliginidae: *Sepioteuthis lessoniana* (Jackson 1989); *Alloteuthis subulata* (Lipinski 1987); *Loligo chinensis* (Jackson 1990, 1995a); *Loligo vulgaris* (Bettencourt *et al*. 1996); *Loliolus noctiluca* (Jackson 1990; Jackson & Moltschaniwskyj 2001); *Loligo plei* (Jackson & Forsythe 2002); *Loligo vulgaris reynaudi* (Lipinski *et al*. 1998; Durholtz *et al*. 2002); *Loligo opalsecens* (Jackson 1994a).
Idiosepiidae: *Idiosepius pygmaeus* (Jackson 1988).

The underlying basis of statolith ring formation is not fully understood, but it is probably driven by changes in the pH and ionic composition of the statocyst fluid following feeding events (Morris 1988, 1991; Lipinski 1993; Durholtz & Lipinski 2000) or environmental influences (Ikeda *et al.* 1998; 1999a, b, c, 2002a, b; Bettencourt & Guerra 2000). The chemical composition of the statolith itself may also vary throughout its growth (Yatsu *et al.* 1998b). The differences observed between species in the strength and regularity of increments may be due to ecological differences between them; those with the most defined increments perhaps having a clear diurnal pattern of feeding activity.

7.1.2 Gladius increments

Other secreted hard structures in cephalopods, notably the gladius (pen) of squid (Hunt & Sherief 1990; LaRoe 1971; Spratt 1978), the cuttlebone of *Sepia* (Choe 1963; Ikeda *et al.* 1999d; Bettencourt & Guerra 1999), the beaks (Clarke 1965; Hernandez-Lopez & Castro-Hernandez 2001), and even the eye lens and the residual shell stylet in octopuses, show periodic or incremental growth lines. The growth lines on the squid gladius offer an important means of tracing the growth history of the individual because gladius length is effectively the same as mantle length (Arkhipkin & Perez 1998). Absolute age cannot be reliably estimated by this method, because the lines cannot be traced back to the hatching point, but if the growth lines are daily, then sequential increment intervals give a reasonable record of growth history back-calculated from the time of sampling (Box 7.2).

Arkhipkin & Bizikoff (1991) investigated the correspondence between statolith and gladius increments in three species of squid. In *Sthenoteuthis oualeniensis* (Ommastrephidae) and *Berryteuthis magister* (Gonatidae), age and growth estimates from the two structures were reasonably consistent, but for the Antarctic *Moroteuthis ingens* (Onychoteuthidae) the number of gladius increments exceeded the number of statolith increments. In a study of cultured and wild-caught *Sepioteuthis lessoniana* (Loliginidae), Jackson *et al.* (1993) found strong corroboration of age and growth data obtained from statoliths and gladii of the same individuals. They also found that the frequency of gladius increments appeared to be less than one per day in young squid, but becoming approximately daily in squid over about 3 months of age. By dye-marking the growing edge of the gladius in cultured animals held under different conditions of feeding, the number of increments subsequently formed was most directly related to the number of days on which feeding took place rather than the number of days lapsed or the feeding episodes alone.

Gladius growth increments have been used to track individual growth histories in a series of studies on squid from different families.

Ommastrephidae: *Sthenoteuthis oualeniensis* (Arkhipkin & Bizikoff 1991; Bizikoff 1995); *Illex argentinus* (Bizikoff 1991); *Illex illecebrosus* (Dawe *et al.* 1985; Perez & O'Dor 1994; Perez 1995; Perez *et al.* 1996).

Gonatidae: *Berryteuthis magister* (Arkhipkin & Bizikoff 1991).

Onychoteuthidae: *Moroteuthis ingens* (Arkhipkin & Bizikoff 1991).

Loliginidae: *Sepioteuthis lessoniana* (Jackson *et al.* 1993); *Loliolus chinensis*, *L. noctiluca* (Jackson 1990; Jackson & Choat 1992).

Box 7.2 Growth history recorded in the gladius

Lying within a sheath of connective tissue below the dorsal surface of the squid mantle is a thin plate of chitin, the gladius or pen. A remnant of the ancestral shell, the gladius now gives shape and rigidity to the elongate mantle. It is formed even in the embryo, and in most squid grows throughout life by the secretion of additional material at the anterior end as the mantle lengthens. For most purposes, mantle length, which is the commonest measure of size in squid, is either numerically the same as gladius length, or there is a close statistical relationship between the two measurements.

Examined microsopically, the semi-transparent gladius exhibits sequential concentric lines following the shape of the anterior end. These lines are interpreted to mark successive increments of growth, and for most squids there is a strong relationship between the number of increments and mantle length (Arkhipkin & Bizikov 1991). The numbers of gladius lines are roughly consistent with the rings of the statolith, and this suggests that the gladius incremental lines are also deposited daily. Support for this interpretation arises from linear studies of cultured animals using markers deposited at intervals in the gladius, an approach which also indicates a daily frequency of deposition.

The early growth lines in the posterior end of the gladius become progressively vague and difficult to interpret. Consequently, gladius lines cannot reliably be used to estimate absolute age, but on the assumption that the size of the gladius increment is proportional to the daily growth increment in length, the growth history of the individual can be read backwards from the time of death (Perez *et al.* 1996). If age can be determined independently from the statolith, a length-at-age growth curve can be derived. As a tool for the reconstruction of individual growth history, investigating growth differences between cohorts and comparing ecological conditions for growth, the technique has considerable potential.

7.1.3 Demographic methods

The widely applied methods of population analysis in fish, based on statistical recognition of size-frequency modes and their tracking over periods of time, have also been used for growth studies in cephalopods. Modes of size-frequency within a population sample are difficult to interpret for reasons arising from population characteristics, e.g.

- recruitment of successive broods within one season, giving rise to microcohorts,
- the plasticity of growth in relation to environmental conditions,
- interactions between growth and maturity,
- individual growth patterns and the lack of a clear asymptote to the growth curve,

- large-scale post-spawning mortality leading to loss of the adult-size mode,
- significant immigration and emigration from the population.

The use of mainly length-based methods to estimate cephalopod growth in the field has its proponents (Pauly 1985), but in practical terms, the resulting length–age-based keys are not reliable (Collins *et al.* 1999). The use of statoliths for age estimation in cephalopods is essential in demographic studies to compensate for the biases due to factors such as selective predation, gear/sampling bias and migration (Caddy 1991; Jackson 1994b; Hatfield & Rodhouse 1994a).

7.1.4 Direct measurement in culture conditions

As cephalopods have been brought into captivity and successfully bred and grown in aquaria, experimentalists have gained new insights into aspects of their biology (Forsythe 2004). Cuttlefish and octopus were initially found to survive better in captivity than squid which are generally more delicate and subject to damage during capture and transport, but intensive efforts led to the successful rearing of loliginid squid for biomedical research. This provided the opportunity for work on aspects of cephalopod growth that has application in ecology and fishery biology. Although culture conditions always differ from those in the wild, experimental work in captivity may provide insights that cannot be obtained in field work.

Studies on cephalopods in captivity have provided consistent evidence for the very high individual growth rates attainable by octopuses, cuttlefish and squid. Forsythe & Van Heukelem (1987) extensively reviewed the literature and compiled growth rates from a series of cultured cephalopods (Fig. 7.1). The basis for growth comparisons was expressed as instantaneous relative (or specific) growth rate, G (% increase in body weight per day).

$$G = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \times 100 \quad \text{(instantaneous relative growth, \% body weight/day)}$$

In most animals, G is inversely related to size, being greatest after an early lag phase and falling off rapidly as body size increases, but Forsythe & Van Heukelem (1987) point out that the cephalopods are unusual in that G usually remains constant over several orders of magnitude of size increase after hatching. This exponential phase of growth is followed by a slower (logarithmic) phase during which growth rate is size-specific. The size at which a change in the growth mode (from exponential to logarithmic) takes place varies widely between individuals, but occurs normally between 10 g and 100 g in weight for most of the species cultured. Up to that point, growth rates of <6% increase in body weight per day are recorded for octopuses (*Octopus cyanea*, Van Heukelem 1973, 1983), <8% for some loliginid squid (*Loligo opalescens*, Yang & Hanlon unpublished data in Forsythe & Van Heukelem 1987), and <12% in sepioids (*Sepia officinalis*, Pascual 1978). The timing of the change from exponential to logarithmic growth is not clearly linked to external factors or internal states, but in many cases growth ceases or becomes erratic coincidentally with the onset of sexual maturity. Species of *Opisthoteuthis* and other cirrate octopuses are exceptional in that both sexes are apparently mature over the greater part of the size range (Villanueva 1992a).

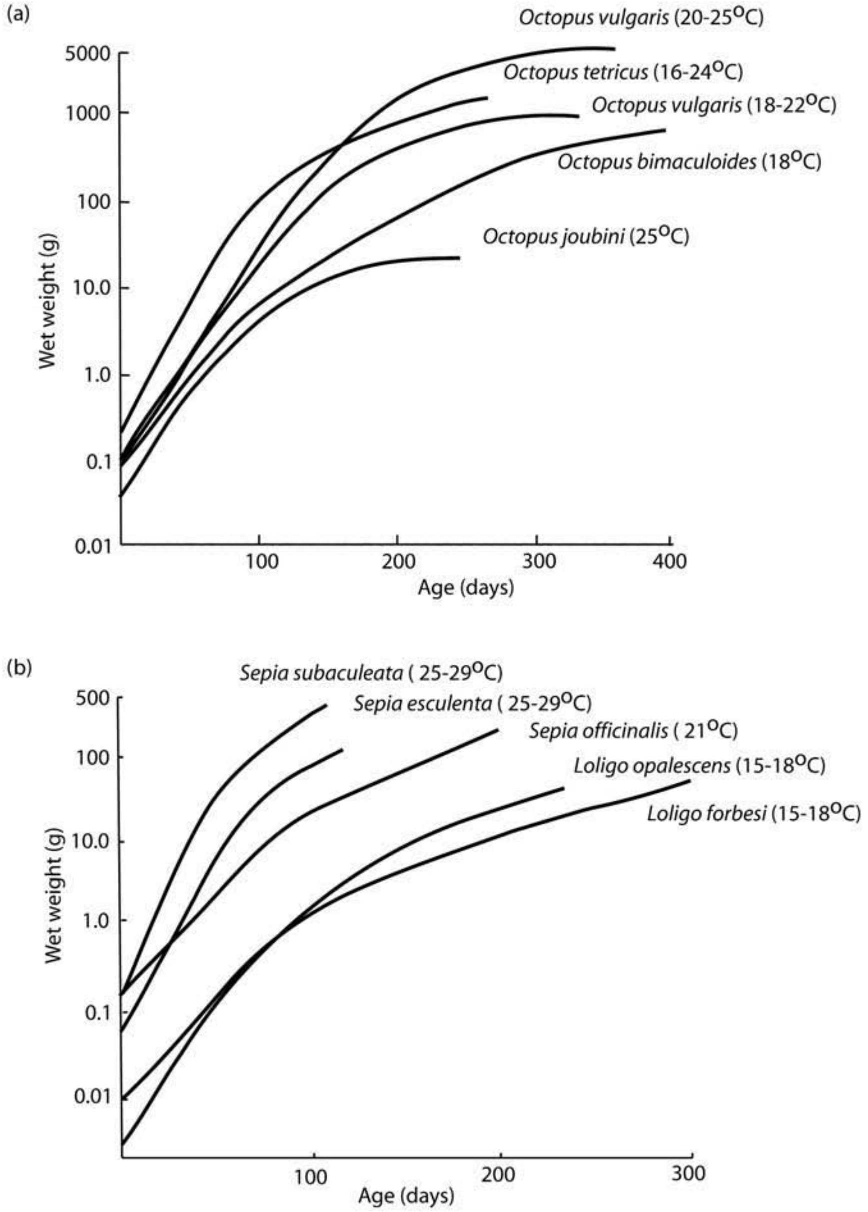


Fig. 7.1 Growth curves of representative (a) octopuses, and (b) cuttlefish and squid, compiled by Forsythe & Van Heukelem (1987).

7.1.5 Direct measurement in field conditions

The high growth rates for cephalopods recorded in captivity are not artefacts of culture conditions. Studies using population length frequency analysis, the use of statolith ageing estimates, and individual tag–recapture programmes for some species have produced ample evidence for comparable growth rates in the field which are consistent with an approximately annual lifespan. It is clear that for most of the coastal octopuses and cuttlefish, as well as the loliginid and ommastrephid squid targeted by fishing, growth rate is high compared with other marine species.

The overall length of the gladius is numerically almost the same as the dorsal mantle length (ML), which is the most frequently used size estimate in fishery studies. This is convenient because the measurement is easily made on large numbers of animals on a simple measuring board and is not subject to much error, but it is not equivalent to total length. Because ML only represents a portion of the total length of the cephalopod, it is subject to relative growth through ontogeny and the wide difference in body form between species. Compare, for example, the elongate mantle form of *Ommastrephes* (see Appendix B, Fig. A28) with the short cap-like mantle of *Histioteuthis* (see Appendix B, Fig. A16). While ML might show continuous growth in squids and cuttlefish because it is internally supported by a hard structure, it does not respond to changes in body weight due to nutritional or reproductive condition, nor is it a good measurement for the globular body of octopuses. Length/weight relationships in cephalopods are relatively weak and thus devalue the use of ML as a single measurement of overall size.

7.2 Growth comparisons

A comparison of cephalopod growth rates with those of other invertebrates and fish will potentially show whether their characteristics are exceptional or within the ranges of other animals. Certainly, within the phylum Mollusca, the large size and high growth rates of cephalopods are unique, as is their level of activity and behavioural complexity. The observation that only in some of the shell-less families of gastropods (Nudibranchiata or sea-slugs) do the majority of the species have an annual life cycle (Boyle 1987b) implies that within the Mollusca this high growth, short lifespan strategy is associated with the loss of the shell. Presumably the external shell requires significant energy and resource for its production and so limits growth rate. This interpretation is consistent with the known growth characteristics of the shelled *Nautilus* (see Chapter 4), and suggests that the very large fossil nautiloids and ammonoids were long-lived animals.

The mean annual weight increase of most of the commercially fished cephalopods, when expressed as a proportion of their maximum body weight, approaches 1. This is a direct consequence of the annual lifespan, and is exceptionally high when compared with most fished teleost fish species of comparable body size (Saville 1987). This is another way of expressing the fact that the biomass of most of the accessible and fished species is a function of the annual recruitment and growth. Calow (1987) plots the absolute growth rate against body weight for some representative cephalopods (Fig. 7.2) and shows that this is probably among the highest in the animal kingdom, and comparable to mammals of an equivalent size.

A different approach was adopted by Jarre *et al.* (1991). In their re-examination of earlier work on the oceanic squid *Kondakovia longimana* (Onychoteuthidae, Clarke 1980), they derived values of the growth parameter *K* from the seasonally oscillating von Bertalanffy growth equation for a number of squid species. When these values are

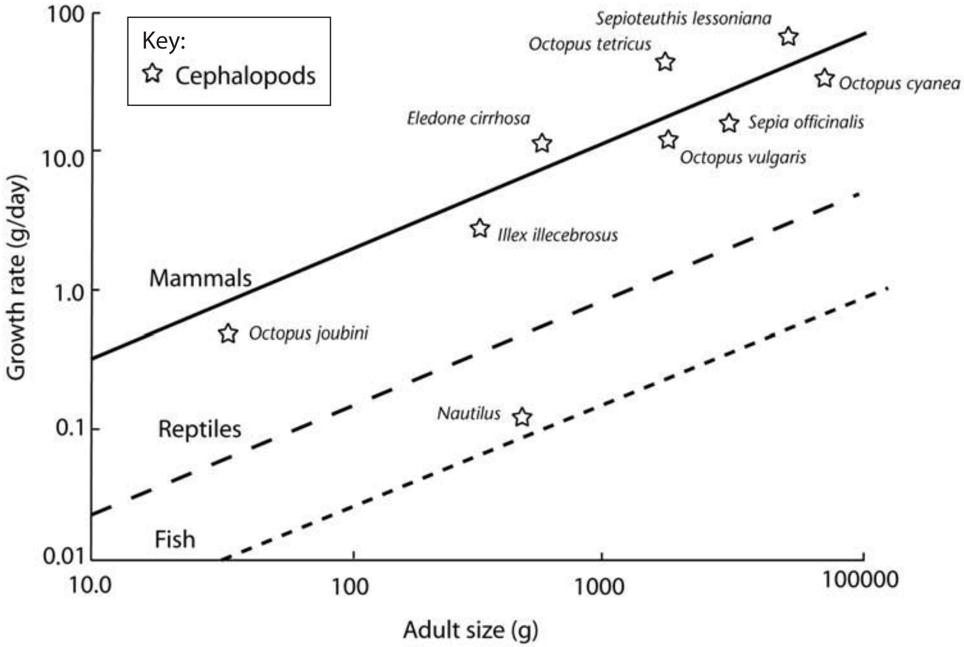


Fig. 7.2 The relationship between mean growth rate and adult body size for a range of cephalopod species compared with the same relationship for mammals (solid line), reptiles (dashed line) and fish (pecked line). From various sources compiled by Lee (1994) after Calow (1987).

plotted against the estimated final size (asymptotic weight) and compared with equivalent values of a range of fish species it appears that squid fall within the ranges of active, fast growing pelagic fish (Fig. 7.3).

Growth data from the largest cephalopod species have been collected and enable us to determine whether they conform to the general pattern of high growth rate and short lifespan of the smaller species.

The giant Pacific octopus, *Octopus dofleini*, regularly grows to an adult size of 50 kg or more (Hartwick 1983), and the largest recorded specimen was 272 kg (Hochberg & Fields 1980). Daily growth rates up to 1.1% in captivity and 1.8% for a tagged octopus in the field have been measured (Hartwick 1983). The longest period between tagging and recapture was 15 months (Kanamura & Yamashita 1967, cited in Hartwick 1983), leading to conjecture that this large species may normally be about 3 years old at reproduction and subsequent death.

The maximum size reached by the jumbo flying squid of the Humboldt Current, *Dosidicus gigas*, has probably been much exaggerated (Nesis 1983). Nevertheless, with a likely maximal mantle length of about 100 cm, this is certainly a very large species. Nevertheless, growth data collected from large samples of statoliths from the fishery off Peru show that the largest squid are no more than one year old. Moreover, up to three size groups may be present in the population at any time but these do not necessarily represent age groups.

Finally, the giant squid, *Architeuthis* spp., remains the object of much speculation. With a mantle of up to about 2 m and weights of <450 kg (Roper & Boss 1982), some

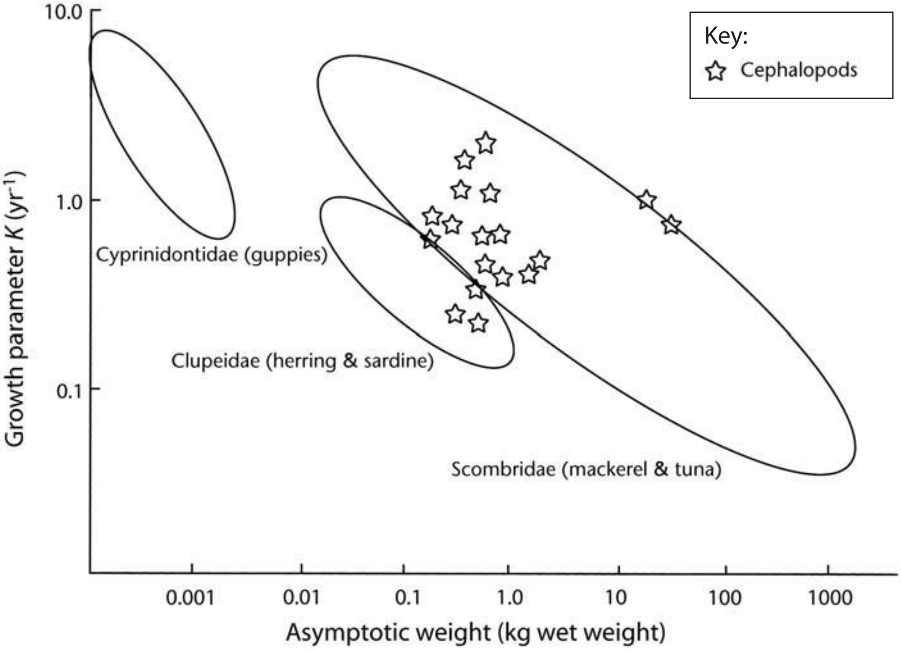


Fig. 7.3 Growth parameter *K* (per year) derived from the von Bertalanffy growth equation plotted against asymptotic body weight (g) for a range of squid species. Compared with values for species from several families of fish, the squid fall within the range of those for active pelagic fish. Figure based on Jarre *et al.* (1991), in which sources of data are listed.

departure from the high growth–short life pattern might be expected. As part of a study of 24 *Architeuthis kirki* stranded in New Zealand between 1983 and 1988, Gauldie *et al.* (1994) sectioned the statolith of a medium-sized specimen (mantle length 1610 mm). They estimated a maximum of 391–395 growth increments in the statolith. Using this evidence and constructing a putative growth curve from the size at stranding, they concluded that the pattern of growth in *A. kirki* could be compatible with a two-phase exponential–logarithmic model (see below), and a lifespan of less than 2.5 years. The statoliths of three smaller specimens (ML 975–1084 mm) of *Architeuthis dux* from Irish strandings (Lordan *et al.* 1998a) gave age estimates of 294–422 days.

Without independent validation of any sort, it could be argued that the increments in statoliths of *Architeuthis* cannot be accepted as daily rings. However, although these very large species may exceed the 1–2-year life of most cephalopods, there is no evidence that they do not conform to the overall pattern of high growth, semelparity and relatively short lifespan of the typical coleoid.

7.3 Growth models

Studies on growth in captive cephalopods have used a variety of mathematical functions to describe the growth pattern, including linear, asymptotic, cyclic, part parabolic, exponential, sigmoidal and exponential followed by logarithmic. Forsythe

& Van Heukelem (1987) reviewed these applications, and found that they emphasise the value of weight rather than length measures to describe cephalopod growth. It is probable that the two-phase exponential–logarithmic growth form is widely applicable, at least to the increase in weight of benthic octopods and loliginid squid. The first (logarithmic) part of the growth curve is followed by a variable period of slower growth described by a power equation. The two-phase growth model is rarely clear in data from field studies (is it a feature of culture conditions?), although it could be argued that it cannot be properly tested owing to the poor representation of juvenile forms in field collections. However, as Forsythe & Van Heukelem (1987) point out, using a single growth equation for the entire lifespan is unlikely to describe adequately and simultaneously both the early and late growth performance.

Field growth data, usually length-based, have frequently been modelled using the von Bertalanffy growth equation, probably because of its widespread use in fisheries (Caddy 1983b). Despite some improvements in its application to cephalopods (Pauly 1985), many authors believe that it does not fit observed data well (Forsythe & Van Heukelem 1987; Day & Taylor 1997). One evident reason for the discrepancy is that von Bertalanffy assumes that individual growth will reach an asymptote, a growth form not recognised in any of the coleoid cephalopods. Whereas mean growth within a population appears to reach an asymptote, this is due to the loss of larger individuals from emigration or post-spawning mortality as the season progresses. Individual growth slows and finally stops with sexual maturation, shortly followed by spawning and death. There is no clear evidence from individual growth studies in the aquarium or the field that growth reaches an asymptote significantly before death, i.e. the interval between gladius increments does not decrease.

Absence of asymptotic growth has been proposed to indicate that coleoid cephalopods are progenic, at least in terms of their physiological energetics (Rodhouse 1998b).

7.4 Determinants of growth

The growth rates of cephalopods depend primarily on their high rate of food intake and on the apparently high efficiency of its conversion into somatic growth. There are relatively few direct estimates of ration size and growth rate, but data assembled by Wells & Clarke (1996) suggest that the maintenance ration for captive octopods is 1.2–1.8% of body weight. Above that level, there is a linear relationship between food intake and growth up to about 8% of body weight per day in octopods and almost twice that for squid (see Table 8.4). Relating mass of food ingested to the change in body mass over the same period gives gross growth efficiency ($[W_2 - W_1]/W_{\text{food}} \times 100$), or food conversion rates, of 40–60% for octopuses (range 20–69%) and 20–40% for cuttlefish and squid (range 13–59%). The apparently lower food conversion in the squid and cuttlefish is largely accounted for by their greater use of energy for active movement. Size-specific feeding rates and food conversion rates are also lower at larger body sizes.

Within a single cohort of animals there may be considerable plasticity in individual growth rates. Semmens & Moltschaniwskyj (2000) took individual *Sepioteuthis* *lessoniana* from extremes of the size range and showed that there were significant differences between them in the proximal composition of digestive gland and mantle muscle and in mantle muscle structure. The differences in biochemical composition were not significantly related to size-at-age of individuals, but there was a strong relationship between the size of mantle muscle blocks and size-at-age, suggesting that larger muscle blocks are related to both body size and faster individual growth rates. The use of size-at-age and size-at-maturity estimates in field populations consequently includes a high degree of variation resulting from differences in individual growth performance.

The size of adult males and females at maturity is frequently quite different. In loliginid squid, cuttlefish and some octopuses, for example *Octopus vulgaris*, the male is significantly larger. Among ommastrephid squid and in other octopuses (*Eledone cirrhosa*), the female may be the larger sex. Sexual dimorphism in size is consistent within a species, and since males and females apparently have similar lifespans, there is presumably a sex-linked genetic influence on growth rate. The onset of sexual maturation in most coleoids marks the end of logarithmic growth. Although some species are known to feed and grow after a first spawning (e.g. *Sepioteuthis lessoniana* and *S. australis*, Pecl 2001), and cirrate octopods are mature over a wide range of body size (Villanueva 1992a), these are not the general patterns for temperate species. The generally observed trade-off between growth and maturity is supported by evidence that the transition is hormonally mediated (Wodinsky 1977; O'Dor & Wells 1978).

The interaction between growth rate and maturity means that the environmental factors affecting the onset of maturity indirectly affect growth. Stimuli known to interact with the control of reproduction and curtailment of growth are day-length reduction (*Sepia*, Richard 1967), temperature (*Octopus*, Forsythe & Hanlon 1988; *Sepioteuthis*, Forsythe *et al.* 2001; Moltschaniwskyj & Martinez 1998) and nutrition (*Eledone*, Boyle & Knobloch 1984) but, as already pointed out (see Chapter 6), the timing of maturation is not determined by a straightforward and universal set of conditions but nutritional status must be an important factor.

The common loliginid squid of the European Atlantic coastline, *Loligo forbesi*, reaches much larger individual body sizes in the isolated population in the Azores (Martins 1982). In this case there is considerable evidence for a genetically distinct population (Brierley *et al.* 1995). In other cases where there are geographical size morphs, such as *Sthenoteuthis oualaniensis* and *Dosidicus gigas*, it is not possible to distinguish between genetically distinct sub-populations or the environmental effects of food and temperature. Some cephalopods reach considerably different body sizes in different parts of their geographic range. The octopus *Eledone cirrhosa* is on average 2–3 times larger at the northern end of its range (Boyle *et al.* 1988), while *Octopus vulgaris* is significantly larger in warmer water. Temperature is therefore not necessarily a factor determining final body size.

In most cephalopods, within the normal temperature range for the species in a given area, higher temperatures promote higher growth rates. The general significance of this to survival and recruitment is most clearly appreciated in the modelling exercise of Forsythe (1993). Based on real data from a number of species, the simulation model shows how the coincidence of later hatching times with warmer seasonal temperatures

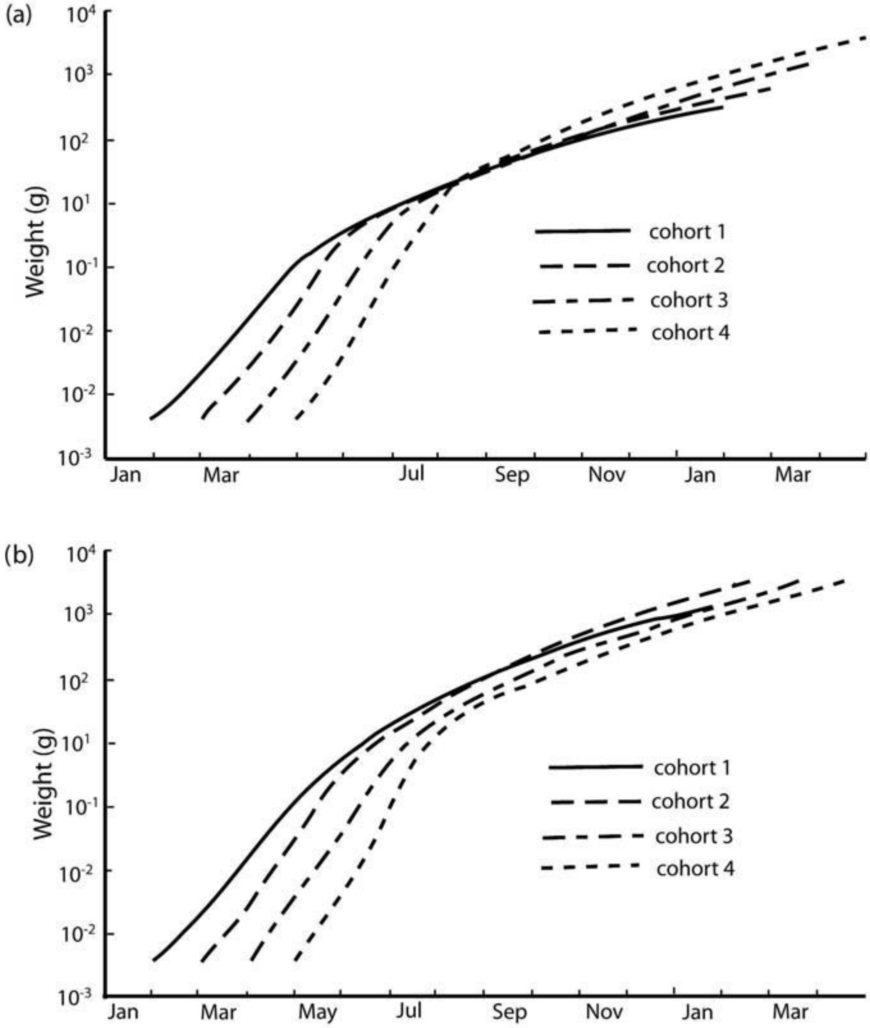


Fig. 7.4 (a) Simulated growth of four cohorts of squid hatching out at successive 30-day intervals each at 1°C increase in temperature for the first 3 months of growth (exponential growth phase). (b) A second simulation under the same assumptions except that the growth rate over the second phase of growth (logarithmic phase) was modified to assume a temperature based on the average for the first 5 months of the logarithmic growth phase (Forsythe 1993).

so influences the predicted growth of the later cohorts that they may grow fast enough to catch up and overtake those hatched earlier in the season (Fig. 7.4).

7.5 Correlates of growth

Growth is not uniform in all parts of the body, and some tissues are more actively involved in the growth process than others and show consequential changes.

Changes in the relative size of various body component parts during the growth of the whole animal (allometry) occur in most cephalopods. Changes in the proportions of arms or mantle, for example, are seen as ontogenetic changes, especially during the growth of paralarval and juvenile squid. In some cases, for example in the relative size of the brachial crown (Rodhouse & Piatkowski 1995), these changes have perhaps evolved in response to the size spectrum of prey available.

The relative growth of organ systems that are responsive to nutritional condition or state of maturity is commonly used as an index of that condition or state. The relative size of the gonad is the gonado–somatic index (GSI) and is a measure of the progress towards sexual maturity, and the relative size of the digestive gland (DGI) has been used as an index of recent feeding history.

Biochemical indices of growth, sometimes applied to larval fish, rely on the principle that faster-growing organisms must have a relatively higher concentration of RNA as messengers for protein synthesis. In the cephalopods, RNA concentration expressed as a proportion of DNA concentration (RNA:DNA ratio) or protein concentration is providing another index of growth, but results are highly variable and correlations are not particularly strong. Aquarium studies providing some degree of calibration of RNA concentration against measured growth are available for *Sepia officinalis* (Clarke *et al*. 1989) and *Eledone cirrhosa* (Houlihan *et al*. 1998). Comparisons between two octopus species in captivity (*E. cirrhosa* and *Octopus vulgaris*), captive squid (*Loligo forbesi*) and wild-caught *Todarodes sagittatus* have been made by Pierce *et al*. (1999). They suggest that there are significant differences in growth rate between species and between male and female animals, and that protein concentration alone (mg protein/g fresh body weight) may provide the best single index of growth status.

Chapter 8

Physiological ecology

Summary: Physiological ecology is the study of energy transformations in whole animals which provides information on growth and metabolic processes in relation to the environment, and insights into evolution, especially the optimisation process which trades off reproductive output against the other energy requirements of the organism. Energy consumed in the food is utilised for growth, reproduction and metabolism, and is lost as excreta and in the faeces. No cephalopod study to date has measured all components of the energy budget at the same time, but there are enough studies of different aspects to allow preliminary composite budgets to be constructed. The feeding rate in cephalopods is primarily controlled by temperature and body size. A 10°C change in temperature alters the feeding rate by a factor of two or more. The relative feeding rate declines with increasing body mass. Most coleoids grow relatively fast, and the allocation of energy to gonad growth is delayed until relatively late in the life cycle. The reproductive effort is lower than theory would expect for short-lived, semelparous organisms, and this appears to be related to the low mortality rates in cephalopod progeny. Some cephalopods utilise energy and nutrient reserves in somatic tissues to fuel gonad growth, and males invest less energy than females in this process. This is probably compensated for by the greater energetic costs of finding and attracting a mate. Females invest substantial energy in the accessory reproductive glands such as the nidamental gland that produces the mucilaginous coating of the egg mass. Metabolism is a heterogeneous process that includes the costs of digestion and absorption of food, maintenance, activity and tissue production. In common with feeding rate, it is determined primarily by temperature and body size. The mass exponent for metabolic rate is greater than for feeding rate, and this underlies a decline in the relative scope for growth with size. Energy loss in the excreta is mainly in the form of ammonia, and cephalopods have high absorption efficiencies and so lose comparatively small amounts of energy in the faeces. Ommastrephid and loliginid squid are less efficient converters of energy consumed to tissue production than octopuses because they utilise more energy actively swimming than the relatively inactive benthic forms. The deepwater and ammoniacal buoyant squid undoubtedly consume less energy for activity than the ommastrephids and loliginids, but the energy partitioning strategies of most cephalopod forms are not known.

This chapter deals with the physiological energetics of cephalopods, which is the study of gains, losses and transformations of energy by whole animals. At other levels of biological organisation, bioenergetics deals with energy flow at the cellular level, and ecological energetics considers energy transformations by populations or whole communities of organisms. This chapter considers the way individual cephalopods balance their energy budgets in response to their life style and environment. It therefore deals with their energy demands and how the energy consumed in the food is allocated between the processes of growth, reproduction and metabolism and is lost as waste products.

The energetics approach is used by physiologists to understand growth and metabolic processes, and also by ecologists to quantify the flow of energy through individuals, as this can be scaled up to populations and hence used, for instance, to examine the role of a species in a particular environment (Rodhouse & Nigmatullin 1996). Evolutionary biologists have also used physiological energetics as a means of understanding the evolution of life history strategies through concepts such as reproductive effort, residual reproductive effort and reproductive cost (Stearns 1992). They analyse how evolution has driven different kinds of organisms, in different environments, towards optimising the allocation of energy resources between components of the energy budget as selection pressures have acted to maximise Darwinian fitness. Calow (1987) has reviewed life-history theory in relation to the cephalopods, especially with respect to their semelparous reproductive strategy. He showed that, contrary to theoretical expectations for short-lived, semelparous animals, cephalopods invest a relatively small proportion of their energy budget in reproduction. He pointed out that most species produce relatively large, well-protected progeny that probably have generally low mortality rates.

8.1 The balanced energy equation

The conventional balanced equation used to describe the energy transformations of marine, and other, organisms was first formulated by Winberg (1956) and is consistent with the first law of thermodynamics, which states that energy can neither be created nor destroyed. It is as readily applicable to cephalopods as to all other animals, and is given as

$$C = P + G + R + U + F$$

where C is the energy consumed in the food, P is the energy invested in somatic tissue growth, G is the energy invested in germinal tissue (gonad), R is respiration or metabolic heat loss, U is primarily energy excreted in the urine, but also includes other losses such as mucus and shed sucker cuticles in octopuses, and F is the energy that is not absorbed by the gut and voided in the faeces. The units are joules (J, or calories in the older literature: 1 cal = 4.2 J) and energy per unit time or power (watts, W). To convert from energy to power units, $1\ \mathrm{kJd^{-1}} = 11.57\ \mathrm{mW}$.

Several other equations derive from the basic energy balance equation. Absorption, A_b, is the energy consumed that is transported across the gut wall, and is calculated from

$$A_b = P + G + R + U = C - F$$

and assimilation, A, is the absorbed energy that is not subsequently lost as excreta but which is transformed into tissue or lost as heat, and is calculated from

$$A = P + G + R = C - (U + F)$$

Readers should be aware that the terms assimilation and absorption, as defined here, are not applied universally. The term assimilation, especially in respect of 'assimilation efficiency', is sometimes used to mean absorption as defined here.

The consumption and production terms of the energy balance equation can also be rearranged to give gross growth efficiency:

$$\frac{P + G}{C}$$

and net growth efficiency

$$\frac{P + G}{C - R_m}$$

where R_m is the basal metabolism which, in energetic terms, is equivalent to the maintenance ration. The different components of the respiration term are discussed in detail later in the chapter.

Finally, the energy available for the growth of somatic and germinal tissue after metabolic costs have been met and waste accounted for is termed the scope for growth (S_G):

$$S_G = C - R + U + F = P + G$$

It may be impossible to measure all the components of an organism's energy budget in the field, especially in the case of highly mobile creatures like cephalopods, and even in the laboratory there are technical problems with making meaningful measurements of feeding and metabolic rate on active mobile forms. Studies of cephalopod energetics have therefore not necessarily attempted to measure all terms in the balanced energy equation, and in cases where a near complete energy or power budget has been derived, the data have been obtained from a combination of field and laboratory observations (Wells & Clarke 1996; O'Dor & Wells 1987).

8.2 Consumption

All living cephalopods are carnivores, and they use their versatile feeding apparatus (arms and tentacles) to feed on a wide variety of organisms of different sizes, especially fish, crustaceans and molluscs.

There is an extensive literature on the proximate biochemical composition and energy content of a wide range of the marine species that comprise the prey of cephalopods or which closely resemble their prey (e.g. Brey *et al.* 1988; Lee 1994). Therefore data on feeding rates on particular foods can readily be approximated to units of energy consumption. However, there are few reliable data on rates of feeding under field conditions, and only limited data from laboratory experiments. It is extremely difficult to study feeding rates in the wild, and even in the laboratory it is problematic because cephalopods prefer live food, although some cuttlefish and octopuses have been habituated to feed on dead food. All cephalopods dismember their prey with their beak prior to ingestion, making it very difficult to quantify consumpton.

When food is readily available, the feeding rate in marine poikilotherms is primarily controlled by two factors, temperature and body size. The effect of temperature on the rate of physiological processes is generally expressed as Q_{10}, where

$$Q_{10} = (R_1/R_2)^{(10/T_1 - T_2)}$$

R_1 and R_2 are measured rates at a higher and lower temperature, respectively, and T_1 and T_2 are the higher and lower temperatures, respectively. By analogy with other marine organisms, including other molluscs and fish, consumption rate in cephalopods is expected to increase with temperature to a Q_{10} of approximately 2.0 (Bayne & Newell

1983; Jobling 1994). Consumption rate also increases with body size, but larger individuals consume relatively less food than smaller ones. There is therefore an allometric relationship between consumption rate and body mass:

$$C = AB_M{}^b$$

where C is the consumption rate, B_M is body mass, A is a constant and b is the mass exponent. In marine and other organisms, b is invariably less than the mass exponent for metabolic rate (see Table 8.3), and this underlies the general reduction in relative scope for growth, and hence relative growth rate, with increasing body size.

There have been suprisingly few systematic attempts to measure the effects of temperature and body size on feeding rate. Data on feeding rates of *Octopus vulgaris* at 10°C and 20°C suggest a Q_{10} value of 3.4 (Mangold & Boletzky 1973). A multiple linear regression equation was fitted to *Illex illecebrosus* feeding rate data in relation to temperature and body size by O'Dor & Wells (1987):

$$F_R = 0.058\,W^{0.79}1.082^T$$

where F_R is feeding rate in g d^{-1}, W is body mass in g, and T is temperature in degrees Celsius. The mass exponent (0.79) is high in comparison with other organsisms, e.g. other molluscs (Bayne & Newell 1983) and fish (Jobling 1994), and the relationship with temperature is equivalent to a Q_{10} of 2.2.

8.3 Production

The production of somatic tissue is a function of growth. Cephalopods generally grow fast and mature rapidly, although there are exceptions, including *Nautilus* and probably some of the deep-sea and high-latitude forms, as well as the very large species. Studies of cuttlefish, squid and octopus in the wild and under laboratory conditions show that temperature and feeding rate and body size are the chief determinants of growth rate. The rate of growth in turn affects the timing of maturation (Wells & Clarke 1996).

Energy invested in growth is estimated from the increase in tissue mass and the energy content of the new tissue generated. The energy content of marine organisms has been estimated in several ways in studies of physiological energetics. The most straightforward approach is to measure heat production during the combustion in oxygen of the dried, homogenised tissue in a bomb calorimeter (Phillipson 1964). A more detailed and informative approach is to assay the proximate biochemical composition of the organism, and then apply values for enthalpy of combustion for typical marine invertebrate protein, carbohydrate and lipid. These values, which by convention are negative, are –23.9, –17.5 and –39.5 kJ g^{-1}, respectively. The energy content of tissue has also been estimated from the elemental carbon content using a functional relationship based on stoichiometric principles, and by using the carbon, hydrogen and nitrogen contents to estimate the proximate composition, assuming average compositions for representative marine invertebrate protein, carbohydrate and lipid, and applying the enthalpy values above (Gnaiger & Bitterlich, 1984).

The proximate biochemical composition and energy content of the whole animal, or of selected parts, of several species of cuttlefish, squid and octopus are given by Lee (1994). Some of these data were collected for the food industry, and so relate to the edible parts only. The most detailed analysis for ecological purposes was carried out by Clarke *et al.* (1994), who measured elemental (carbon, hydrogen and nitrogen) and proximate biochemical composition (Table 8.1) for all the major organ systems in *Illex argentinus* from the fishery on the feeding grounds on the southern Patagonian Shelf. They then used the biochemical composition and carbon content data to calculate the energy content. In most cases, the composition of somatic tissues did not change significantly during sexual maturation.

8.4 Gonad

All cephalopods appear to be monocyclic, but eggs may be spawned over a short period in a single, terminal event or produced in batches. Egg size ranges from <1 mm to >10 mm between species. Males of many species probably mate several times with different females so the sperm, which is packaged into spermatophores, is also effectively released in batches over an extended period. As females and males mature, resources are increasingly allocated to the growth of gonads and associated organs at the expense of other tissues. From an evolutionary standpoint, the function of adult organisms is to ensure that their genes are spread as widely as possible through the genepool of the next, and subsequent, generations. We should expect, then, that the energy budget of any species will have been shaped by natural selection, and evolution will have tended to optimise gamete production, trading off other energetic requirements against the production of eggs and sperm.

The proximate biochemical composition, elemental composition and energy content of male and female *Illex argentinus* gonads (Clarke *et al.* 1994) are given in Table 8.1. The composition of the ovary changes significantly during sexual maturation, whereas that of the testis does not. As well as the eggs, female cephalopods develop large glands: the nidamental gland, the accessory nidamental gland (in sepiids, sepiolids and loliginids) and the oviducal gland, which secrete egg coatings at the time of release. These contribute to the direct energy cost of reproduction and hence should be included in any calculation of energy budgets. In ommastrephid squid, the nidamental glands represent the largest investment of energy among these glands, e.g. in mature *Illex argentinus* they may account for >7% of body weight, but in loliginids the oviducal gland may be as, or more, important. The composition of the nidamental gland changes significantly during sexual maturation. When mature it contains a large quantity of the mucosubstance which forms the viscous gel coating of the eggs at spawning. About 35% of the nidamental gland mucosubstance is a mucin-type glycoprotein in *Illex argentinus*, and this contains 23% protein, 73% carbohydrate and 4% ester sulphate (Kimura *et al.* 1994).

The energetic cost of reproduction has been analysed for squid from the winter-spawning population of *Illex argentinus* using data on growth of tissues (Rodhouse & Hatfield 1990a, 1992; Hatfield *et al.* 1992) and their energy content (Clarke *et al.* 1994).

Table 8.1 Proximate biochemical composition, elemental composition and energy content (estimated from carbon content) of *Illex argentinus* tissues (after Clarke *et al.* 1994).

Tissue	% wet mass				% dry mass				Energy (kJ/gram dry mass)
	Water	Protein	Lipid	Carbohydrate	Carbon	Nitrogen	Phosphorus	Ash	
Males									
Testis	78.9	10.6	1.2	1.0	42.4	13.3	2.1	9.8	–15.4
Spermatophoric complex	77.4	9.5	1.6	1.7	42.1	13.1	2.0	10.3	–15.1
Digestive gland	45.0	–	27.6	1.3	54.9	5.9	0.6	3.4	–24.6
Mantle	–	–	1.7	0.4	43.8	12.3	1.3	–	–16.9
Head	79.1	17.2	1.6	0.3	–	12.9	1.1	8.0	–18.4
Viscera	77.3	–	–	–	–	9.1	1.0	8.0	–19.9
Females									
Ovary	–	13.2 (II) 41.8 (V)	1.5 (immature) 8.2 (mature)	0.8	–	–	–	9.2 (immature) 4.9 (mature)	–21.7
Nidamental gland	–	–	–	–	–	–	–	–	–17.1
Digestive gland	42.1	–	31.3	1.2	58.6	5.3	0.6	2.6	–27.1
Mantle	78.1	14.8	1.9	0.03	43.3	12.2	1.2	–	–16.5
Head	79.0	16.0	1.8	0.3	45.8	12.6	1.0	7.9	–17.9
Viscera	78.2	–	–	–	43.9	–	1.0	7.7	–15.1

This species grows and matures on feeding grounds on the southern Patagonian Shelf, in the southwest Atlantic, and then migrates to spawning grounds on the northern part of the shelf (Brunetti & Dranovic 1992; Haimovici *et al.* 1998). On the feeding ground, the squid prey on rich zooplankton stocks (Ivanovic & Brunetti 1994) and grow actively at the same time as they are maturing. In the last 7–8 weeks an average female incorporates 935 kJ into new tissue, the majority of which is somatic tissue (23% to the mantle, 17% to the head arms and tentacles and 46% to the digestive gland). Reproductive tissues receive only 16% of ingested energy. Males grow more slowly and reach a smaller size. During the same period they accumulate only 250 kJ, of which about 6% is allocated to reproductive tissues. In this species it is clearly important that a substantial proportion of the energy budget is allocated to somatic tissues (muscles and reserves) which are needed to undertake the long migration to the spawning area. Comparison with other species suggests that some appear to utilise nutrients derived from the somatic tissue for gonad growth and others do not. *Moroteuthis ingens*, from cool water in the southern hemisphere, appears to utilise somatic tissue (mantle muscle) immediately before spawning (Jackson & Mladenov 1994). In the tropical *Photololigo* sp., however, there is little evidence that there is any storage of energy in, or transfer from, the mantle or digestive gland for reproduction (Moltschaniwskyj & Semmens 2000). It is not known whether *Illex* uses somatic reserves for gonad production once the spawning grounds have been reached.

Octopus vulgaris spawns once and dies after the eggs have been brooded. The onset of sexual maturation is associated with secretion from the optic glands which simultaneously accelerates gonad growth and catabolism of other, somatic, tissues (Wells & Wells 1959; O'Dor & Wells 1973, 1978). As muscle breaks down, amino acids flood into the blood and the animal wastes away even faster than if it had been starved. Other octopuses lay smaller numbers of eggs in separate clutches before dying, and the deep-sea cirrate octopuses probably produce single eggs over an extended period.

The energy invested in reproduction has been estimated for female *Octopus cyanea* by Van Heukelem (cited in Wells & Clarke 1996). This species produces a large number of planktonic young. A mature female with a body mass of 600 g live weight had a total energy content of 3082 kJ, of which 32% was ovary. While guarding the spawned eggs the octopus shrank and the energy content of her body was reduced from 2100 kJ to 721 kJ, so 45% of her pre-spawning energy content was attributed to metabolic costs. In *Octopus maya*, which produces a relatively small number of benthic young, the energetic cost of reproduction was similar to that of *O. cyanea*.

The energetic cost of reproduction in male octopuses has not been assessed. Male *Octopus vulgaris* start to produce spermatophores when they reach about 250 g body weight and this continues until death, but the number of spermatophores produced, and the energy content, have not been measured, so the energy cost is not known. However, Wells & Clarke (1996) conclude that because males die at the same age and mass as females, the final cost of reproduction is probably similar in both sexes. The difference is that females expend energy brooding the eggs, whereas males incur an energy cost in seeking mates.

8.5 Respiration

Respiration is a measure of the instantaneous demand for oxygen to act as an electron receptor for the prodution of adenosine triphosphate (ATP). Energy reserves are metabolised to make ATP and the heat produced can be measured by direct calorimetry (Widdows & Johnson 1987), but respiration is more usually estimated from measurements of oxygen consumption. Estimating heat production from oxygen consumption makes assumptions about the type of energy reserves being utilised, and calculations are based on conversion factors that give heat production per milligram of oxygen consumed (Elliot & Davison 1975). The metabolism of different energy sources can be descibed by thermochemical equations. The oxidation of one mole of glucose is given by

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 = H_2O$$

a reaction accompanied by the release of 2833 kJ in the form of heat. The combustion of 1 mole of glucose thus requires 6 moles (192 g) of oxygen, so 14.76 kJ energy is released as heat per gram of oxygen consumed. The ratio of carbon dioxide molecules produced to oxygen molecules consumed (the respiratory quotient R_Q) is 1.0 in this reaction. This equation ignores the fact that free energy is trapped as ATP, which is used for mechanical or chemical work. This work results in heat loss, so given the rapidity of turnover of ATP, it is not unreasonable to summarise the process using the equation and ignoring ATP cycling.

The oxidation of lipids is given by

$$CH_3(CH_2)_{14}COOH + 23O_2 = 16CO_2 + 16\ H_2O$$

and this is accompanied by the release of 13.7 kJ per gram of oxygen produced. The R_Q is 0.7.

The oxidation of protein results in the release of nitrogenous and sulphurous compounds as well as carbon dioxide and water, e.g.:

$$C_{43}H_{70}O14N_{12}S_{0.3} + 44.4CO_2 = 43CO_2 + 12NH_3 + 17H_2O + 0.3H_2S$$

In the case of protein metabolism, the oxygen to energy conversion factor will depend on the proportion of the different forms of nitrogenous excretion (ammonia, urea and uric acid) that are produced. Cephalopods are predominantly ammonotelic, and under these conditions approximately 13.36 kJ is released per gram of oxygen consumed. If ammonia is the only nitrogenous waste produced, the R_Q is approximately 0.95.

The oxygen consumption method of estimating metabolic heat loss is only applicable if all metabolism is aerobic. If there is anaerobic metabolism, then heat loss will be underestimated. However, cephalopods have very little capacity for anaerobic metabolism (Pörtner 1994), so the oxygen method is likely to be reliable in most situations. R_Q values can provide an indication of the type of substrate being metabolised, but as this is usually a mix the method can only be a guide. If R_Q is close to 1.0 it suggests a largely carbohydrate energy source, and values close to 0.7 indicate lipid. Measuring the ratio of oxygen consumed to nitrogen excreted (O:N) provides a means of assessing the relative amount of protein metabolism (Mayzaud & Conover 1988).

Table 8.2 Q_{10} values for maintenance metabolism in selected cephalopods.

Species	Body mass (g)	Temperature range (°C)	Conditions	Q_{10}	Source
Nautilus pompilius	378–734	17–25	Resting/unfed	3.0	Redmond *et al.* 1978
Loligo opalescens	0.003–40	10–20	Resting/unfed	2.7	O'Dor 1982
Sepioteuthis lessoniana	0.04–4.28	10–30	Resting/unfed	2.0	Segawa 1995
Octopus briareus	345–348	20–30	Resting/unfed	2.2	Borer & Lane 1971
Eledone cirrhosa	300–323	4.5–11.5	Resting/unfed	3.1	H. Daly, unpublished data, 1996

Respiration (R) is a heterogeneous process, and includes the energy costs of digestion and absorption of food, maintenance (R_m), activity (R_a), soma production (R_s) and gonad production (R_g) (Wells & Clarke 1996). Maintenance, or basal turnover (R_m), is the respiratory cost of of maintaining life in the absence of locomotor activity, growth or reproduction, and includes protein, DNA and membrane turnover, osmotic work and circulation. The production of new somatic and germinal tissue incurs thermodynamic costs associated with the movement of raw materials around the body and into cells, as well as the cost of assembling new macromolecules.

Maintenance costs can be measured in one of three ways: by measuring the routine oxygen consumption rate of individuals that are just maintaining their body mass, by measuring the rate of decrease in mass of starved individuals, or by measuring the feeding rate that just maintains a constant body mass.

Maintenance metabolism in cephalopods, in common with most marine invertebrates, is dependent on temperature and body size. Measured Q_{10} values for several species of cephalopod are given in Table 8.2. Values range from 2 to 3.1. Measured Q_{10} values between species of octopus from different latitudes and ambient temperatures have shown that in cold environments maintenance metabolism is reduced and could be predicted from Q_{10} values derived from their warmer-water equivalents, i.e. there is no metabolic cold adaptation *sensu* A. Clarke (1983).

There is an allometric relationship between metabolic rate and body mass of the form

$$R = AB_{M}b$$

where R is the metabolic rate, B_M is the body mass, A is a constant and b is the mass exponent. The mass exponent for metabolic rate in most marine invertebrates is approximately 0.75. Measured values for cephalopods are given in Table 8.3. Octopuses have mass exponents for metabolic rate that are close to the generally observed value of ~0.75, but most squid seem to have higher values, often approaching 1.0. Zeuthen (1953) predicted that small organisms <50 mg should have a mass exponent for metabolism close to 1.0, and in larger organisms it should approach 0.75. Squid appear to fall between these values, and we can only speculate why this should be so. O'Dor & Wells (1987) suggest that it may reflect the fact that the squid that have been studied are negatively buoyant and so need to expend energy to remain in the water column. Reynolds' number effects on sinking rate would mean that this cost increases with size. They also suggest that because jet propulsion is less efficient than undulatory

Table 8.3 Mass exponents for metabolic rate for selected cephalopods.

Species	Mass exponent, *b*	Reference
Sepia officinalis	0.91	Johansen *et al.* 1982
Loligo pealei Male	1.03	Macy 1980
Female	0.61	
Loligo forbesi	0.91	Segawa & Hanlon 1988
Lolliguncula brevis	0.85	Segawa & Hanlon 1998
Sepioteuthis lessoniana <0.5 g body mass	0.94	Segawa 1991
>0.5 g body mass	0.81	
	0.93	Segawa 1995
Illex illecebrosus	0.87	Kao 1970
	1.0	DeMont & O'Dor 1984
	0.73	Webber & O'Dor 1985
Histioteuthis heteropsis	0.80	Seibel *et al.* 1997
Vampyroteuthis infernalis	0.70	Seibel *et al.* 1997
Octopus cyanea	0.83	Maginniss & Wells 1969
Octopus vulgaris	0.74	Wells *et al.* 1983b
Octopus maya	0.9	Segawa & Hanlon 1988
Japatella diaphana	0.73	Seibel *et al.* 1997

swimming in fish, and because maximum speeds relative to body size do not increase as rapidly in cephalopods as in fish, competition may have meant that larger squid have to maintain a relatively higher metabolic rate at large sizes.

The metabolic costs of locomotor activity (R_a) are clearly likely to be quite different in the highly active squid and the relatively sedentary octopuses. The negatively buoyant squid *Illex illecebrosus* swimming continuously in an experimental pool at 0.15 m s^{-1} consumes oxygen at a rate equivalent to burning 3.8% body mass per day (Webber & O'Dor 1986). This is less efficient than has been recorded for fish of equivalent size at the same temperature because jetting is less cost-effective than undulatory swimming (O'Dor & Webber 1986). The ammoniacal, buoyant squids avoid the cost of continuous swimming. Deep-living cephalopods have significantly lower metabolic rates and capacity for glycolytic energy production than shallower species, probably because in the darkness of the deep sea there is less reliance on locomotion for prey capture (Seibel *et al.* 1997). Octopuses sometimes swim, but locomotion is usually by walking on the seabed. Continuous walking in an exercise wheel elevates the metabolic rate in *Octopus vulgaris* to about 2.4 times maintenance levels when resting (Wells *et al.* 1983a). In the wild they are active for about 11% of the time (Mather & O'Dor 1991), and it is thought that data from the exercise wheel probably overestimates the actual cost of normal activity.

The energetic cost of production of new tissue in marine invertebrates has been estimated by Parry (1983) to take about 120–130 kJ to produce 100 kJ of new tissue. This cost of tissue production is probably the major component of the post-prandial elevation of metabolic rate, or specific dynamic action (SDA), in cephalopods. In *Octopus vulgaris*, the post-prandial rise and fall in energy consumption depends on the size of the meal consumed (Best 1981; Best & Wells 1983, 1984; Wells *et al.* 1983b) and amounts to about 4.3% of the energy content of the ingested food (Wells & Clarke 1996). Longer term, but reversible, increases in routine metabolic rate in actively feeding octopuses take a higher percentage of energy consumed. Houlihan *et al.* (1990) estimated that in *Octopus vulgaris*, growing at a rate of 6% body mass day^{-1}, over 90% of the protein synthesised after a meal was incorporated in growth in the short term. However, when the longer-term increase in metabolic rate was included, the total thermodynamic cost of production increased to some 18% of the energy content of the food consumed.

It is not clear whether the energetic cost of producing gonad (R_g) by cephalopods is the same as the cost of growing somatic tissue (R_s). There may well be differences because ovarian oocytes, for instance, have a much higher lipid content than somatic tissues, but this question has not yet been addressed.

8.6 Excreta

Cephalopods excrete nitrogen mainly in the form of ammonia, and this is largely via the gills. In *Octopus vulgaris*, about two-thirds of all nitrogen is excreted as ammonia, and in *Illex illecebrosus* about three-quarters is ammonia. The remaining nitrogen in the urine is largely in the form of urea and a small amount of uric acid (Andrews 1988; Hoeger *et al.* 1987; Boucher-Rodoni & Mangold 1994). The daily loss of energy in the urine of *Octopus vulgaris* has been shown to amount to some 1.5 kJ kg^{-1} d^{-1} in immature and starving specimens, and 3.1 kJ kg^{-1} d^{-1} in mature females (Wells & Wells 1990). No data are available for squid, but rates of loss have been assumed to be the same as for octopus, and it has also been assumed that rates of energy loss through excretion are proportional to metabolic rate (Wells & Clarke 1996).

Some energy is also lost by octopuses in the form of protein in the urine, which is produced by metazoan parasites in the renal sacs. Tait (1986) found the protein concentration in the urine of immature *O. vulgaris* to be 515 mg l^{-1}, increasing to 1407 mg l^{-1} in mature females. In starved specimens, the concentration was 662 mg l^{-1}. This represents a loss of energy from the cephalopod via its parasite load, and has to be considered in constructing energy budgets of infected cephalopods.

Other energy losses that are also included in the excretion term in the energy balance equation are mucus losses from the body surface and in the faeces and, in the case of octopuses, shedding of sucker cuticles. Mucus production has never been quantified in cephalopods, but in other molluscs it can be a significant proportion of the total energy budget (Peck *et al.* 1993). *Octopus cyanea*, with a mean body mass of 1380 g, sheds 2.4 g of sucker discs d^{-1} with a dry matter content of 3%. They have an energy content of 19.7 kJ g^{-1}, so the energy loss is some 0.34 kJ d^{-1} (Van Heukelem 1976, cited in Wells & Clarke 1996).

8.7 Faeces

Faecal energy loss is generally relatively small in cephalopods. Van Heukelem estimated that *Octopus cyanea*, with a mean body mass of 1380 g, had an absorption efficiency of >96% and produced some 2.7 g d^{-1} of faeces, or 5.9 kJ d^{-1}, which is equvalent to about 3.5% of the total energy budget (cited in Wells & Clarke 1996).

It has been suggested that cephalopods have a limited capacity to metabolise lipids (Mommsen *et al.* 1981), and common observations of cephalopods held in tanks indicate that when fed a high lipid diet the faeces are oily and so float. It has therefore been suggested that the absorption efficiency of cephalopods might be less when they are feeding on prey with a high lipid content (O'Dor & Wells 1987). However, some cephalopods, e.g. *Illex argentinus*, regularly feed on high-lipid prey such as crustaceans and lantern fish (myctophids), and they accumulate large quantities of lipid in the digestive gland (Clarke *et al.* 1994). The digestive gland grows at a much higher rate relatively than the rest of the somatic tissues in *I. argentinus* (Rodhouse & Hatfield 1990a), pointing to a role in energy storage, or possibly in increasing buoyancy, prior to making the spawning migration. On the other hand, in two species of loliginid squid the role of the digestive gland appears to be excretion of lipid rather than storage (Semmens 1998). The loliginids have comparatively smaller, less oily digestive glands than the ommastrephids, and it is possible the ommastrephids differ in this respect because they make longer, more energetically costly migrations than the loliginids. The role of lipids in cephalopod energetics is clearly not yet fully understood and probably differs with different life-cycle patterns.

8.8 Energetic efficiencies

Cephalopods generally seem to have high absorption efficiencies, which explains their relatively low production of faeces. High absorption efficiency is related to the exclusively carnivorous diet of cephalopods (animals are generally more digestible than plants, which contain quantities of refractory cellulose in fibrous matter) and their ability to reject relatively indigestible materials, such a bone, when they are cutting up prey with the beak. The cephalopod alimentary tract is also well adapted for rapid digestion and high absorption efficiency (Boucher-Rodoni *et al.* 1987).

The difference between the mass exponents for feeding rate and metabolic rate in animals means that the proportion of energy consumed that is available for growth, after metabolic needs are met, decreases with size. Gross growth efficiency (conversion efficiency) therefore decreases in all animals as they grow larger. Table 8.4 gives conversion efficiencies for 15 species of cephalopod growing at rates between about 0.7 and 6.5% body mass d^{-1} and feeding at rates of 1.6–15% body mass d^{-1}. These animals were all large enough to have passed the early, exponential growth phase, but were not necessarily sexually mature. Although these conversion rates are relatively high, they are not exceptional by comparison with carnivorous fish (Jobling 1994). Although, as shown earlier, feeding rates increase with temperature, there is no evidence to suggest that food conversion rates are temperature-dependent (Mangold & Boletzky 1973; Van Heukelem 1983).

Comparisons of gross and net growth efficiencies of octopus (*Octopus maya*) and squid (*Illex illecebrosus*) in Table 8.5 show that squid are substantially less efficient converters than octopus. This is primarily because of the greater energetic cost of activity associated with the pelagic life style of squid compared with the more sedentary benthic octopus. When net growth efficiency is compared, conversion efficiency in

Table 8.4 Growth rates, feeding rates and gross conversion rates of selected cephalopods (after Wells & Clarke 1996).

Species	Temperature (°C)	Relative growth rate (% body mass per day)	Body mass (g)	Feeding rate (% body mass per day)	Conversion efficiency (%)	Food	Reference
Sepia officinalis	24	6.5	–	11.0	59	Shrimp	Forsythe *et al.* 1994
Sepiola affinis	13	2.4	2	6.4	38	–	Gabel-Deickert 1995
Loligo forbesi	14	0.7	10–60	4.6	16	Crustaceans	Hanlon 1990
Loligo opalescens	15	1.7	50	15	13	Crustaceans	Yang *et al.* 1986
Sepioteuthis lessoniana	25	7	100	–	25	Crustaceans and fish	Hanlon 1990
Illex illecebrosus	7	11.3	104	5.2	35	Fish	Hirtle *et al.* 1981
Todarodes pacificus	16	0.6	384	3.3	19	Fish	Sakurai *et al.* 1993
Octopus cyanea	24	2.5	500	6.0	48	Crabs	van Heukelem 1976*
Octopus dofleini	12	1.0	2700	1.3	69	Crabs and bivalves	Hartwick 1983
Octopus maya	25	4.1	300	9.2	40	Crabs	van Heukelem 1976*
Octopus vulgaris	10	0.9	300	1.6	56	Crabs	Mangold & Boletzky 1973
	15	1.7	300	3.3	55		
	20	2.9	300	5.4	48		
Eledone moschata	15	0.8	250	3.4	37	Crab	Mangold 1983c
Eledone cirrhosa	15	0.7	250	2.0	35	Crab	Boyle & Knobloch 1982a

* Cited in Wells & Clarke (1996).

Table 8.5 Growth rates and gross and net growth efficiencies in a squid and an octopus. Data from Hirtle *et al.* (1981) and van Heukelem (1976, cited in Wells & Clarke); table modified after Wells & Clarke (1996).

Species	Feeding rate (% body mass/day)	Growth rate (% body mass/day)	Gross conversion efficiency (P/C%)	Net conversion efficiency ($P/(C - R_b)$%)
Illex illecebrosus	4	0.6	15	43
(crustacean diet)	8	2.2	28	41
	12	4.0	30	43
Illex illecebrosus	4	0.9	23	30
(fish diet)	8	2.1	26	30
	12	3.4	28	31
Octopus maya	4	1.4	35	64
	8	4.3	54	69
	12	7.0	58	69

both squid and octopus is independent of consumption rate, indicating that the metabolic costs of growth are independent of the size of the meal. These are the costs measured by the post-prandial increase in respiration and the longer-term increase in resting metabolism after feeding discussed above (Wells *et al*. 1983b).

8.9 Power budgets

Preliminary power budgets for an octopus (*Octopus vulgaris*) and two species of squid (*Loligo opalescens* and *Illex argentinus*) have been constructed from composite data sets by Wells and Clarke (1996), and these are summarised in Table 8.6. The budgets for the two squid species are based on incomplete information so it would be unwise to draw detailed conclusions, but they do broadly illustrate some key features of the energy partitioning strategies of these different cephalopods.

The squid power budgets represent: (a) a starving but active *L. opalescens*; (b) a feeding and growing *L. opalescens*; (c) an actively migrating *I. illecebrosus* on its way to the spawning grounds, towards the end of the life cycle when growth is complete. The budgets for *O. vulgaris* are representative of animals that are: (a) starving, having not

Table 8.6 Preliminary power budgets for 500 g *Octopus vulgaris* at 22°C, 40 g *Loligo opalescens* at 14°C and 400 g *Illex illecebrosus* at 15°C. Units are mW, and data in parentheses are percentages of the total power requirement; table modified after Wells & Clarke (1996).

	Loligo opalescens starving	*Loligo opalescens* growing	*Illex illecebrosus* mature	*Octopus vulgaris* starving
Maintenance metabolism, R_m	56 (66)	56 (27)	695 (43)	147 (75)
Costs of activity, R_a	16 (19)	31 (15)	815 (50)	8 (4)
Energy content of new tissue, $P + G$	–	32 (16)	–	–
Costs of synthesis and breakdown, $R_s + R_g$	–	54 (26)	–	10 (5)
Excretory losses, U	5 (6)	13 (6)	46 (3)	6 (3)
Faecal and sucker losses, F+	8 (9)	19 (9)	69 (4)	26 (13)
Total power requirement, $P + G + R + U + F$	85 (100)	205 (100)	1625 (100)	197 (100)

been fed for several days; (b) feeding at maintenance level and so maintaining body mass but not growing; (c) feeding and growing at 2% body mass per day, which is a typical rate for an octopus in the sea; (d) fully mature, female and ready to lay eggs.

In both octopus and squid the power budget of starved animals is dominated by maintenance metabolism, but when they are actively growing the emphasis shifts to the production of new tissue. In the squid, which are almost constantly swimming, the energy costs of activity are considerably higher than in the more sedentary octopus, and this is at least partly reflected in the relatively smaller proportion of the overall budget that is allocated to tissue growth in squid compared with octopus when they are actively growing.

The relatively inactive octopus and the fast-swimming muscular squid probably represent fairly extreme examples of energy partitioning strategies among the coleoid cephalopods. The species that have secondarily evolved ammoniacal buoyancy mechanisms, and the deep-ocean forms, have undoubtedly reduced the proportion of total energy needed for activity, but we can only guess the strategies that have evolved in other forms. It is probably safe to assume that the diversity of morphology and life style of the class is reflected in their physiological energetics.

Physiological energetics of the long-lived iteroparous nautiloids is probably much closer to that of the other shelled benthic molluscs. Depending on the species, they can take 5–15 years to reach sexual maturity (Landman & Cochran 1987; Ward 1987) and they may live for 10 years after attaining maturity. They remain inactive for a relatively large proportion of their time, especially during daylight (O'Dor *et al.* 1993), they are neutrally buoyant and they swim by jet propulsion, mostly at their most economic speed. They have an energy demand of as little as 40.5 mW, and at this rate their large crop could probably hold enough food to sustain them for 6 weeks or more (O'Dor *et al.* 1993).

Chapter 9

Reproduction

Summary: The reproductive systems of cephalopods are rather similar in cuttlefish, squid and octopuses. The sexes are always separate, and no hermaphroditism or sex change has been found. Maturation in the female is principally a process of egg growth by the accumulation of large amounts of lipoprotein yolk, and the enlargement of the accessory reproductive organs: the oviducal, nidamental and accessory nidamental glands. Routine assessment of the state of maturity is usually based on a descriptive scale, supported by indices of the relative development of reproductive tissues. In males, mature spermatozoa are packaged into complex spermatophores stored in the spermatophoric (Needham's) sac. Fertilisation is achieved after individual matings in which spermatophores are transferred from the male to the female using an arm which is usually specially modified for the mating process (hectocotylus). There may be competition for mates, but multiple mating is common. The potential for sperm storage by the female leads to delayed fertilisation and the production of eggs at one spawning arising from matings with several different males. Egg masses are attached to the sea bed (most octopuses, loliginid squid and cuttlefish) or released into the water column in fragile gelatinous masses (most squid families). Reproduction in most cephalopods occurs seasonally, but there is no overall consistency of the timing cues for breeding. Individual females may spawn all their eggs over a short period of time (terminal spawning), or there may be distinct bouts of spawning (batch or repeated spawning). Some species (particularly the deep-water cirrate octopods) apparently spawn continuously over a wide range of adult sizes. Estimates of individual fecundity vary widely between species, and there is a trade-off between egg size and fecundity. Compared with other marine invertebrates, the eggs of cephalopods are large, well-protected and produced in relatively low numbers, leading to low mortality and low egg numbers.

9.1 Basic patterns

The organisation of reproduction follows a very similar pattern throughout the Coleoidea. The sexes are separate (dioecious or gonochoristic), and unlike the gastropod and bivalve molluscs, there are no known cases of hermaphroditism or sex change. Comprehensive accounts of coleoid reproductive systems are given by Mangold (1987), and also by Wells & Wells (1977b) for the octopods and Arnold & Williams-Arnold (1977) for decapods.

9.1.1 Female maturation

The eggs produced by the female are grown in the single median ovary (Fig. 9.1). This arises during embryology from paired cell masses in *Octopus* (Marthy 1968), or a single mass in the squid and cuttlefish (Fioroni & Sunderman 1983). When fully mature, the eggs become detached from their blood supply and the stalk connecting them to the germinal epithelium, and are shed loose into the proximal oviduct(s), where they temporarily accumulate. The adult oviducts are paired structures in the ommastrephid squid and incirrate octopods, while in sepioids, myopsid squid (*Loligo*) and cirrate octopods only one develops. At spawning, the eggs travel through an enlarged section

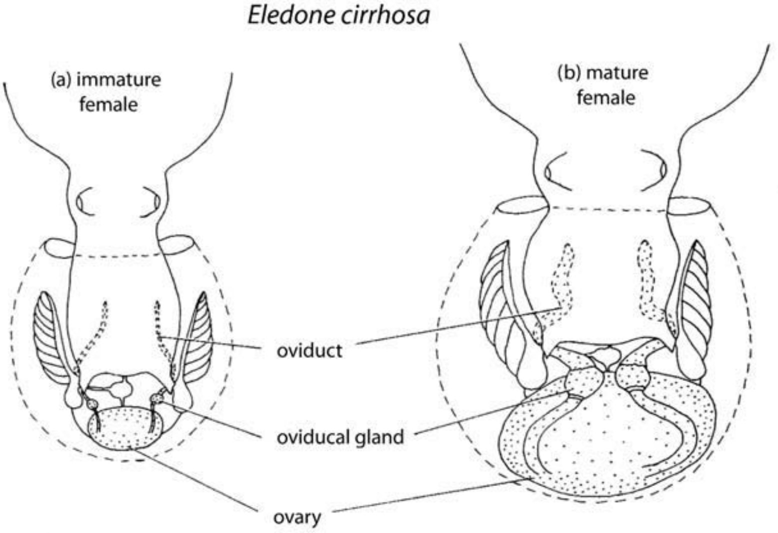


Fig. 9.1 Layout of the reproductive organs of a female octopus (*Eledone cirrhosa*) seen from the dorsal surface. (a) Immature, and (b) at reproductive maturity showing the relative enlargement of the ovary, ducts and oviducal glands (after Boyle & Knobloch 1982b).

of oviduct, the oviducal gland, into the distal portion. The function of the glandular region of the oviducal gland is the secretion of the final protective egg coats, although in *Octopus* it also stores the sperm after impregnation by a male (Froesch & Marthy 1975). Female squid also have paired nidamental glands which secrete the mass of jelly material surrounding the deposited spawn strings of loliginids, or the fragile gelatinous globes encasing the egg masses of ommastrephids.

Oogenesis, the production of eggs, is described for representative types such as *Sepia* (Richard 1971; Dhainaut & Richard 1976), *Loligo* (Selman & Arnold 1977; Selman & Wallace 1978; Knipe & Beeman 1978), several ommastrephid squid species (Lipinski 1979; Schuldt 1979; Takahashi 1978) and *Octopus* (Bolognari *et al.* 1976). Small oocytes first arise from a germinal epithelium and are present from a very early stage. Three phases of oocyte development are recognised, which are used to sub-divide the continuous process of oocyte maturation (see Bottke 1974 for the loliginid *Alloteuthis*; Boyle & Chevis 1992 for *Eledone cirrhosa*). *Stage I*: the oocytes are very small (<1 mm in length), and each is attached by a short stalk to the connective tissue core of the ovary. *Stage II*: flattened follicle cells migrate from the stalk in a single layer over the surface of the oocyte underneath the covering connective tissue; the oocyte begins to increase in volume, but the proliferation of the follicular cell layer increases at a greater rate than can be accommodated by the increase in surface area of the oocyte, and consequently it forms a deeply infolded double layer well supplied with blood vessels, giving the egg an externally striped or reticulated appearance (Fig. 9.2). *Stage III*: cells of the follicular cell layer become more columnar and secrete proteinaceous yolk into the lumen of the oocyte; the egg (oocyte/follicular cell complex) increases rapidly in volume; when yolk accumulation is complete, the follicle cell layer degenerates and the chorion is formed.

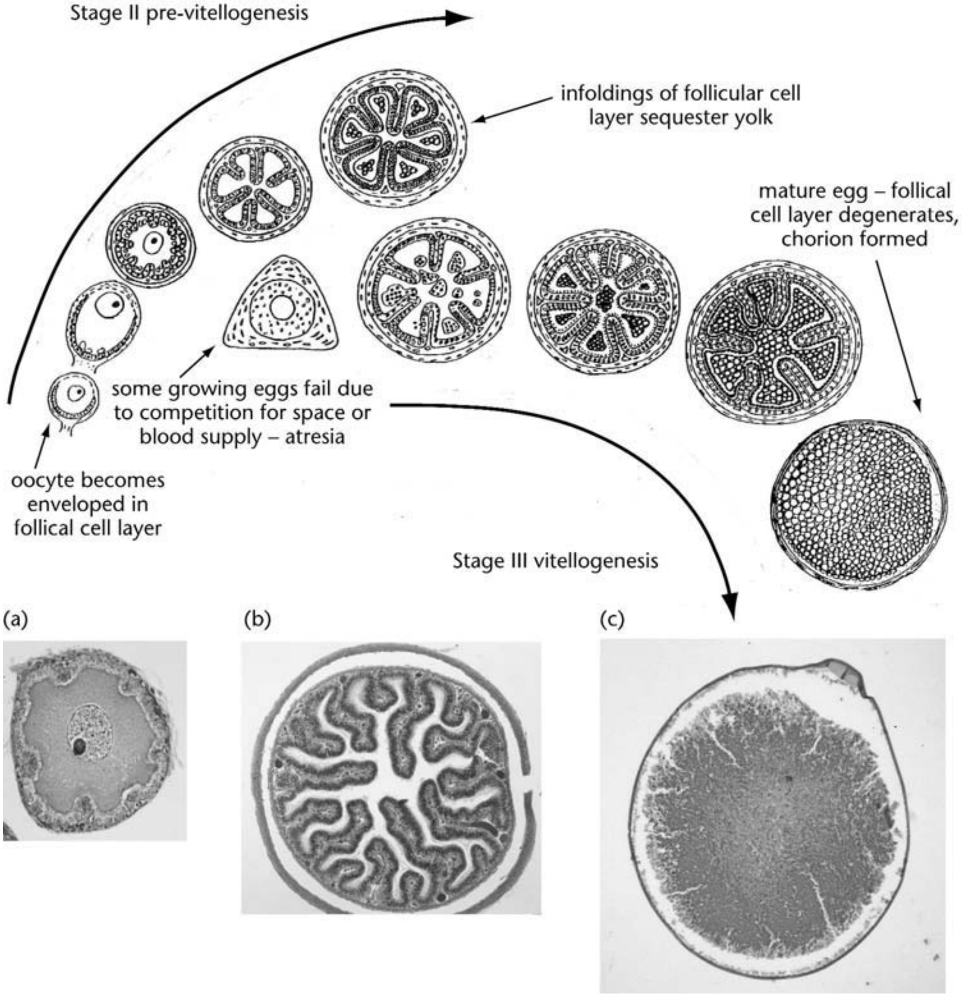


Fig. 9.2 Stages of oocyte development in the octopus *Eledone cirrhosa* to show sequential changes during egg formation (oocyte/follicular cell complexes) and the sequestration of yolk (after Boyle & Chevis 1992). Diagrams are schematic cross sections of the egg from about 200 µm to 2 mm in diameter, illustrated with representative light micrographs. Descriptive key in Table 9.1.

The key to the rapid growth of the cephalopod ovary during sexual maturation seems to be the formation of the intermediate oocyte/follicular cell complex to accelerate the process of vitellogenesis, i.e. yolk sequestration into the lumen of the oocyte. The extraordinary rate of development of the follicular cell layer is achieved by high rates of follicular cell division, with many nuclei becoming polyploid at this time (Boyle & Chevis 1991). Eggs growing from the same string of germinal epithelium in the ovary may grow at different rates and vary considerably in size along the length of the string. The distribution of egg sizes within the ovary is a further index of the stage of maturation of the animal (Table 9.1). Not all the eggs in the ovary will reach maturity because the total number normally appears to exceed the physical capacity of the ovary for all of them to grow to a mature size. This gives rise to 'competition' between

Table 9.1 Microscopic characteristics of developing eggs in the ovary of the octopus *Eledone cirrhosa* during the process of vitellogenesis (yolk formation), as shown in Fig. 9.2, after Boyle & Chevis (1992). The normal course of egg development is boxed; a proportion of eggs will become atresic (degenerate, shown in shaded boxes).

State of ovarian maturity	Egg length					
	<1 mm	1–2 mm	2–3 mm	3–4 mm	4–5 mm	5–6 mm
Ovary: pre-vitellogenic <1% GSI	*Eggs* stage II: follicle cells cuboidal, little RER, some lipid	*Eggs* stage II: little RER, increasing lipid				
Ovary: early vitellogenic 2–4% GSI	*Eggs* stage II: follicle cells cuboidal, little RER, some lipid	*Eggs* stage II: little RER, increasing lipid	*Eggs* stage II: follicle cells more columnar and closely packed, increasing RER and lipid, yolk accumulating in oocyte	*Eggs* stage III: follicle cells columnar and enlarged, increasing yolk accumulation, chorion developing		
Ovary: late vitellogenic 8%		*Eggs* stage II: follicle cells vestigial, oocyte degenerate, eggs triangular in section	*Eggs* stage III: follicle cells degenerating, pycnotic nuclei accumulating	*Eggs* stage III: follicle cells columnar and enlarged, increasing yolk accumulation, chorion developing	*Eggs* stage III: follicle cells columnar and enlarged, increasing yolk accumulation, chorion developing	*Eggs* stage III: follicle cell epithelium regresses, yolk accumulation complete, chorion formed

GSI, gonado-somatic index; RER, rough endoplasmic reticulum.

them for resources (blood supply) and space, and the consequent degeneration of some eggs, a process similar to that of the atresia seen in the gonads of fish. This competition within the ovary is known for octopus (Boyle & Chevis 1991) and squid (Sauer *et al.* 1993). At full maturity, the chorion is fully formed and encloses the egg, which detaches from its formative epithelial stalk. The mature eggs pass into the proximal oviduct and may be spawned in a single or several episodes (batch spawning).

9.1.2 Male maturation

Sperm is produced by the male in the single, median testis. Mature spermatozoa are shed into the proximal portion of the vas deferens where, in the convoluted and glandular tubing of the spermatophoric organ, they are packaged into spermatophores and stored in the spermatophoric (Needham's) sac. During mating, the spermatophores are pumped peristaltically along the distal portion of the vas deferens into the single excurrent duct. The terminal portion of the vas deferens becomes free from the body surface shortly before its ending just within the mantle opening of the left side. This detached portion of the vas deferens is often called a 'penis', a term that is strictly incorrect because the excurrent duct does not function as the intromittent organ. Instead, the spermatophores are transferred to the female by one of the arms, which is specially modified when the animal is sexually mature as the hectocotylus (Fig. 9.3).

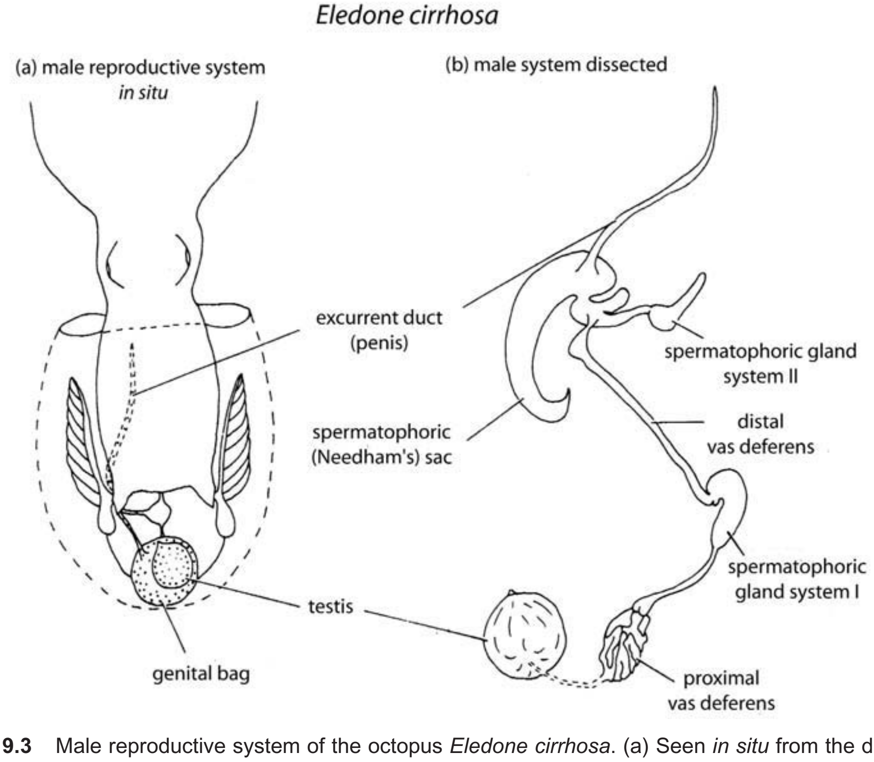


Fig. 9.3 Male reproductive system of the octopus *Eledone cirrhosa*. (a) Seen *in situ* from the dorsal surface. (b) With the components of the male duct dissected free from the genital bag (after Boyle & Knobloch 1982b).

Spermiogenesis is also divisible into stages describing the development and maturation of spermatozoa from the germ cells (spermatogonia). The mature sperm often has a species-characteristic morphology, and detailed descriptions are available for several squid, cuttlefish and octopus species (Healy 1989, 1990, 1993; Fields & Thompson 1976; Franzen 1955, 1956, 1967; Maxwell 1974, 1975; Richard 1971).

When fully differentiated, the spermatozoa pass into the proximal vas deferens and then into the thickened regions of the complex spermatophoric gland system where the cylindrical spermatophores are formed. Each spermatophore consists of a tightly coiled mass of sperm and an ejaculatory apparatus enclosed within a tunic. At maturity, the diverticulum which forms the spermatophoric sac is tightly packed with ripe spermatophores (Fig. 9.4a). After transfer to the female or release into seawater, the spermatophore swells and bursts, ejaculating the contained sperm by the spermatophoric reaction (Mann 1970). The mechanism of sperm transfer in all coleoids appears to be by one of the male arms, usually specially modified as the hectocotylus. The particular arm involved may differ (generally third right in octopuses, fourth left in loliginids), and the form of the tip of the hectocotylus, the spadix, is a species-specific modification. The morphological details of the hectocotylus tip are differentiated, presumably as part of a selective mating process (Cigliano 1995; Hanlon *et al.* 1999c), and the tip is a key recognition character for males throughout cephalopod systematics (Voight 2002; Fig. 9.4b).

9.2 Control of reproductive maturity

The essential processes of the onset and progress of reproductive maturity in the female are the production and sequestration of yolk in the oocyte (vitellogenesis), and the development of organs for the formation of protective individual egg coats (oviducal glands) and the encapsulation of the spawned egg mass (nidamental glands). In most of the shelf species of cuttlefish, squid and octopus, the enlargement of oviducal and nidamental glands marks the beginning of breeding competence and reproduction. The control of this process and the possible role(s) of environmental cues are of considerable significance to the life cycles of cephalopods.

Most of the evidence for the hormonal control of vitellogenesis has been obtained from a series of studies on *Octopus vulgaris*. In the course of studies on the central nervous system, it was noticed that individual females in which an experimental lesion severed the optic tract, or affected the innervation of the optic lobes, became precociously sexually mature within a few weeks (Boycott & Young 1956; Wells & Wells 1959). Subsequent experiments showed that the secretion(s) from the optic glands of *Octopus* increased the rate of protein synthesis for yolk production and was essential for vitellogenesis (Wells *et al.* 1975). The suggestion that in some squid the process of copulation itself induces female maturation has not been confirmed (Ikeda & Shimazaki 1994). Male sexual maturity, however, has also been shown to depend on the secretion(s) of the optic gland (Wells & Wells 1972a).

Optic gland material transplanted from one octopus to another apparently stimulates the recipient regardless of the sex of the donor. Implants from other octopus

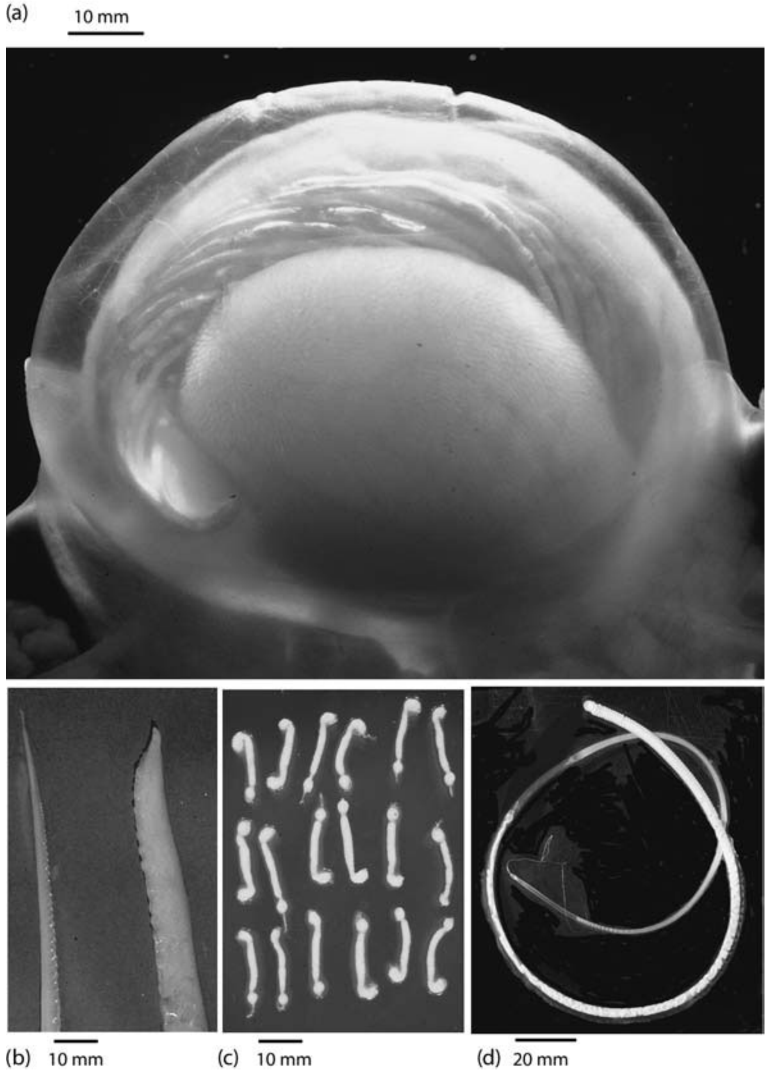


Fig. 9.4 (a) Genital bag of the octopus *Eledone cirrhosa* in a fixed and cleared specimen to show the testis (central) and mature spermatophores lying within the spermatophoric (Needham's) sac. (b) Hectocotylised 3rd right arm (right) of the male *E. cirrhosa* compared with the unmodified 3rd left arm tip (left). (c) 18 spermatangia (ruptured spermatophores) retrieved from the ovary of a mated female *E. cirrhosa*. (d) Single spermatophore of *Octopus dofleini*.

species (*Octopus macropus*, *Eledone cirrhosa*) are also effective (Wells & Wells 1975). Removal of the optic glands from maturing *Octopus* has been shown to cause the gonads to regress, although mating behaviour is apparently unaffected (Wells & Wells 1972b). Since reproduction is the terminal event for these species, it seems that the sequence of physiological processes brought about by the optic gland hormone cannot naturally be reversed. This idea received some direct support from the experiments of Wodinsky (1977) and Tait (1986), in which the excision of optic glands from maturing octopuses caused gonad regression and a subsequent resumption of feeding and growth. The nature of the optic gland secretion and its mode of action are still to be discovered, and it is also possible that the glands have other, catabolic functions (Froesch & Mangold 1976; Mangold & Froesch 1977).

In captivity, some cephalopods reduce their feeding rate or stop feeding altogether as sexual maturity progresses. This is consistent with the view that, at least in octopodids, the physiology of the pre-spawning female switches over from somatic growth to vitellogenesis in the ovary. The rapid secretion of large amounts of protein-rich yolk while food intake is reduced or stopped is apparently achieved by the re-mobilisation of somatic protein (O'Dor & Wells 1978). This results in the flaccid and weakened muscular tissues of 'spent' animals. In field populations of squid in which this effect has been examined, the results have been inconsistent. In *Alloteuthis (Loligo) subulata* (Rodhouse *et al.* 1988), *Nototodarus gouldi* (McGrath & Jackson 2002) and *Illex argentinus* (Rodhouse & Hatfield 1992), evidence for loss of somatic protein was lacking, but for *Photololigo* spp. (Moltschaniwskyj 1995) and *Moroteuthis ingens* (Jackson & Mladenov 1994), wasting of somatic musculature was associated with breeding. It is unlikely that the loss of musculature alone can result in the high level post-spawning mortality so characteristic of cephalopods, but it seems that the process of re-mobilisation of nutrients, mainly proteins to be sequestered in yolk, cannot be reversed.

9.3 Assessment of maturity status

Ecological and fishery studies require clear and detailed estimations of the state of sexual maturity for large numbers of individuals. The timing and location of breeding aggregations, the size at maturity, the sex ratio at breeding, and many other population characteristics all require swift and consistent assessment of the state of sexual maturity. These assessments usually involve several aspects of reproductive development, e.g. the state of the gonad and the accessory reproductive structures, and are based either on indices (semi-quantitative size relationships between the reproductive components and body size) or scales (descriptive sub-division of the reproductive process into arbitrary but recognizable stages). Either approach provides a guide to the rate of progress of reproductive maturity, but neither is solely fully descriptive of the process.

9.3.1 Maturity scales

The reproductive scales commonly used in population biology and fishery studies on cephalopods are mostly adapted from the universal scale of Lipinski (1979). Most scales adopt a simple five-stage system; examples for a loliginid and an ommastrephid squid are given in Table 9.2. Many studies are available which link the descriptive scales to quantitative indices of relative development or the histological appearance of the reproductive structures.

A remarkable correlate of the maturation process in female loliginids is the development of the orange-red colouration of the accessory nidamental glands, an easily recognised feature of progressing reproductive maturity. This is due to the growth of plaques of pigmented symbiotic bacteria (Bloodgood 1977), and is specifically linked

Table 9.2 Descriptive maturity scales for *Loligo forbesi* (after Boyle & Ngoile 1993) and *Todarodes sagittatus* (after Borges & Wallace 1993).

	Male	Female
Loligo forbesi		
Stage I	Microscopic characters: testis transparent and appears as an enlargement of the genital aorta; spermatophoric organ appears as a clear droplet by the base of the left gill; penis opening dorsal to base of left gill	Microscopic characters: ovary transparent and membranous; oviduct and oviducal glands appear as droplet post. to left gill; nidamental glands appear as two strands ant. to stomach and below digestive gland; accessory nidamental glands not distinguishable
Stage II	Visible components: testis translucent and soft; spermatophoric organ translucent and distinguishable into component parts; penis opening anterior to base of left gill; no spermatophores visible; vas deferens transparent and not easily visible; hectocotylisation of 4th left arm begins	Ovary translucent and 'fluffy', appears to emanate from genital aorta; oviduct opening visible dorsal to base of left gill; oviduct and oviducal gland transluscent and not distinguishable from each other; nidamental glands opaque; accessory nidamental glands appear with scarlet specks
Stage III	Testis extends to posterior apex of mantle, and is opaque and ridged; vas deferens full of sperm and creamy white; spermatophoric complex with a white streak, but sac without spermatophores; penis extends half the length of the ink sac, hectocotylised arm clearly recognisable	Ovary with visible eggs; oviducal gland opaque; oviduct large and transparent with opening halfway along inksac; nidamental glands enlarged and opaque; accessory nidamental glands mottled scarlet and tinged reddish-brown, partly obscured by anterior tips of nidamental glands
Stage IV	Testis extends anteriorly past post. tip of stomach, opaque and ridged; spermatophoric sac packed with spermatophores; penis extends to level of anus and ink sac opening; vas deferens full of sperm; hectocotylisation complete	Ovary with eggs of different sizes, some free eggs in body cavity; eggs in proximal oviduct, oviducal glands creamy white with brown patch at posterior end; nidamental glands exude viscous fluid with cut; accessory nidamental glands mottled scarlet, reddish brown and orange, overlain by nidamental glands
Stage V	As Stage IV, but with spermatophores in distal vas deferens and penis	As Stage IV, but with eggs in distal oviduct, spermatheca with sperm
Todarodes sagittatus		
Stage I	Sexual organs microscopic; spermatophoric complex appears as a single organ, as a transparent or translucent spot	Sexual organs microscopic; nidamental glands appear as very fine transparent strips
Stage II	Spermatophoric complex (spermatophoric organ, spermatophoric sac and vas deferens) clearly distinguishable; testis small	Nidamental glands translucent and whitish; oviduct visible
Stage III	Vas deferens white, enlarged and convoluted; spermatophoric sac lengthened but empty; surface of testis striped	Nidamental glands enlarged; oviduct extended; oviducal glands small but clearly visible; ovary with immature eggs visible
Stage IV	Spermatophores present in spermatophoric sac	Nidamental glands large; voiduct extended with obvious eggs present; oviducal glands enlarged; ovary swollen and packed with eggs
Stage V	As Stage IV, but with spermatophores present in distal vas deferens.	Nidamental glands large and overlying other organs; eggs in distal oviduct; oviducal glands swollen

to the onset of maturation (Lum-Kong 1992). It is possible that this association with a coloured symbiont is similar to the symbiotic luminescent bacteria known from elsewhere (McFall-Ngai 1994).

9.3.2 Maturity indices

The most frequently and widely used index of maturity is the gonado-somatic index (GSI), in which the weight of the gonad is expressed as a percentage of body weight. This is defined as

$$\text{GSI\%} = \text{gonad weight (g)/total body weight (g)} \times 100$$

or

$$\text{GSI\%} = \text{gonad wt. (g)/(body wt.} - \text{gonad wt.) (g)} \times 100$$

Because gonad weight is used variously to mean including or excluding the mass of the genital ducts (oviduct or vas deferens), with or without their glandular and storage portions (oviducal glands or spermatophoric sac), comparability between studies of even such simple measures as GSI% cannot be assumed. Scales based on weight relationships are not favoured for field studies because of the difficulties of making rapid and accurate weighings, especially at sea. However, length-based indices, such as the relative length of the nidamental gland (NGL/ML), may be readily applied in the field (Rodhouse *et al.* 1994b).

9.3.3 Timescale for maturity and reproduction

Direct evidence for the rate of progress of sexual maturity of individuals in the laboratory or field environment is lacking, but the impression from all the laboratory work suggests that vitellogenesis and maturation of the eggs (maturity stages II–IV) occurs rapidly. Population sampling on species that are strongly seasonal breeders is generally consistent with this timing. In loliginids, mature males appear earlier in the fishery, either due to an earlier onset of maturity or to earlier arrival in the breeding areas. At the start of the breeding season the sex ratio is also frequently biased towards males. The use of these maturity scales, i.e. their incidence in the population, is the main tool for assessments of the timing and locations of breeding.

9.4 Mating strategies

Unusually among marine invertebrates, reproduction in cephalopods always takes place through individual matings. The spermatophores of the male are transferred from the terminal organ of the excurrent duct to a groove along the hectocotylus formed from a fold of skin. Pumped along the arm by muscular action, the spermatophore is delivered to the female by the modified tip of the hectocotylus, or spadix.

In mating octopods, the tip of the hectocotylus is inserted into the mantle of the female. Spermatophores are deposited in the cavity and, at least in *Octopus vulgaris*, they enter the oviduct and become lodged in the oviducal gland (Froesch & Marthy 1975). This provides considerable potential for sperm storage, and allows for a significant time-interval between mating and fertilisation. Joll (1976) records up to 113 days between an observed mating and the laying of fertilised eggs in *Octopus tetricus*. In some octopuses (*Eledone cirrhosa*, Boyle 1983b), the spermatophores pass completely along the oviduct and through the oviducal glands before finally bursting in the ovary itself. The eggs in this species are thus fertilised before beginning their passage down the oviduct. The mating behaviour of deep-water cirrate octopuses remains mysterious. Females of these octopuses apparently lay eggs continuously over most of their growth period and lifespan (Villanueva 1992a; Daly *et al.* 1998). Because of this breeding pattern, and their dispersed distribution in deep water, it would be logical to expect female cirrates, in particular, to store sperm in the reproductive tract. Although there is no hectocotylus in these cirrates, the spermatophores could presumably be transferred via the funnel. Despite a report of sperm in the female reproductive tract in *Cirrothauma* (Aldred *et al.* 1978), active searching in the oviducal glands of *Opisthoteuthis* (Boyle & Daly 2000) failed to find clear evidence.

After mating, some squid, e.g. the loliginids, retain the spermatophores in a seminal receptacle, i.e. a pouch-like structure in the arm web close to the buccal membranes. Others deposit the spermatophores inside the mantle, where they are often attached near the gills, and even same-sex spermatophore transfers are reported (Norman & Lu 1997). Presumably fertilisation is achieved at the time of egg laying when the eggs are passed out from the funnel. It is apparent from these examples that in both squid and octopuses, fertilisation is finally achieved by the actions of the female at spawning, although very little is actually known about the details of the process.

Mating takes place with few preliminaries in octopuses, but in cuttlefish and loliginid squid, elaborate courtship behaviours have been described (Hanlon & Messenger 1996). Mated pairs will swim side by side for hours while the female spawns the eggs, during which time the male (usually the larger animal) interposes himself between the female and other males which may approach while continuing to display intense and moving chromatophore patterns.

On the spawning grounds of *Loligo vulgaris reynaudi* (Hanlon & Messenger 1996), the very interesting phenomenon of the ‘sneaker’ male has been described. These are much smaller but mature adult males, which remain on the edge of the spawning area, apparently unnoticed by the large mating male. As the female approaches the egg attachment site the ‘sneaker’ dashes forward and mates with her. Using molecular genetic markers, Shaw & Boyle (1997) have shown that single egg strings of *Loligo forbesi* females may be successfully fertilised by at least two males. Competition for females and multiple paternity of the offspring may be a general mechanism in the loliginids (Hanlon *et al.* 1997; Hanlon 1998; Maxwell *et al.* 1998; Maxwell & Hanlon 2000). New genetic techniques for the assignment of paternity have allowed Emery *et al.* (2001a) to show that mated *Loligo forbesi* may be carrying the spermatophores from at least four males. Moreover, genotyping of the hatchlings emerging from single egg strings in this species (Boyle *et al.* 2001) has shown multiple paternity within the 90–120 offspring emerging. The mating strategy of the species in this instance is a matter of speculation, but it can be assumed that mixing the paternal genotypes within

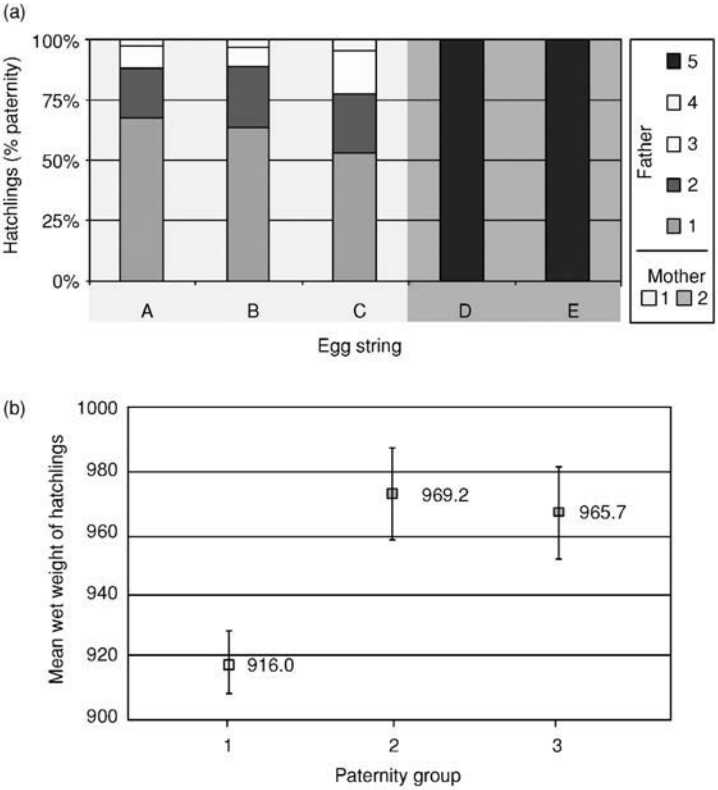


Fig. 9.5 Multiple paternity of offspring from females of *Loligo forbesi*. (a) Distribution of paternity (fathers 1–5) among hatchlings from five egg strings (A–E) from two females. (b) Mean wet weight of hatchlings (µg ± SE) of three paternity groups (fathers) from one egg string (C) (after Emery *et al.* 2001b).

the reproductive output of a single female must increase the phenotypic diversity of her offspring, and thus increase the chance that at least a portion of the brood will possess the phenotypic characteristics for survival. Confirmation of this interpretation was found by Emery *et al.* (2001b), who compared the mean size of all hatchlings from single egg strings of *Loligo forbesi*. They showed that at least in one case, the mean size of the offspring from one male at hatching was significantly smaller than that of the offspring of another three males fertilising the eggs within that string (Fig. 9.5). Size is such a fundamental phenotypic character that it is safe to assume that this strategy of multiple paternity within broods conveys important phenotypic diversity.

9.4.1 Spawning modes of individuals

The apparent semelparity (monocycly) of the modern coleoids, and its significance for their life cycle, is a popular subject for debate, and much of the uncertainty surrounding the issue of whether all are semelparous (single breeding) or some are iteroparous (repeated breeding) arises from variations in the mode of spawning. Whether the eggs of an individual female are fully spawned in a single episode (*Loligo opalescens*) or sequentially in batches (*L. forbesi*, *L. vulgaris* Rocha & Guerra 1996; *L. vulgaris reynaudi*, Melo & Sauer 1999; *Photololigo* spp., Moltschaniwskyj 1995) does not alter the argument that loliginids are also semelparous. Cuttlefish, too, may spawn intermittently or over an extended period of time (Boletzky 1987b). Ommastrephids such as *Stenoteuthis oualaniensis* (Harman *et al.* 1989) and *Illex* spp. (Laptikhovsky & Nigmatullin 1993) are also batch (sequential) spawners, but with no evidence for alternating regression and regeneration of the germinal tissue of the gonad.

The situation is more difficult to interpret in those species in which eggs are produced by individuals over a very extended period of time or over a large range of body sizes. The small tropical sepioid *Idiosepius pygmaeus*, for example, produces eggs in as many as 11 sequential batches, and spawning may take place in individuals ranging in size over 80% of the total adult size range (Lewis & Choat 1993). Remarkably, Lewis & Choat (1993) found that, on average, females of this species incorporated 5.1 times their body weight (organic weight/dry weight) into reproductive material (eggs and coatings) spawned over a period of 18 days.

Typical incirrate octopods such as *Octopus* spp. and *Eledone cirrhosa* confine their egg laying to a period of only a few days or weeks, and all observations consistently show that death follows shortly after the eggs have hatched. Tropical octopods like *Octopus chierchiae* (Rodaniche 1984) have been found to alternate several episodes of egg laying with mating activity (Rodaniche 1984). These examples lead some authors (Rodaniche 1984; Harman *et al.* 1989; Lewis & Choat 1993) to propose the case for true iteroparity. If these arguments are accepted, then it would still be true that this version of iteroparity takes place over a short period of time and within a single annual cycle (monocyclic).

A further special case is presented by deep-water cirrate octopods of the genus *Opisthoteuthis* (Villanueva 1992a; Boyle & Daly 2000). Both sexes are fully mature over the major part of their size range, and females always have a single egg in the distal oviduct apparently ready to be spawned. A sequence of decreasing egg sizes is present along the proximal oviduct and in the ovary itself, suggesting a continuous spawning mode. Nothing is known of the age and lifespan of these bathybenthic species, but the evidence for continuous spawning fits neither the semelparous nor the iteroparous conventions, although they could still be considered as monocyclic.

9.4.2 Seasonality and timing

Temperate cephalopod species appear to have more or less seasonally defined breeding, and this is probably also the case for high-latitude species. Although environmental cues for the onset of vitellogenesis are implicit in much of the experimental work, the factors controlling breeding in cephalopods are by no means clear or consistent.

A short photoperiod has been shown to have a stimulatory effect on gonad development in *Sepia officinalis* (Richard 1967), but in *Illex illecebrosus* longer daylengths induce or accelerate maturation (O'Dor *et al.* 1980). Higher temperatures accelerate gonad development in *Sepia* (Richard 1966a, b) and *Octopus* (Van Heukelem 1979), and lead to sexual maturity at smaller sizes. A restriction of food intake in early life may delay maturation and extend lifespan in *Eledone moschata* (Boletzky 1975) and *Sepia officinalis* (Boletzky 1979), but poor nutrition in the later stages accelerates the onset of maturity in *Eledone cirrhosa* (Mangold & Boucher-Rodoni 1973). Notably, in *E. cirrhosa*, aquarium-held animals have greater gonad development than freshly caught specimens at all sizes (Boyle & Knobloch 1984a, b). The actions and interactions of temperature, photoperiod and nutritional state in different species in captivity do not currently allow a consistent hypothesis linking these factors and the mechanism of maturation.

The optic glands of field-caught mature *Octopus vulgaris* appear enlarged and pigmented (Wells & Wells 1959). A multivariate analysis of body components in the octopus *Eledone cirrhosa* showed that the size of the optic glands varied seasonally in phase with the reproductive components rather than with a neural or somatic component (Boyle & Thorpe 1984). Most data on the timing and seasonality of reproduction arises from field studies of the incidence of mature stages in the population.

Mangold (1987) proposes that cephalopod spawning at the population level can be categorised as (1) strict seasonal spawning, (2) extended seasonality with or without peaks of spawning activity, (3) year-round seasonality with or without activity peaks, or (4) two spawning periods within one year occurring in species with a life cycle of about 6 months.

Some species with exceptionally wide distributions may have quite different spawning patterns in different parts of their range, which confounds the idea that environmental factors are the sole or main control on breeding season. Despite evidence for seasonality in the breeding cycles of most boreal and shallow-water cephalopods, it is also the case that in most examples where year-round sampling of a representative population has taken place, some mature animals are found at almost any period of the year. These findings imply that whatever the environmental cues tending to bring the breeding population into phase, some portion of it is always competent to breed. This capacity may provide an essential safeguard for a monocyclic seasonal species in the event that conditions at the peak breeding season in any year do not favour reproductive success or recruitment of the offspring. The life-cycle plasticity provided by the combination of variable reproductive characters in individual animals and populations is key to cephalopod survival in highly variable environments.

9.5 Reproductive output (fecundity)

Reproductive output, i.e. the number of viable eggs spawned, attracts considerable attention in most organisms. On theoretical grounds it represents the lifetime investment in the continuity of genetic material, and is a critical stage in the production of the next generation. In practice, the success of annual reproduction is the basis for the growth of biomass and recruitment to adult (fished) populations.

There are few data on actual fecundity, i.e. the number of eggs spawned by individual females. Nearly all estimates are of *potential* fecundity, i.e. the maximum number of oocytes in the ovary prior to spawning. This approach is relatively easily standardised, but does not estimate the number of eggs reaching full maturity and successfully fertilised and spawned. Some authors have attempted to overcome the over-estimate inherent in this method by counting only mature oocytes in the oviduct and ovary. However, the evidence for sequential batch-spawning of eggs in several species undermines this approach also. Fecundity estimates for a range of representative

Table 9.3 Estimates of female reproductive output by representative cephalopods (fecundity) and the method by which the data were obtained. Egg dimensions are gross external measurements and may include capsular sheaths in the case of the sepioids. Difficulties in size estimation also arise due to swelling of the eggs after spawning*; generally the maximum sizes are given, but the sizes of the species and of individual females are also important variables. There is a range of estimates in the literature for both the numbers and the sizes of eggs of individual species. This table summarises these estimates for the species listed as reviewed by various authors in Boyle (1983a) who have aggregated data from many individual sources.

Species	Egg number (approx.)	Egg size (mm)
Sepioids		
Sepia officinalis	500 spawned	1.2 × 3.0
Sepiola robusta	35–54 spawned	3.5 × 4.5
Euprymna scolopes	300 spawned	4.0 × 4.0*
Sepietta oweniana	<160 spawned	4.5 × 5.0*
Loliginid squid		
Loligo opalescens	<4250 spawned	1.6 × 2.5
Loligo pealei	3500–6000 female count 21 000–53 000 spawned	1.0 × 1.6
Loligo vulgaris	<7000 spawned	2.2 × 2.7
Ommastrephid squid		
Illex illecebrosus	<100 000 spawned	0.8 × 1.0
Todarodes pacificus	320 000–470 000 female count	0.7 × 0.8
Dosidicus gigas	<650 000 female count	0.9–1.1
Octopods		
Octopus briareus	200–500, <955 spawned	5.0 × 14.0
Octopus cyanea	<700 000 spawned	<3.00 long
Octopus dofleini	18 000–70 000 spawned	<8.0 long
Octopus joubini	<321 spawned	4.0 × 8.0
Octopus maya	3000–5000	3.9 × 11.0
Octopus tetricus	<15 000 spawned <700 000 female count	0.9 × 2.4
Octopus vulgaris	100 000–500 000 spawned	1.0 × 2.0
Eledone cirrhosa	2000–54 000 female count	2.5 × 7.5
Eledone moschata	100–500 spawned	5.0 × 16.0
Bathypolypus arcticus	20–80 spawned	6.0 × 14.0

cephalopods are given in Table 9.3, with the caution that these estimates may not be directly comparable owing to methodological differences.

Based on the measure of gonado-somatic index (GSI), the individual investment in reproduction rarely exceeds about 30% of body weight. Compared with many other semelparous marine animals this has been considered to be rather low (Calow 1987), and leads to the assumption that the mortality of eggs and juveniles must also be low. All cephalopod eggs are relatively large and yolky (Table 9.3), and there is naturally some trade-off between egg size and number. Many authors have also measured potential fecundity at a range of body sizes. While a statistically significant relationship between fecundity and body size is found in some species, it is generally weak and highly variable. The study of Lewis & Choat (1993) is unique both in quantifying the total spawning output of individual *Idiosepius pygmaeus*, and in demonstrating that it may considerably exceed the body weight of the female. By feeding groups on different rations, they also showed that the reproductive output was directly responsive to nutritional conditions.

Chapter 10

From egg to recruitment

Summary: Study of the complete life cycle between spawning and recruitment to the adult population is hindered by difficulties of representative sampling and of species' identification at early stages. Those cephalopods with egg deposits attached to the seabed (shallow-water octopods, cuttlefish and loliginid squid), have yolky, well-protected eggs and long development times. Changing environmental conditions during development, especially temperature, directly influence developmental rate and hatching success. Cephalopods releasing eggs in the water column, either freely (families Brachioteuthidae, Enoploteuthidae) or in neutrally buoyant gelatinous masses (families Ommastrephidae, Gonatidae), produce small eggs with relatively short development times which become part of large-scale current-assisted migrations of the population. Cephalopods do not have highly differentiated larval stages. The hatchling larvae and early young are sometimes called 'paralarvae', a term which recognises the ecological differences between this stage and the adult. Many benthic and nektobenthic adult forms have planktonic paralarvae. Temperature has a considerable effect on the rate of egg development and of paralarval and juvenile growth. These stages occupy a substantial proportion of the total lifespan of any species, and the effects of temperature may be paramount in affecting the timing of hatching and recruitment to the adult population. The culture of cephalopods in captivity, based on the maintenance and rearing of wild-caught juveniles and sub-adults, has limited commercial potential because of their predatory habit and dependence on supplies of live food. Rearing of larvae hatched in captivity is possible using a combination of specially reared live food and frozen supplies. There is scope for the integration of managed culture with management of the coastal environment for mixed cultivation of cuttlefish, loliginid squid and octopuses.

In common with most marine animals, the lives of cephalopods between spawning and the attainment of an appreciable body size are not well known. Since all cephalopod eggs have been fertilised at or before the point of spawning, embryonic development is already in progress when the eggs are released by the female. In contrast to the other molluscan classes, there are no morphologically specialised larval stages or any profound metamorphoses between hatching and adult. The general pattern is of a relatively large hatchling emerging directly as a miniature adult. These 'paralarval' forms usually have different ecological requirements from the adults and frequently comprise the main distributional stage of oceanic species (e.g. Vecchione *et al.* 2001b). Reviews of the embryonic (Boletzky 1987a) and juvenile (Okutani 1987; Vecchione 1987a) stages and their biology in culture (Boletzky & Hanlon 1983) are available. The comprehensive work by Boletzky (2003) treats the embryonic stages and their transition to free-living young as an integrated life phase.

10.1 Spawned eggs

The eggs of coleoids are spawned in one of two basic modes. For those species which are mainly restricted to coastal and shelf habitat, most octopuses, cuttlefish and loliginid squid eggs are attached to the seabed or other surfaces.

Cuttlefish eggs are individually enclosed in a tough protective external coating, often pigmented black from the ink-sac secretions. These form distinctive clusters of lozenge-shaped capsules attached to rock surfaces and disguised among the many other encrusting organisms. Several females may deposit eggs at the same site, and Zatylny *et al.* (2000) have shown that the egg capsules themselves release a peptide pheromone which induces spawning in other mature females. It should be noted that the egg capsules of *Sepia apama* often contain bacterial populations originating from the accessory nidamental glands of the female (Cronin & Seymour 2000, Chapter 9), although the significance of this is obscure.

Loliginid squid ensheath their eggs with material from the nidamental glands, embedding them into finger-like capsules each containing some 90–120 eggs in *Loligo*, but as few as 3–10 in *Sepioteuthis*. Large numbers of these conspicuous white capsules are attached by the female to a hard surface (Fig. 10.1). Individual females progressively attach their capsules to the same site in concentrated bouts of spawning, and in those species which aggregate densely at breeding (*Loligo opalescens*), many females use the same area, resulting in large areas of seabed covered with spawn. Some loliginid species such as *Loligo vulgaris reynaudi* (Sauer & Smale 1993) and *Loligo plei* (Vecchione 1988) are less dependent on solid surfaces for egg-laying, and may simply insert the egg

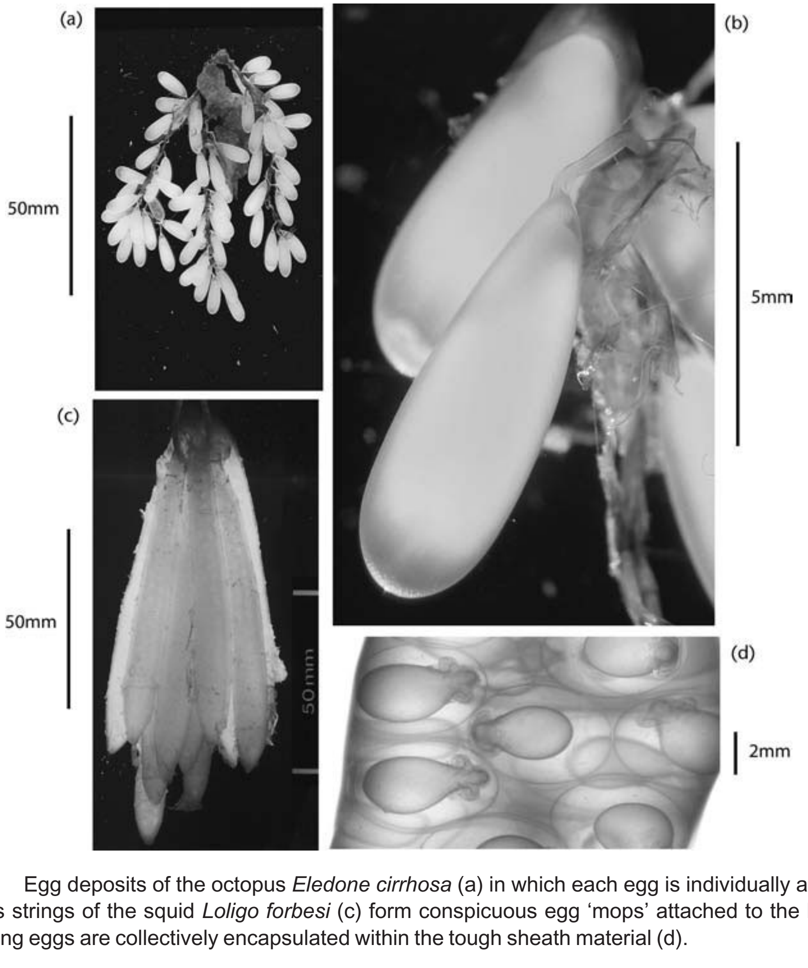


Fig. 10.1 Egg deposits of the octopus *Eledone cirrhosa* (a) in which each egg is individually attached (b). Eggs strings of the squid *Loligo forbesi* (c) form conspicuous egg ‘mops’ attached to the bottom. Developing eggs are collectively encapsulated within the tough sheath material (d).

capsule into sandy or gravel sediment. Boletzky (1986) compares the various forms of encapsulation of cephalopod embryos and the mechanisms of their formation.

Less is known about spawning by squid species which are mainly pelagic in habit. Ommastrephids such as *Illex illecebrosus* and *Todarodes pacificus* in captivity extrude their eggs in a continuous fragile gelatinous mass, which expands on production by absorption of water to form masses up to 1 m in diameter (O'Dor *et al.* 1982a; Bower & Sakurai 1996). Apparently these masses are almost neutrally buoyant in seawater and probably float at horizontal density discontinuities between water masses (O'Dor & Balch 1985). Oceanic squid of other families, such as the Gonatidae are also described as spawning mid-water gelatinous egg masses (Okutani *et al.* 1995; Bjørke *et al.* 1997), and in some cases even to brood them (Seibel *et al.* 2000a). The persistence of these structures in nature is in doubt since they are not captured in nets. Sakurai *et al.* (1996) report that the egg masses of *Todarodes pacificus* disintegrate 4–10 days after spawning. A few squid from other families, notably *Brachioteuthis* spp. (Brachioteuthidae) and members of the Enoploteuthidae, are known to release eggs singly into the water (Young *et al.* 1985).

Octopus eggs are individually attached by a short stalk into strings, which are themselves attached to the bottom on hard surfaces (Fig. 10.1). Typically, the female *Octopus* will deposit her spawn under an overhang or within an enclosed space that will enable her to gain some protection during the time she will brood the eggs. Exceptions to this pattern are the bathybenthic cirrate octopuses, such as *Opisthoteuthis*, whose eggs are apparently deposited freely and individually onto the sea bed (Boletzky 1982). The most remarkable exception is the pelagic octopus *Argonauta*, in which the female secretes a thin calcareous brood chamber, the paper nautilus, within which the eggs are attached and brooded while being held continuously by the female (Bello & Rizzi 1990). In other pelagic octopods, such as *Tremoctopus violaceus*, the female retains the eggs in specialised egg carriers formed from the dorsal arms or even, in *Ocythoe tuberculata*, becomes ovoviviparous (Boletzky 1998).

There are profoundly different ecological consequences for the benthic or pelagic spawning modes. Spawned eggs attached to the bottom are exposed to any changes in physical conditions imposed by changing water masses. Only the hatchling, paralarval and juvenile stages are transported and dispersed by coastal currents in relatively well-mixed shelf water. In contrast, pelagic eggs will be carried in the water mass and conditions in which they were spawned, but owing to the advective transport possibilities of ocean currents they may be dispersed over far wider geographic areas as Lagrangian particles living in relatively constant conditions (Bower 1996). The trade-off between egg size and fecundity (see Chapter 9) generally means that the pelagic-egged species produce much larger numbers of small eggs. These drifting eggs are less well protected than benthic spawn deposits and may suffer higher rates of mortality.

10.2 Developmental processes

The large size and robust nature of the encapsulated eggs of coastal cephalopods has prompted studies of the embryonic development in many species. Naef (1923, 1928) figured and described their embryonic stages, and formalised the main steps in the process into a series of numbered stages from the earliest cell division through to hatching. A modified form his scheme provides the framework for comparative studies (Arnold 1965; Arnold *et al.* 1972; Baeg *et al.* 1992; Blackburn *et al.* 1998; Boletzky *et al.* 2001; Guerra *et al.* 2001b; Mangold *et al.* 1971; Segawa *et al.* 1988; Shigeno *et al.* 2001b, e; Watanabe *et al.* 1996) and reviews (Arnold 1971, 1990; Boletzky 1987a, 1998, 2003) on different species.

In these short-lived species, the time for embryonic development may be a significant fraction of the total lifespan of the individual. During this phase, the nutritional requirements of the embryo are provided by the yolk supplied by the female. The earliest stages of embryonic development appear to be unaffected by the volume of the yolk mass. Cell division envelops the uncleaved yolk in a single layer of cells to form the cellular envelope of the outer yolk sac (Boletzky 2002). As the embryo proper grows and organogenesis proceeds, the yolk is clearly sub-divided into outer and inner yolk sacs connected to each other through the buccal cavity (Fig. 10.2).

Large-egged species take longer to develop between spawning and hatching (Mangold-Wirz 1963) and emerge as larger, more competent hatchlings. At an early stage in development, pulsation of the yolk sac is seen, which may be functioning as both a food reserve and a respiratory surface (Boletzky 1989), followed by activity of the embryonic heart and blood vessels. At later stages, mechanical stimulation will cause whole body movements of the developing embryo and spasmodic chromatopore expansion (Fig. 10.3). It appears that movements of the *Loligo* embryo are chemically inhibited by a substance within the embryonic fluid (Weischer & Marthy 1983), and that the egg-string jelly of loliginids also has a generalised effect inhibiting ciliary action (Atkinson 1973).

Embryonic development times vary considerably between the different types of cephalopod egg, ranging from 5–10 days for small, unprotected eggs, to 50–100 days for large yolky-egged species. Total development times are highly dependent on egg size and temperature, and may be over 1 year in cold-water large-egged octopods (Voight & Grehan 2000; Wood *et al.* 1998; Boletzky 2003). Whatever the optimum development time for a species, the temperature at which development takes place is a very significant variable, since higher temperatures shorten development time. Many studies have established specific time–temperature relationships for different species (e.g. McMahon & Summers 1971; O'Dor *et al.* 1982b; Sakurai *et al.* 1995, 1996), and some of these are shown in Fig. 10.3. Whatever the relative effects of temperature and egg size on the duration of the embryonic phase, the expectation is that larger eggs have longer development times and, within the temperature limits for any species, a higher temperature shortens the period between spawning and hatching.

Although few data are available, the influence of temperature in accelerating or retarding embryonic development in the field is expected to be of key importance to the life cycle (Fig. 10.4). The interaction between the timing of egg-laying and the development temperature will clearly fix the time of hatching, which, in turn, determines the conditions for survival and growth met by the hatchling. Especially at low (Boletzky 1994) or fluctuating (Boyle *et al.* 1995) seasonal temperatures, this interval may be a critical component in completion of the life cycle. The influence of temperature

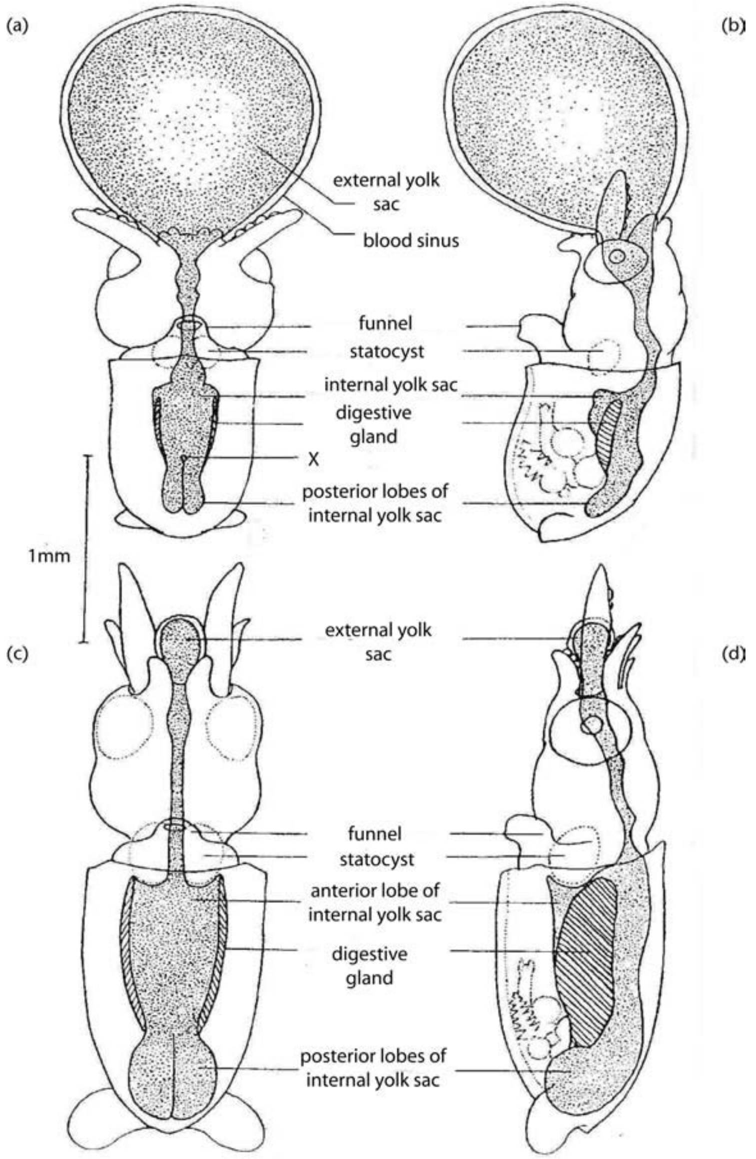


Fig. 10.2 Developmental stages of the squid *Loligo vulgaris* to show the disposition of the external yolk sac in a stage-XVI embryo. (a) Dorsal, and (b) lateral views, and later transfer of the yolk into the inner yolk sac at the point of hatching. (c) Dorsal view, and (d) lateral views. X marks the point at which the fore-gut passes between the posterior lobes of the internal yolk sac. After Boletzky (2002).

continues as a main determinant of the growth rate of the hatchling. Forsythe (1993) models how this effect may so accelerate the growth rate between hatching and juvenile stages that later-hatched broods may overtake those hatched earlier, thus dominating the early recruitment to the adult population.

Eggs develop normally within a defined species-specific temperature range, although at different rates. Towards the upper and lower limits of this temperature envelope,

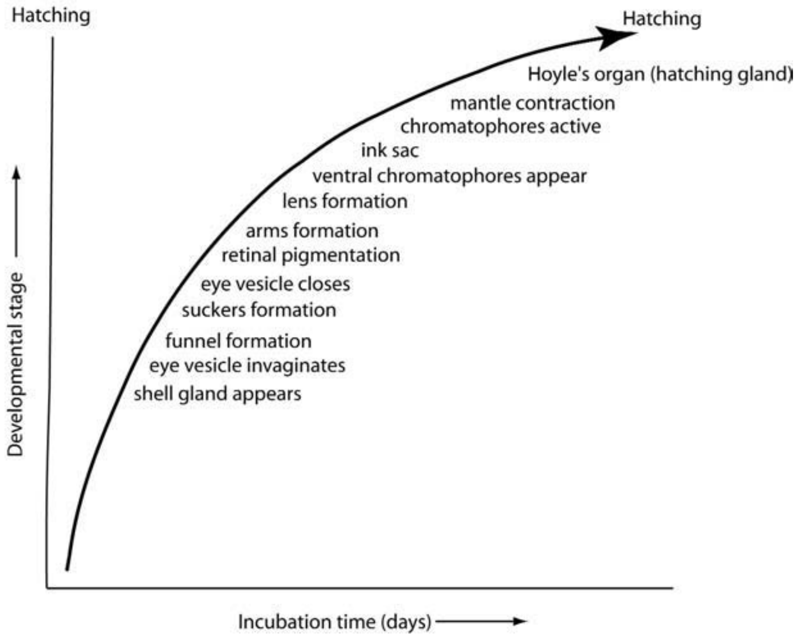


Fig. 10.3 Approximate sequence and developmental timing of significant embryonic features during organogenesis for a typical *Loligo* species (after Baeg *et al.* 1992).

however, the incidence of developmental deformities increases rapidly (Gowland *et al.* 2002a, b). Variations in salinity and the ionic composition of the seawater have a significant effect on embryonic survival and rates of hatching (D'Aniello *et al.* 1989).

10.3 Hatching and hatchlings

When organogenesis is complete, which occurs before all the yolk contained in the outer yolk sac has been absorbed and incorporated, the embryo may be competent to hatch. The process of hatching, or eclosion, when the young are released into the sea, takes place by a combination of muscular contractions, release of enzymes from the hatching gland (organ of Hoyle) and the action of stiff bunches of cilia (Kölliker's tufts). If this occurs before all the yolk has been transferred into the embryo (Fig. 10.5), then there will be loss of nutrient available for embryonic growth since, after hatching, the remains of the outer yolk sac is normally shed (Boletzky 2002). The likelihood of premature hatching is reduced by the tranquilising properties of the perivitelline fluid bathing the embryo and preventing muscular movement (Marthy *et al.* 1976).

Immediately post-hatching the embryo is active and swimming, surviving on the food supplies remaining in the inner yolk sac. Foraging activity may start at once, and many free-swimming hatchlings are competent planktonic predators within hours. This early individual experience becomes incorporated into the development of the nervous system and the learned improvement in behaviour (Dickel *et al.* 1997, 2000). It appears that their capability to locate and attack relatively transparent prey in low

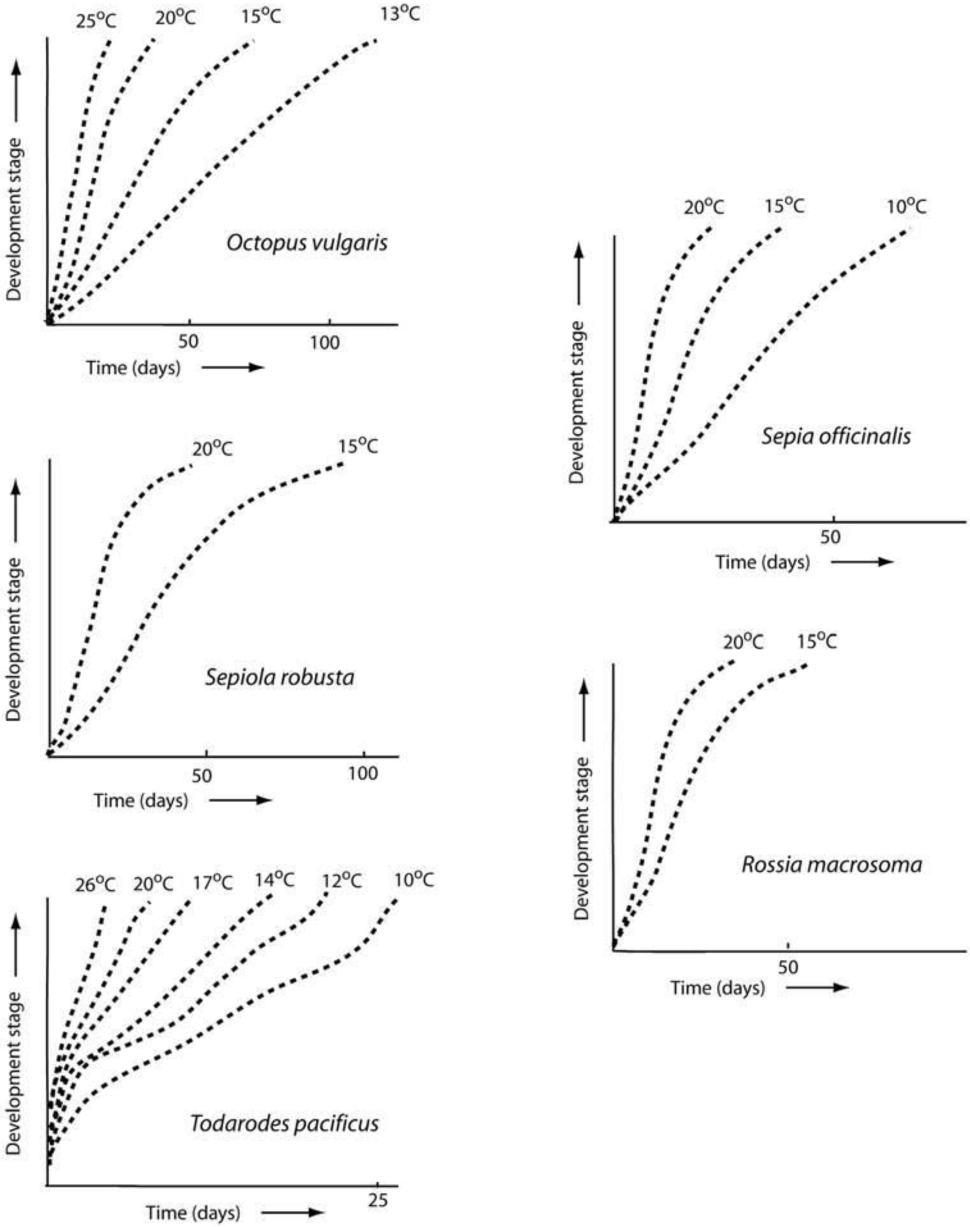


Fig. 10.4 Developmental time as a function of temperature for a range of species (modified after Boletzky & Hanlon 1983, data from earlier sources), and the course of embryonic development for *Todarodes pacificus* at a range of incubation temperatures (after Sakurai *et al.* 1996).

light conditions may be enhanced by sensitivity to polarised light. Shashar *et al.* (1998) found that loliginid squid hatchlings could detect and attack planktonic prey at greater distances when illuminated with polarised light. At this stage their nutrition can be both lecithotrophic and planktotrophic (Boletzky 2003). Although it has been suggested that hatchlings (Vecchione & Hand 1989) and young cephalopods (de Eguilor *et al.*

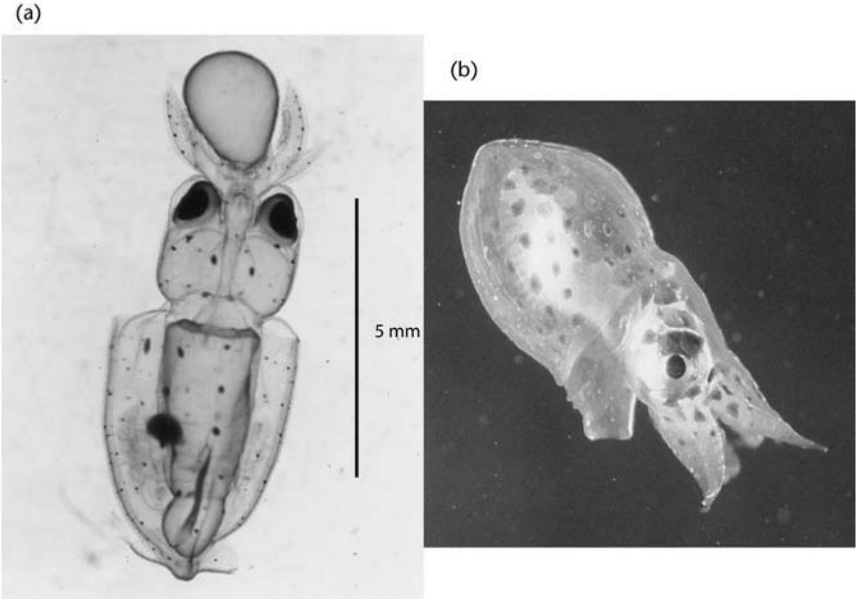


Fig. 10.5 (a) Premature hatchling of *Loligo forbesi* showing remaining outer yolk sac (photograph courtesy of Stephen Craig). (b) A planktonic larval octopus.

2000) are capable of direct absorption of dissolved nutrients from seawater or suspension feeding (see p. 228), it is not clear whether these mechanisms are important compared with the wealth of evidence demonstrating that a rich food source is necessary in the immediate post-hatching phase (Koueta *et al.* 2002; Piatkowski & Hagen 1994; Segawa & Hanlon 1988; Vidal *et al.* 2002). Experiments with hatchlings of *Sepia*, *Loligo* and *Octopus* fed on enriched cultures of the brine shrimp *Artemia* have established the requirement for the diet to be rich in phospholipids, polyunsaturated fatty acids (PUFAs) and cholesterol, with a moderate content of neutral lipids (Navarro & Villanueva 2000).

10.4 Larva and 'paralarva'

The terminology of the developmental stages between hatching and full adult size is inconsistent in the literature. Historically, the term larva has been used to describe the hatchlings and young juveniles, and is still in wide usage (Mangold & Boletzky 1985). The problem arises because, unlike other marine invertebrates, there are no distinctly larval morphological characteristics that are lost or changed by radical metamorphosis during post-hatching development (Boletzky 1974). To accommodate the ecological differences between the early young stages and the adult forms, particularly the planktonic young of many benthic cephalopods, Young and Harman (1988) introduced the term 'paralarva'.

Based mainly on ecological criteria, the term paralarva recognises the distinct lifestyle of the early young without replacing larva, and juvenile, as conventional

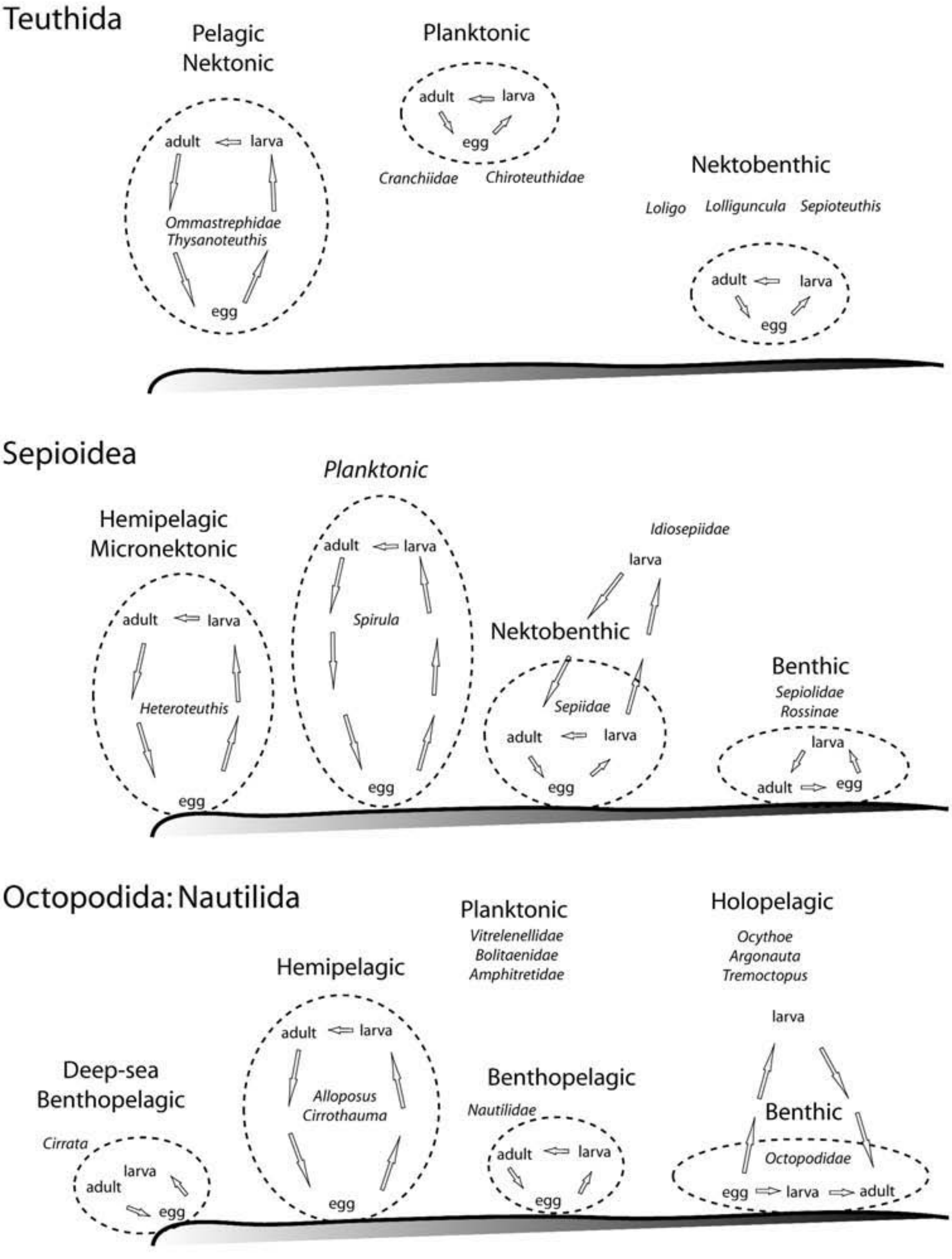


Fig. 10.6 Summary of the habitat relationships between adult, paralarval and egg stages in the main cephalopod groups (after Arkhipkin 1992 and Nesis 1995). Generic and family names in italics.

developmental terms (see Boletzky, 2003, for a comprehensive discussion of the use of this terminology). In Fig. 10.6, the relationships between adult, paralarva and egg stages is summarised. For the predominantly benthic incirrate octopuses especially, the planktonic paralarval form is clearly an ecologically distinct stage (Villanueva *et al.* 1995, 1996; Vecchione *et al.* 2001b).

An exception to the absence of specialised larval forms is found in the hatchlings of the oegopsid squid (Order Teuthoidea, Suborder Oegopsida). In some, such as *Onychoteuthis borealijaponica* (Okutani & McGowan 1969), the arms are incompletely differentiated, and develop only later as the animal grows. Hatchlings of the family Ommastrephidae also appear with some arms lacking and with the two tentacles fused together in a proboscis-like structure (Okutani 1987) which, in *Todarodes pacificus*, only differentiates some 1–2 days after hatching. These distinct early forms are named rhynchoteuthions, and are characteristic members of oceanic plankton. The rhynchoteuthion stage ends with separation of the two tentacles at hatchling sizes up to 15 mm mantle length.

Few studies have been made of the stimuli inducing hatching. For *Loligo* spp. (Paulij *et al.* 1990) and *Sepia* (Paulij *et al.* 1991) in laboratory conditions photoperiod is important, and the majority of hatching occurs during the hours of darkness. At hatching, the larval cephalopod retains the yolk in the stomach, which provides the energy source for the first few days of active life until the transition to dependence on external feeding.

Within a day or so of hatching, the young cephalopod is a competent predator, and on first presentation of live food will attack and consume prey of appropriate sizes. Many species have been hatched in captivity and reared through to the adult stage (Nabhitabhata & Nilaphat 2000; Nabhitabhata *et al.* 2001; Mangold & Boletzky 1985; Boletzky & Hanlon 1983; Hanlon 1990). The main problem for laboratory rearing is the provision of live food of an acceptable kind in the rapidly increasing quantities required by the growing brood, and this has been the main obstacle to routine culture. Significant advances have been made in the managed provision of crab zoeae as food (Villanueva 1994), but young cephalopods are very selective of the prey they will take, with relative size being an important criterion (Blanc & Daguzan 2000). Nevertheless, laboratory studies provide the main source of information on the behaviour and development of the paralarvae.

10.5 Juvenile ecology

The lack of adequate sampling methods and the uncertainties of species identification are major limitations to study of the ecology of these young stages.

Paralarvae are notably rare in coastal plankton samples. Although relatively large and robust, these stages are significantly under-represented. Even in studies targeted at loliginid squid, whose concentrated spawning areas would be expected to yield dense swarms of paralarvae into the water column, very few examples are retrieved (Collins *et al.* 2002), and that means that larval surveys are not widely used for pre-season fisheries assessment (see Chapter 19).

Of the various methods of plankton collection, the bongo net has been the most successful (Diekmann & Piatkowski 2002; Harman & Young 1985; Young *et al.* 1985; Vecchione 1981; Vecchione & Lipinski 1995; Vidal 1994). These rigs consist of paired metal rings holding open two symmetrical cone-shaped plankton nets. Towed from the connection between the two nets, it is the absence of bridle wires crossing the net

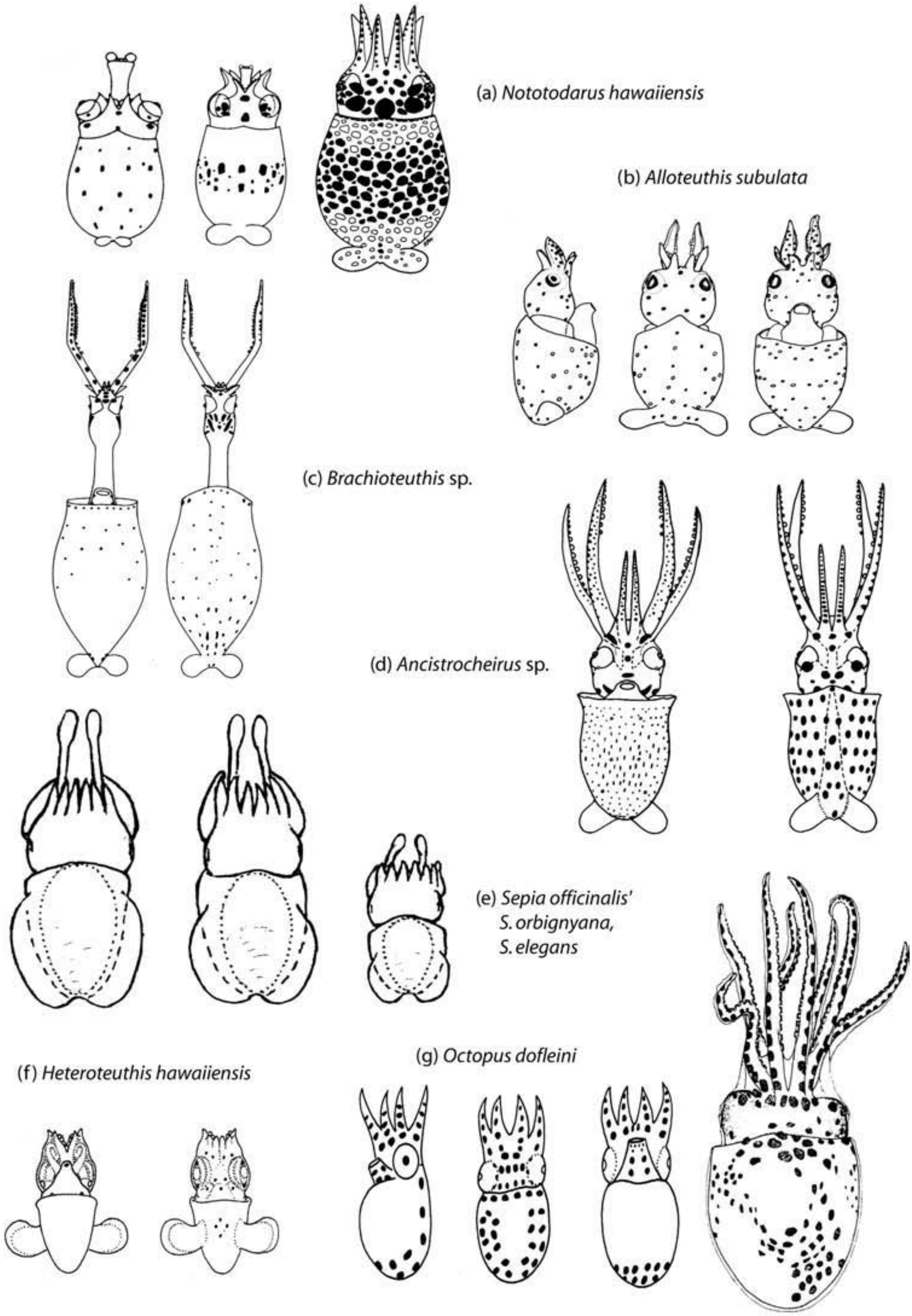


Fig. 10.7 Views of various cephalopod larval types and hatchlings, not to scale (after Sweeney *et al.* 1992 after earlier sources). (a) *Nototodarus hawaiiensis* (Ommastrephidae) – dorsal views of planktonic larvae ranging from 1.7 to 9.2 mm ML, showing the fused tentacles in the early 'rhynchoteuthion' larva. (b) *Alloteuthis subulata* (Loliginidae) – 2 mm ML, lateral, dorsal and ventral views. (c) *Brachioteuthis* sp. (Brachioteuthidae) – 9.2 mm ML, ventral and dorsal views. (d) *Ancistrocheirus* sp. (Ancistrocheiridae) – 2.8 mm ML, ventral and dorsal views. (e) From left to right, hatchlings of *Sepia officinalis*, *S. orbignyana, S. elegans* (Sepiidae). (f) *Heteroteuthis hawaiiensis* (Sepiolidae) – ventral and dorsal views. (g) *Octopus dofleini* (Octopodidae) from left to right – lateral, dorsal and ventral views of a young post-hatchling, 3.0 mm ML, and later young 14.0 mm ML.

aperture which is assumed to be the feature giving these nets their greater efficiency. In mid-water and for larger juveniles or small adults, the usual gear is the Isaacs–Kidd midwater trawl (IKMT), which features an angled depressor plate allowing it to be towed relatively fast while maintaining constant depth (Kubodera 1989). Other succesful gears include the various forms of rectangular mid-water trawls or RMT (Rodhouse & Clarke 1986; Rodhouse *et al.* 1994a). In sheltered inshore waters, the use of light traps originally developed for fish larvae can prove very successful for paralarvae and juveniles (Moltschaniwskyj & Doherty 1994, 1995).

An on-going problem in studies on planktonic and juvenile cephalopods is that of species identification. The difficulties of recognising consistent systematic characters, and the normal variability or plasticity of these features, are exaggerated for paralarval and juvenile specimens. Few of these specimens can be readily identified by the non-specialist, and even the most authoritative of guides (Sweeney *et al.* 1992; Fig. 10.7) admit that ‘it is entirely reasonable to expect that not every specimen in a given collection can be identified to the desired taxonomic level’.

Despite these problems of sampling and identity, the distribution of paralarval forms in oceanographic surveys is an important component of life-cycle studies. For the commercially exploited species characteristic of the shelf break, such as *Illex illecebrosus*, *Illex argentinus*, *Todarodes pacificus*, *Nototodarus gouldi* (see Chapter 18), understanding the timing of spawning, the ecology of the hatchlings, the larval distribution and the growth conditions for the juveniles is of paramount importance to the interpretation of the location and life cycle of the adult population.

10.6 Recruitment

In the terminology of fisheries, recruitment is defined as the number of individuals that reach a specified stage of the life cycle, e.g. metamorphosis, settlement or joining the fishery (Jennings *et al.* 2001). In practice, it is a metric for the relative success of breeding and the contribution made to the continuity of the population. Different measures of recruitment are valid, and the choice often depends on the ease of quantitative measurements. There is no precise biological meaning for recruitment, but use of the term, without an exact definition, is universal in population and fisheries studies. Since so many marine populations breed on an annual cycle, recruitment is often taken to mean the appearance of the ‘young of the year’ into the fished population when they first become susceptible to the fishing gear.

Recruitment is an important concept in the sense that it is an arbitrary measure of population breeding success, and the growth and survival of the resulting offspring to sub-adult and adult sizes. The biological processes that promote breeding, and those leading to the survival of the juveniles, their growth to adult sizes, sexual maturation, and aggregation into breeding concentrations are strongly influenced by the physical and biotic conditions of the environment. These conditions are likely to vary significantly year-on-year, and as a consequence, the strength of recruitment may be highly variable and reflect a combination of impacts on all the stages in the life cycle thus far. Frequently it is the timing of spawning and the ‘match–mismatch’ of the hatchling brood with its planktonic food that are the critical variables (Cushing 1982; Grahame 1987), as well as the influence of the physical environment on the early life stages, rather than the size of the spawning stock (see Chapter 19).

In the case of temperate zone, short-lived, annual species such as many of the common cuttlefish, squid and octopus, there is little or no overlap of generations, so the size of the population depends very largely on the strength of the annual recruitment. This determines the numerical size of the annual population, and is the major factor setting its potential for growth in biomass and the availability of resources to higher predators or fishing. This situation contrasts with that of longer-lived species in which recruitment represents the annual increment in numbers to a much larger population of multi-annual-aged cohorts (see Chapter 13). Inter-annual fluctuations in recruitment strength are of less overall significance in these species.

Among cephalopod populations, the importance of environmental variability to the strength of recruitment is well known (e.g. Bakun & Csirke 1998; Dawe *et al.* 2000; O'Dor 1998b; Waluda *et al.* 1999, 2001), but there is no generally agreed criterion for the recognition of 'recruits'. Typically, recruits are defined simply by body size, especially in trawl fisheries where the net mesh size sets a distinct lower limit to the size of animals caught and the timing of their appearance in the catch. Despite the apparently simple life cycle of most of the fished cephalopod species, analysis of the size- or age-frequency of the catch frequently resolves a series of cohorts (Hatfield 1996; Collins *et al.* 1999), presumably representing successive sub-annual waves of recruitment. The explanation of this episodic recruitment is not usually unclear, but is perhaps often due to the presence of more than one seasonal cohort or to immigration from distant sites.

10.7 Cultivation

With their large eggs and hatchlings compared with other molluscs, direct development, high rates of growth and food conversion efficiency, cuttlefish and octopuses have been the subjects of considerable attention as candidate species for commercial aquaculture. A few squid species have been cultured for experimental purposes, notably the coastal loliginids (see Hanlon 1987b, 1990), and some ommastrephids such as *Todarodes pacificus* (Sakurai *et al.* 1993, 1995) and *Illex illecebrosus* (O'Dor *et al.* 1980, 1982b). Squid generally, as pelagic animals, require too much space, attention and expensive live food for their cultivation to attract commercial interest, although this may change with the increased development of artificial and specially reared food supplies (Castro *et al.* 1993; Castro & Lee 1994; Minton *et al.* 2001). Research into cultivation has been stimulated by the continued uses of cephalopod material for biomedical research (Hanlon & Hixon 1983; Hanlon & Forsythe 1985; Hanlon 1990), which potentially might absorb the high production costs. For nautilus cuttlefish and several small octopus species there is also a lively trade in animals for aquarium display.

Many species of wild-caught cuttlefish and octopus have been maintained and grown in seawater circulation systems. In their 1983 review of the literature, Boletzky & Hanlon standardise use of the terminology as follows: *maintenance*, holding wild-caught late juvenile or adult stages in the same approximate developmental stage for varying periods of time; *rearing*, growing over a period of time without achieving a second generation; *culture*, growing from hatching, through the complete life cycle, to hatching of the first filial (F_1) generation.

10.7.1 Maintenance and rearing

The coastal benthic cuttlefish and octopuses adapt readily to captivity, can be held at high densities, disease problems are minimal and there would be a ready market for the product. In selected situations, where the supply of juveniles and market conditions are suitable, there is a limited commercial supply from cultivated animals. For example, the northwest region of Spain produced 32 tonnes from this source in 1998 and 1999 (FAO 2000, 2001). However, their apparent suitability for aquaculture is blighted by the inherent problem that these animals are predatory and carnivorous. The supply of food for the growing stock is therefore only obtained at considerable effort and cost, which undermines the commercial viability of the process. Despite the high rate of food assimilation and growth (see Chapters 7 and 8), the ecological inefficiency of feeding high-quality marine protein to produce a small quantity of cephalopod species high in the food chain is clear.

For these reasons, the provision and acceptability to cephalopods of alternative non-living food is of significant interest. Pioneering work by Van Heukelem (1977) on the Yucatan octopus *Octopus maya* showed the potential of this species for consuming trash fish (from fish processing) instead of live food, and led to many further critical studies on the diet requirements of captive animals fed in this way (e.g. Garcia & Giminez 2002). A systematic evaluation of artificial food supplies for other species (DeRusha *et al.* 1989) shows that prepared pelleted food or surimi (finely minced fish) are palatable in cultivation conditions, but the growth rates achieved have been only 25–30% of normal (Lee 1994). The general conclusion is that the provision of non-living or artificial food supplies for the growth and rearing of captive cephalopods, although feasible, has not yet reached a point of general commercial viability.

10.7.2 Culture

Egg deposits from cuttlefish, loliginid squid and octopuses are readily obtained either by collection from the wild or, with more difficulty, from those spawned in captivity. The embryonic stages and the factors affecting development have been extensively studied, but a systematic approach to the provision of larval food was missing. Villanueva (1994) and Villanueva *et al.* (1995) then showed that the larvae of *Octopus vulgaris* could be successfully fed in the aquarium on a sequence of crab zoea of appropriate size from hatching to settlement (Villanueva 1994).

The use of both live and frozen food supplies, artificially provided or wild-caught, has allowed successful cultivation of cuttlefish *Sepiella intermis* (Nabhitabhata 1997), *Sepia pharaonis* (Nabhitabhata & Nilaphat 1999; Minton *et al.* 2001) and *Sepia officinalis* (Domingues *et al.* 2001; Forsythe *et al.* 2002), as well as the loliginid squid *Sepioteuthis lessoniana* (Walsh *et al.* 2002), through several generations. These species are valuable commercial products, and it can be expected that there will be further development in this field.

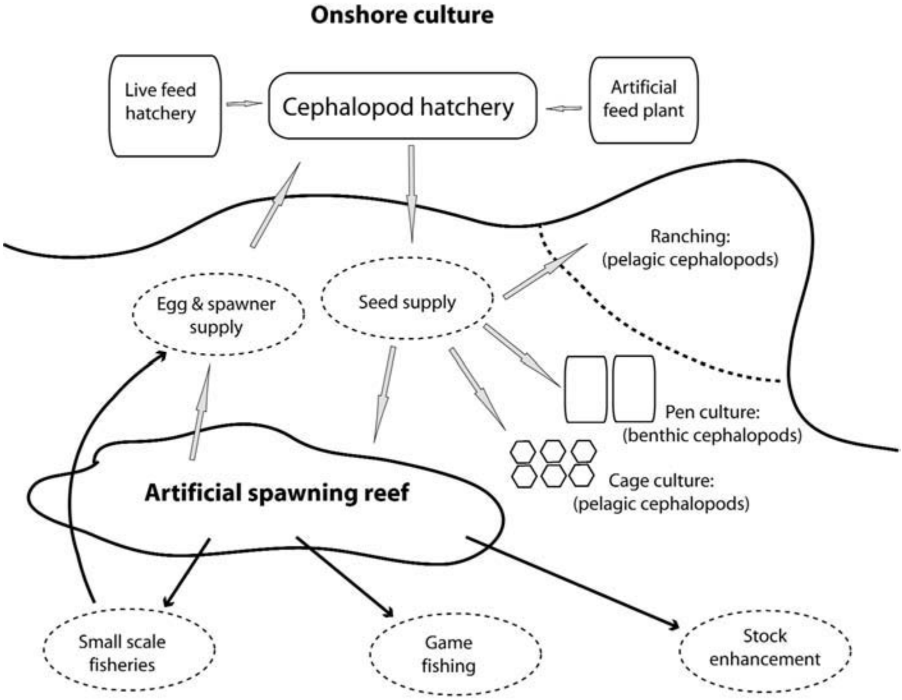


Fig. 10.8 Possible scheme for integrated aquaculture and habitat management in Thailand to give simultaneous production of a variety of cephalopod species (after Nabhitabhata 1994). An on-shore culture facility for hatching and rearing cephalopods, together with associated plants for live and artificial feed, is managed in conjunction with an off-shore reef providing spawn and spawning animals. The reef can also be managed for other purposes such as small-scale fisheries, and the surrounding area provides space for the on-growing of cephalopods to market product.

10.7.3 Integrated aquaculture

In selected areas it may prove possible to integrate the technology of aquaculture with management of the local environment for fisheries. Coastal areas that have traditionally utilised cephalopods may be showing the way with proposals that allow for the wild collection of egg deposits or spawner animals from managed reefs, and the production of hatchlings and juveniles in terrestrial hatchery conditions based on live feed supplies, followed by on-growing in pens (benthic cephalopods), cages or ranched enclosures (pelagic cephalopods). Such a scheme of integrated aquaculture and habitat management, as shown in Fig. 10.8, is proposed as suitable for the production of a combination of cuttlefish, loliginid squid and octopus species.

Aside from the commercial potential, the known environmental consequences of intensive aquaculture associated with feeding animals high in the food chain at high stocking densities suggests that the viability of any large-scale aquaculture industry for cephalopods is still open to question.

Chapter 11

Coastal and shelf species

Summary: The inshore coastal neritic zone, with its mixed seabed substrates of rock sand and mud and highly mixed water column, is the most physically diverse and biologically productive of the marine habitats. The octopuses, cuttlefish and myopsid squid endemic here (e.g. *Octopus*, *Sepia*, *Loligo*) use the close availability of the seabed for attachment of their eggs. The abundance and variety of fish and invertebrate food sources available to them support regional concentrations of great cephalopod species diversity and biomass. Adaptations to life in this inshore coastal environment include the complex prey capture and prey handling mechanisms of octopuses and cuttlefish, exploitation by octopuses of opportunities for shelter by the occupation and improvement of homes or dens, and the use of highly specific colour and pattern displays for crypsis and communication. Underwater observations by divers are beginning to describe the full range and functions of cephalopod behaviour. The coastal octopuses and squid, which are typically associated with the seabed, may extend down the continental slope. Here they overlap with the distribution of octopuses such as *Pareledone*, *Bathypolypus* and *Alloposus*, of which some species range continuously downwards to <3000 m. Squids of genera such as *Illex*, *Todarodes*, *Todaropsis* and *Nototodarus* (family Ommastrephidae) comprise major populations in the shelf-break zone. Here, the oceanographic features associated with western and eastern boundary currents and the associated mesoscale and downwelling features such as eddies and upwelling cells promote enriched food supplies. Egg masses of these species are produced in fragile gelatinous masses thought to float at depth on the horizontal boundary between water masses of different densities. Mechanisms for the maintenance of these populations geographically within the powerful current systems involve postulating long distance return migrations to breeding areas. These ommastrephid squid are present seasonally over the continental shelf in large shoals of young animals making use of the rich feeding conditions for growth and maturation.

The cephalopod fauna of the continental shelf and coastal regions includes all of the familiar forms, i.e. those whose life cycles, ecology, physiology and behaviour are best known, and which are the sources of most of the generalisations which can be made about cephalopod biology. Although oceanic genera such as *Todarodes* and *Illex* may make major migratory incursions over the shelf and into coastal waters, this chapter will review the ecology of those cephalopods in which there is dependence on the bottom for attachment of the eggs at spawning. This remit includes the incirrate octopuses (*Octopus*, *Eledone*, etc.), the myopsid squid (*Loligo*, *Sepioteuthis*, etc.) and the sepeiods (*Sepia*, *Sepiola*, *Rossia*, etc.). The neritic marine province is conveniently defined as that part of the oceans overlying the continental shelf, normally limited to a depth range down to about 200 m. These essentially coastal animals comprise many valuable fisheries and share a number of ecological themes relevant to their exploitation.

The cephalopod families and genera typical of the neritic habitat and having the greatest number of species, as listed by Sweeney & Roper (1998), are the Octopodidae (23 genera, 194 species, >100 species of *Octopus*), the Sepiidae (3 genera, 102 species, >100 species of *Sepia*), the Sepiolidae (15 genera, 61 species, 13 species of Sepiola) and the most speciose of the squid families, the Loliginidae (5 genera, 43 species, 14 species of *Loligo*). Clearly the richness and diversity of the coastal zone has promoted extensive speciation in these recent cephalopod types (Fig. 11.1).

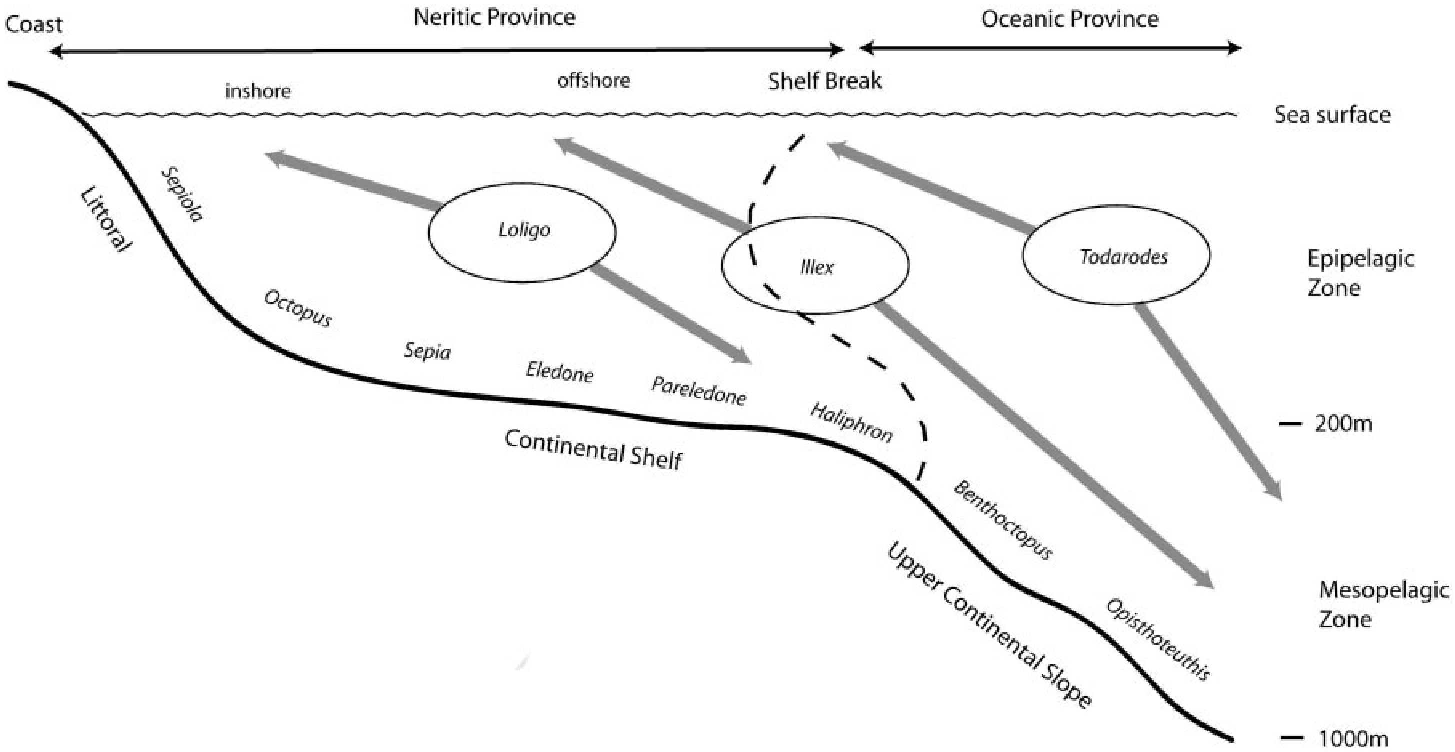


Fig. 11.1 Distribution with habitat and depth of selected cephalopod genera characteristic of the neritic zone and the shelf slope (not to scale). Squid of the family Loliginidae are characteristic residents of the neritic zone for their entire lives; members of the family Ommastrephidae such as *Illex* and *Todarodes* make periodic but major feeding excursions over the shelf. The benthic and epibenthic cuttlefish and octopuses are shown sequentially over the seabed for clarity, but in reality they have overlapping depth ranges over the continental shelf and into the upper region of the continental slope.

11.1 The coastal habitat

Although the area of the continental shelf accounts for only about 3% of the global ocean area, the marine environment of the neritic province is the most diverse and generally productive of all marine habitats. The reasons for this include:

- the high proportion of the habitat falling within the photic zone of sunlight penetration, and hence primary production by marine algae;
- the contribution to habitat diversity of the various rock and sedimentary bottom types;
- the inputs of inorganic and organic nutrients from terrestrial sources via rivers and other run-off, including contaminants;
- the well-mixed nature of the water column, due mainly to tidal- and wind-generated movements re-suspending nutrients from the sediment and contributing to their rapid cycling through food chains;
- the generation of rich microbial food sources in the sediments which supports the dense and diverse benthic fauna of invertebrates and fish;
- the importance of the rich diversity of bottom-living animals to the food sources available for predatory cephalopods and their input of larval and juvenile forms into the plankton.

Benthic marine habitats range from steep rocky canyons to fields of broken boulders, and from highly mobile coarse sands to undisturbed plains of soft fine mud, and include kelp forest, coral reef and mangrove swamp. They extend from the shoreline to the shelf break, an average distance of 130 km from the coast, ranging from a few kilometres off California to >1000 km in the Arctic (Pinet 1992). These environments are subject to:

- relatively wide temperature fluctuations;
- lowered salinity due to estuarine influences or temporary inundation by fresh water;
- high loads of sediment settling from the water;
- relatively high current speeds and tidal oscillations;
- violent water movements due to storm forces;
- erosion by coastal ice sheets or grounded icebergs.

11.2 Ecology of the coastal forms

The full range of coastal habitats is colonised somewhere in the world by cephalopods, although there are distinct preferences for habitat type. Cephalopods are not usually present in water of lowered salinity. Exceptions are loliginids such as *Lolliguncula brevis*, a common species in the Gulf of Mexico in water down to at least 22‰ S. On the fringes of the Indian Ocean and seas of the Indo-Pacific is another species, *Loligo duvauceli*, which may be densely present as juveniles in lower salinity water over inshore mud banks and fringing mangroves. In the western Baltic Sea, where salinity may be as low as 16‰ S, *Loligo (Alloteuthis) subulata* occurs seasonally, but most sea areas of lowered salinity are not colonised at all, and there are no cephalopods endemic to the estuarine environment. Smaller octopods, particularly of tropical regions, may be widely present in the intertidal zone, sheltering in pools or under small stones and rocks when the shore is exposed by the tide. Perhaps because they avoid water that is truly estuarine, inshore cephalopods have seldom been examined for the effects of human pollution. However, in those areas where the bottom fauna has become contaminated by organic pollutants (Lee *et al.* 1997) or radionuclides (Yamada *et al.* 1999) squid have been found to be also as susceptible to their uptake.

All the octopodids, sepioids and loliginid squid of the shelf have strong associations with the sea bottom. Their eggs are encapsulated in tough protective sheaths and firmly fixed to a surface for the duration of development. Attachment is typically on to the hard surfaces of rocks and stones, but eggs may also be attached to the stipe of kelp plants, and to artificial surfaces such as fishing traps and lines, buoys and rafts. Some of the loliginid squid species may use open sandy bottoms for spawning, vigorously inserting the attachment end of each string into the sediment where small pebbles or shells may form sufficient attachment (*Loligo vulgaris reynaudi*, Sauer *et al*. 1992, 1993). The localised availability of bottom substrate for suitable breeding, coupled with the benefit obtained from the simultaneous presence of many breeding animals, leads to major spawning aggregations of sepioids and loliginids in specific areas. Conspicuous among these species is *Loligo opalescens*, which congregates in immense spawning aggregations at certain times and in highly localised areas (Fields 1965) along the California coast, where they are highly vulnerable to fishing. Seasonal movement to selected breeding areas by cuttlefish may give rise to pronounced coastal migrations, for example those of *Sepia officinalis* (Boucaud-Camou & Boismery 1991).

In addition to the use of the bottom for spawning, the coastal cephalopods are mostly bottom feeders. The rich diversity of other invertebrates and fish associated with the bottom provides ideal hunting grounds for predators. Octopuses and cuttlefish hunt actively on prey species such as shrimps, crabs, shelled molluscs and fish, using visual and chemical cues. Octopods, in particular, have evolved a sophisticated range of behaviours and prey-handling mechanisms to deal with the diverse problems presented by the variety of prey available. The loliginids also make full use of the water column for feeding. Studies on *Loligo forbesi* and *L. vulgaris* (Pierce *et al.* 1994c) have shown that fish or pelagic crustaceans such as euphausids may dominate in the diet (see Chapter 14). These loliginids are also strongly diurnal in behaviour, usually resting or feeding close to the bottom during day, and dispersing upwards into the water column through the hours of darkness.

The physical nature of the bottom is also highly significant for the shelter it offers from superior predators. Octopuses use the shelter of crevices and holes temporarily to escape from predators. They also establish semi-permanent homes, which may be improved by drawing in other material such as small stones. These are operational bases from which the octopus makes its feeding excursions, returning to the home to disarticulate and ingest the prey. Some octopuses and typically the cuttlefish are able to burrow into the surface of soft sediments, forming a depression or pit below the surface and partially covering themselves with loose sand.

11.3 Adaptations to the coastal habitat

All the coastal forms are active, muscular and strong-swimming. None have the flaccid body form and sluggish movements of the mesopelagic and bathybenthic types. Clearly their mode of life is adapted to the neritic environment with its relatively strong water currents. The incirrate octopods, cuttlefish and loliginid squid all have a tough corneal covering to the eyes, which is suggested to be an early adaptation to protect the eyes from suspended sediment.

11.3.1 Shelter

Homes, dens or lairs are the terms used to describe the stable shelters occupied by most coastal octopus species. Numerous accounts of the behaviour of octopus in homes (e.g. Lane 1957; Cousteau & Diolé 1973) suggest that this is a normal and widespread behaviour. Homes constructed or improved by the accumulation of stones or other objects by *Octopus vulgaris* (Woods 1965; Yarnall 1969) are readily recognisable by divers. Less well known are the homes excavated in firm sand or mud by *Octopus dofleini* (Hartwick *et al.* 1978a) and *O. macropus* (Hochberg & Couch 1971), or in coral rubble (*O. cyanea*, Yarnall 1969). The distinction is carefully drawn by Hanlon & Messenger (1996) between this *burrowing* behaviour of octopuses to form stable homes, and the *burying* behaviour of cuttlefish in sand for temporary concealment.

Relatively little information is available on the occupancy rates of octopus homes. Diving studies such as those by Altman (1966–67) have recorded continuous occupation of the same home in the field by *Octopus vulgaris* for 4 days, while Kayes (1974) found some holes to be occupied by the same animals for at least 10 days. Observing *O. cyanea* in a large pool, Yarnall (1969) found that individuals occupied the same home for up to 23 days. There is no clear evidence for the establishment of the home and its surrounding feeding grounds as an individual 'territory', although Woods (1965) observed two animals apparently disputing the occupancy of a home, and it is possible that these complex animals exhibit a degree of individual preference in home selection (Cigliano 1993; Mather 1994). Experiments on pairs of male *Octopus vulgaris* in captive conditions in which two homes were provided found that neither home was exclusively occupied by one animal, although usually one was preferred and most likely to be occupied by the larger animal (Boyle 1980). A size-based dominance hierarchy in the use of space (not homes) has been described in *Octopus* (Mather 1980) and *Sepia* (Adamo *et al.* 2000).

In a field experiment, Hartwick *et al.* (1978b) removed *Octopus dofleini* from dens within a study area, measured the size of all dens and recorded their re-colonisation by immigrating octopuses. There was a clear positive relationship between den volume and the size of the octopus colonising it. Moreover, small octopuses tended to be found in newly dug dens, with the larger specimens being more likely to occupy natural dens. Presumably the main function of this behaviour is to provide secure protection from predators. It is carried to extremes in the tiny *Octopus micropyrsus*, that is known only from within the holdfasts of the giant kelp *Macrocystis* of the California coast (Hochberg & Fields 1980).

11.3.2 Camouflage

There are many other ways in which the coleoids use the characteristics of the bottom to hide themselves, thus using it as primary defence against predators. Hanlon & Messenger (1996) classify and summarise the various means of hiding as described below.

11.3.2.1 Background resemblance

Matching of overall body brightness and colour to that of the background by the selective use of chromatophores and the underlying reflecting elements is a common form of disguise amongst octopuses. Octopuses have been shown to be sensitive to small differences in the brightness of their background, but it is not clear how colour matching can occur, unless the colour contrast presented differs in colour density, since they appear to be colour-blind (Messenger 1977a). The grading of pattern scale, i.e. the relative areas of light and dark patches, also makes an important contribution to the degree of background resemblance (Packard 1969; Packard & Sanders 1969, 1971; Packard & Hochberg 1977; Hanlon & Messenger 1996). Octopuses have been seen to hold adventitious material against themselves, such as weed or shells, to contribute to their resemblance to their background (Packard 1969). The small sepiolid *Euprymna scolopes* has a specially sticky epidermis to which sand grains adhere, helping to hide its appearance when out hunting in daylight (Shears 1988).

11.3.2.2 Countershading

Most marine species active in the water column have some counter-shading pattern distribution to reduce the effect of silhouette or shadow due to the generally downwelling light. Even benthic octopuses (*Octopus*, *Eledone*) have typically lighter ventral surfaces, and in *Sepia officinalis* and *Lolliguncula brevis* this appears to be due to specific arrangements of iridophores (reflecting elements) in the skin (Hanlon & Messenger 1988; Hanlon *et al.* 1990). Cuttlefish resting on the bottom eliminate their shadow by using the edge of fin the along the body and the flange on the ventro-lateral part of the 4th arm (Hanlon & Messenger 1988).

11.3.2.3 Disruptive colouration

Cuttlefish, most notably *Sepia* spp., use disruptive colouration to break up the outline of the body shape and render themselves almost invisible against backgound patterns (Corner & Moore 1980; Mauris 1989; Roper & Hochberg 1988). Octopuses frequently combine disruptive pattern elements with a general background resemblance pattern. Loliginids also use this form of crypsis, and Hanlon and Messenger (1996) point out that species such as *Sepioteuthis sepioidea*, which spends a large proportion of its time close to the variegated bottom of the coral reef, has the greatest repertoire of disruptive pattern components.

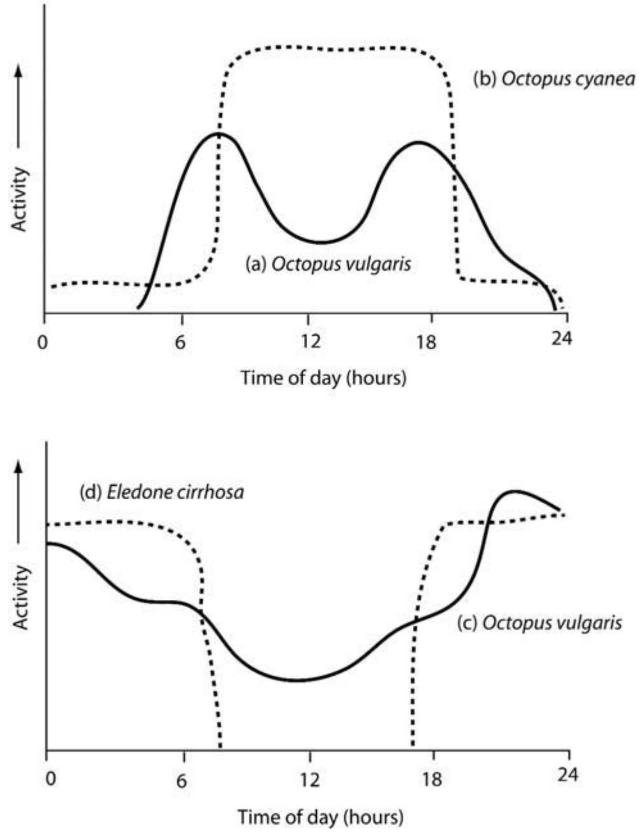


Fig. 11.2 Patterns of daily activity in shallow-water octopuses. (a) Observations of Mediterranean *Octopus vulgaris* alert and hunting in the natural environment (after Kayes 1974). (b) *O. cyanea* in Hawaii (after Yarnall 1969, dashed line). (c) Daily rhythm of *O. vulgaris*, unfed, in laboratory conditions (Wells *et al*. 1983a). (d) Active behaviour of aquarium *Eledone cirrhosa* (after Cobb *et al*. 1995, dashed line).

11.3.2.4 Deceptive resemblance

An extension of the general resemblance pattern principle is when an animal combines elements of colouration, pattern and body shape or posture to resemble specific objects in the environment. To the human observer, young *Sepia* often resemble small encrusted stones, the sepiolid *Idiosepius pygmaeus* is described as closely resembling floating seagrass debris (Moynihan 1983; Natsukari 1970), and the loliginid *Sepioteuthis sepioidea* can resemble branching soft corals or seaweed (Moynihan & Rodaniche 1982). Some of the coral reef squids and octopuses may show strong distinctive patterns of longitudinal stripes considered by some authors (Moynihan & Rodaniche 1982; Hanlon & Messenger 1996) to resemble the patterns of striped reef parrotfishes.

It is in the rich variety of displayed patterns and other behavioural reactions to predators and prey (Hanlon & Messenger 1996) that the full range of cephalopod behavioural adaptations to the shallow-water habitat can be fully appreciated. There is apparently a high selective advantage in the characterisitics of camouflage, signalling, escape jetting and inking in all the shallow-water species. In tropical waters, recognition of the rich variety of patterning and the capabilities of the system for rapid change and signaling is being used as an essential tool for species identification (Roper & Hochberg 1988; Norman & Sweeney 1997), in contrast to traditional systematic descriptions based only on the characters of preserved specimens. In the giant cuttlefish, *Sepia apama*, small males avoid the attention of large males and gain access to females by using their pattern capabilities to mimic the opposite sex rather than signal aggressively to the guarding male (Norman *et al.* 1999). Shallow-water tropical octopuses have especially excellent disguise capabilities (Hanlon *et al.* 1999b), and some specialise in the mimicry or 'impersonation' of other species such as fish and sea snakes (Norman 2000).

11.3.3 Feeding

Aristotle (*c.*330 BC; translated by D'Arcy Wentworth Thompson 1910) noted that 'Molluscs are all carnivorous; and of molluscs the calamary and the sepia are more than a match for fishes even of the large species. The octopus for the most part gathers shellfish, extracts the flesh, and feeds on that; in fact, fishermen recognise their holes by the number of shells lying about'. This octopus habit of returning from feeding excursions to the home and there disarticulating the skeletons of Crustacea, and opening the shells of molluscs and removing the flesh, is the major source of data on octopus diets and their dependence on the diverse benthic fauna.

Field studies on species such as *Octopus vulgaris* (Smale & Buchan 1981; Guerra & Nixon 1987), *O. dofleini* (Hartwick *et al.* 1978a), *O. briareus* (Aronson 1989) and *O. bimaculatus* (Ambrose 1983, 1984) have established the wide range of benthic species normally taken as prey and the apparent preference for crustaceans. These findings are supported by numerous observations on octopuses in captivity (e.g. *O. vulgaris*, Buchan & Smale 1981; *Eledone cirrhosa*, Boyle & Knobloch 1982a, Boyle *et al.* 1986).

The intrinsic biological interest of the elaborate detail of prey-handling mechanisms and their significance to the trophic ecology of octopuses have given rise to many studies on their hole-drilling behaviour (e.g. Arnold & Arnold 1969; Ambrose 1988b; Mather & Nixon 1990; Nixon & Maconnachie 1988; Boyle 1990a; Grisley *et al.* 1996; Runham *et al.* 1997; Harper 2002). Complex mixtures of toxins (Cariello & Zanetti 1977; Dulhunty & Gage 1971; Freeman & Turner 1970; Key *et al.* 2002; McDonald & Cottrell 1972; Songdahl & Shapiro 1974) are used to immobilise the prey and enzymes to loosen and extract the flesh (Grisley & Boyle 1987, 1990; Morishita 1978).

Crustacea are generally susceptible to octopus predation; even the large and powerful lobsters will fall prey to octopuses of about their own weight. Ross (1971) found that hermit crabs (*Dardanus arrosor*) are effectively protected from attack by octopus (*O. vulgaris*) when carrying the commensal sea anemone *Calliactis parasitica* attached to the shell. Remarkably, this behaviour on the part of the crab is actively stimulated in response to chemical traces of octopus in the seawater. Ross & Boletzy (1979) go on to show that in the aquarium, *D. arrosor* loses its behavioural activity towards *C. parasitica*, but that the association is restored when effluent water from a tank containing *O. vulgaris* is run into a tank containing crabs and anemones. Repeating the experiment with three different *Octopus* species and *Sepia* showed that all were effective in restoring the association, apparently solely by chemical cues. The results go some way towards explaining the apparently facultative nature of the commensal association in the field between the crab and the sea anemone; the presence of octopuses is also required if the association is to be maintained.

Direct observations of feeding behaviour in sepioids are less readily available. In cuttlefish (*Sepia*), feeding seems to involve a 'lie in wait' tactic. Lying on the sandy bottom, partially covered with sediment flicked over the body by the lateral fins, the cuttlefish waits for suitable prey to approach. Sometimes the first pair of arms is waved just above the surface, apparently to provide a source of attraction for curious prey. When close enough, the cuttlefish emerges from the sand and, hovering just above the bottom, manoeuvers into range for an attack principally using visual cues (Messenger 1968). Although scuba divers in the field and observers in aquarium conditions typically point to shrimps and other small crustaceans as prey of *Sepia*, Nigmatullin (1975) records a significant proportion of commercial fish species in the diet such as *Pagellus* and *Dentex*. Although descriptions of feeding behaviour for loliginids are similarly lacking, many authors (Collins *et al.* 1994; Hixon 1983; Macy 1982; Lipinski 1987; Martins 1982; Pierce *et al.* 1994c; Rocha *et al.* 1994) show the dominance of fish species in their diet.

For each of the typically neritic groups of cephalopods, the incirrate octopuses, sepioids and the loliginid squid, the diverse benthos and the associated demersal fish fauna is their major source of food (see Chapter 14).

11.3.4 Diurnal behaviour

In the shallow-water environment (although also in the open ocean), where light intensity is a strong and regular, diurnal patterns of activity are expected. In a diving study, Altman (1966–67) found *Octopus vulgaris* to be most active at night and in daylight, with relatively little activity at dawn and dusk. Working on home occupancy in the same species, Kayes (1974) found the octopus to be actively hunting at night with only limited excursions during the day. A similar pattern of nocturnal activity was found for *O. joubini* by Mather (1988). Other studies have shown a preference for twilight in *O. cyanea* (Yarnall 1969), and for the daytime activity of *O. vulgaris* in Bermuda to be concentrated in the morning between 08.00 and 10.00 h (Mather 1988). The direct influence of moonlight is implied by Voight (1992), who found that fewer specimens of *O. digueti* were foraging in the intertidal zone during moonlit nights. Species-specific behavioural differences with respect to light may be an important factor in the ecology of benthic octopuses by temporal spacing of habitat use among sympatric species (Houck 1982; Norman 2000).

The shoaling behaviour of loliginids in shallow water is often related to diurnal changes in light intensity. Shoals of the Caribbean reef squid *Sepioteuthis sepioidea* generally disperse at dusk and re-form by dawn (Moynihan & Rodaniche 1982). In *Loligo* species, however, shoals may occur day or night (Hanlon & Messenger 1996). Moonlight causes squid shoals to go deeper, while in some fisheries (*Loligo opalescens*) artifical lights are used at night to cluster squid around fishing vessels. Diurnal light rhythms even affect the egg stages of coastal species. In aquarium studies with controlled photoperiods, the eggs of *Loligo vulgaris* and *L. forbesi* (Paulij *et al.* 1990) and *Sepia officinalis* (Paulij *et al.* 1991) each showed an increased incidence of hatching during the period of darkness.

11.3.5 Reproduction

The use of the substratum for the attachment of the spawned egg masses is the key to the ecology of the truly coastal neritic cephalopods. The incirrate octopuses seek secluded locations for spawning, e.g. under natural overhangs, in rock crevices, or within artificial enclosures such as pots or cans. The female lays the spawn in a tightly localised area which she can then occupy and protect the eggs. During the period of development, she aerates them with seawater, maintains them free of epigrowths and defends them against predators. To protect herself during this period she needs a defensible space within which to lay the eggs. Some elements of competition for space in the use of homes have been described (Boyle 1980), and it seems a reasonable speculation that in some localities, the scarcity of suitably protected sites for spawning may be an important limitation on the breeding female population. Certainly, brooding females are likely to be found occupying fishing pots set for octopus, and the female requirement for brooding sites may underlie the imbalance in the sex ratio at capture.

Cuttlefish and sepiolids have stoutly protected egg capsules. Perhaps as a consequence they are less selective over their spawning sites, and females are not known to remain after spawning to protect the eggs. Rock surfaces, stones, seaweeds and assorted debris may all form suitable sites for sepiolid spawning.

The loliginid squid lay their very conspicuous finger-like spawn capsules attached to a variety of substrates without apparently seeking especially sheltered sites. The same range of sea bed surfaces are used, together with such introduced materials as anchors, ropes, rafts, buoys, wooden and netting traps, etc. Species such as *Loligo opalescens* off California are known to breed in dense aggregations at highly specific sites within the overall distribution range (Fields 1965; Butler *et al.* 1999). Probably the function of these spawning aggregations is more connected with concentrating the population for mating and fertilisation than with any very specific advantages offered by the site for spawn attachment. Indeed, the closely related *Loligo vulgaris reynaudi* seems quite careless of the security of the individual spawn deposits. This species breeds on a series of spawning grounds inshore around the coast of South Africa. The spawned egg capsules are thrust by the female into mobile sandy bottoms, where many of them are loosened and lost by the activities of subsequently spawning females or current-driven sand movement. Those loliginid squid which aggregate for breeding can exhibit a complex repertoire of pattern changes adapted to mating strategy (Hanlon *et al.* 1994, 1999a).

Localised migrations are typical of the coastal species. Mangold (1963) found that the octopuses *Octopus vulgaris* and *Eledone cirrhosa* made onshore shallow-water migrations in spring to concide with breeding activity. *Sepia officinalis* and other sepioids also make onshore shallow-water migrations to favoured breeding areas, while the highly targeted breeding migrations of the loliginid squid are well known and exploited by fisheries. These breeding migrations are considered further in Chapter 16.

11.4 Susceptibility to fisheries

Cephalopods in coastal waters are largely demersal in habit. Fishing activities exploit this dependency with the use of targeted methods such as baited and unbaited traps for octopus and jigs for squid, as well as by general methods for demersal species such as trawls. These general and specific fishing methods and the impacts of fishing are considered in Chapter 16.

11.5 The shelf break

The true coastal neritic species are not strictly limited to the depth of the shelf. The octopus *Eledone cirrhosa* has been recorded at least to 770 m (Massy 1928), and *Loligo forbesi* egg masses have been trawled up from 507 m (Lordan & Casey 1999), where they were presumed to have been laid. Remarkably, *L. forbesi* is also present in fishable quantities in the Azores, 1500 km off the European coast. These volcanic islands fall steeply to >2000 km deep within a few kilometers of the coastline, and known fishing grounds (jigging) extend out to the 500-m isobath (Martins 1982; Hanlon 1987a). There are sufficient population and genetic differences between the populations to suggest long isolation from each other (Pierce *et al.* 1994e; Brierley *et al.* 1995; Shaw *et al.* 1999), and the finding of fresh egg mops (Porteiro & Martins 1992) further supports the view that the Azorean population is self-maintaining in oceanic water.

11.6 Occupation by ommastrephid squid

The edges of the continental shelves, at about the 200 m isobath, are locations where the highly mixed water of the shelf abuts the more stable oceanic water, or fronts the residual currents of the oceanic or tidal circulation. For nektonic squid and fish, these shelf-break areas comprise particularly favourable habitats owing to a combination of at least three types of environmental factors (Bakun & Csirke 1998):

(1) enrichment of the food supply by physical processes (upwelling, mixing, etc.);
(2) the opportunity for a concentrated patch structure of food particles to accumulate (stable structure, convergent flow patterns, frontal formations, etc.);
(3) flow mechanisms that enable a population to maintain itself, through adaptive responses, in a continually moving fluid medium.

The hydrography of the shelf break forms a high-energy, highly variable environment. Members of the squid family Ommastrephidae have exploited this habitat with adaptations to lifestyle and distribution that both maintains them within the shelf-break environment and provides them with opportunities to exploit its productivity and the rich feeding grounds of the adjacent shelf. Particularly in those zones of the world where western boundary currents create powerful shear and mixing forces between oceanic and coastal waters, the ommastrephids comprise major global fisheries. Particular examples are *Illex illecebrosus* off the eastern coasts of the USA and Canada, *Illex argentinus* off the eastern coast of Brazil and Argentina, *Todarodes pacificus* in the Japan Sea, and *Nototodarus* spp. of the western Pacific and New Zealand. It has been suggested (Nigmatullin & Laptikhovsky 1994) that the reproductive strategy of these offshore ommastrephids is more K-selected than the true oceanic forms (e.g. *Ommastrephes*, *Sthenoteuthis*, *Dosidicus*, see Chapter 12). They have generally lower fecundity and slower growth rates, and are thought to represent the more primitive evolutionary strategy within the family.

11.7 Pelagic egg masses

The life cycle of the ommastrephid squid seasonally present over the continental shelf is completed in deep water offshore. Slight differences in temperature or salinity throughout the water column partition the pelagic environment vertically or horizontally. These differences give rise to boundaries between water masses characterised by step density gradients. The ommastrephid squid which utilise these environments produce pelagic egg masses of close to neutral density in sea water. This enables the large gelatinous mass of eggs to retain its location in the water column by floating at the interface between water layers of slightly different densities, the isopycnic surface or pycnocline.

Direct evidence for the nature of these pelagic egg masses is hard to come by because their fragile gelatinous nature makes them difficult to sample. In captivity, female *Illex illecebrosus* (O'Dor & Balch 1985) have been seen to extrude an egg mass that, once fully hydrated, was almost neutrally buoyant. In a natural environment, Bower & Sakurai (1996) have seen the process underwater for *Todarodes pacificus*, brought the egg masses into captivity and estimated the contents at <200 000 small eggs. This mode of formation of large pelagic egg masses (<1 m diameter) is assumed to be the normal pattern for the family Ommastrephidae and to be the principal way in which their life cycle can be completed within the hydrographic dynamics of the shelf break (Sakurai *et al.* 2000).

11.8 Life cycle and habitat dynamics

Details of the interaction between the short cephalopod life cycle and the strong water movements in these frontal formations are uncertain for most species. There is little doubt, however, that many ommastrephid squid species exploit the opportunities for production arising along the shelf break, and that this pattern of association is typical at the margins of all major ocean systems.

A schematic general model describing how squid paralarvae, hatching from the egg mass 'floating' mid-water off the shelf at the isopycnic surface (Fig. 11.3), can recruit

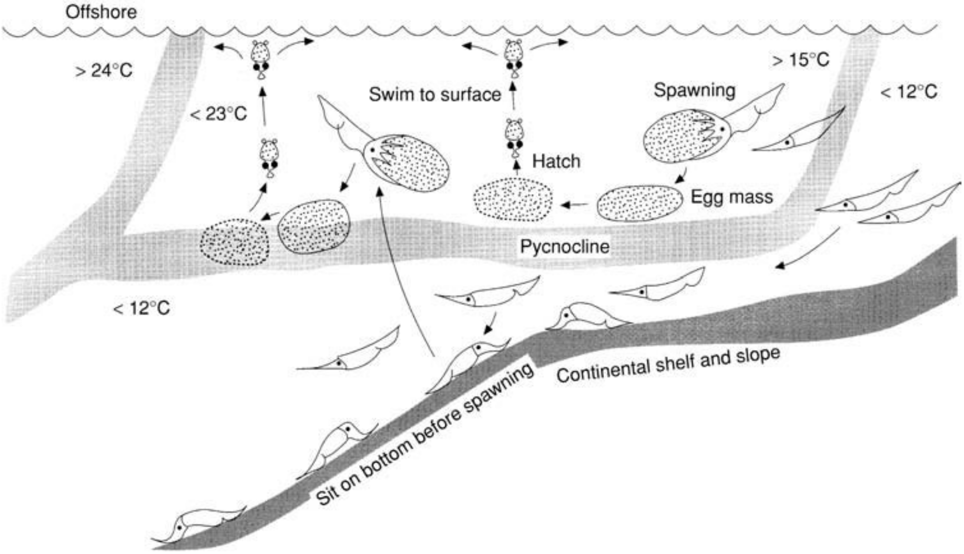
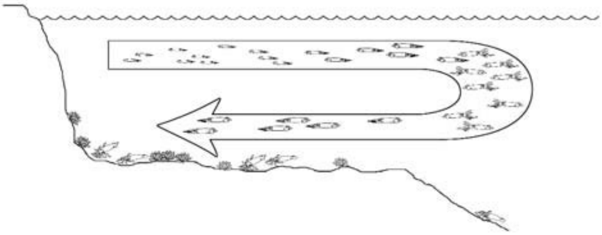


Fig. 11.3 Schematic view of the reproduction of *Todarodes pacificus* showing the spawning of gelatinous egg masses 'floating' on the isopycnic surface which is presumed to be typical of many ommastrephid squid (reproduced with permission from Sakurai *et al.* 2000). Larvae ascend into surface waters. Growth in the rich convergent features at the interface between oceanic and coastal waters is followed by the ontogenetic descent of sub-adults to mature and spawn at depth, off the continental shelf.

into the rich convergent features at the surface is provided by Bakum & Csirke (1998, based on *Illex illecebrosus* in the Gulf Stream of the northwest Atlantic). The model links the location of paralarvae in surface waters (Young 1985) with the major fisheries on growing squid migrating along frontal processes at the shelf edge (Sakurai *et al.* 2000), and the laboratory evidence suggesting that the gelatinous eggs masses will be neutrally buoyant at isopycnal surfaces. To confirm this model of the life cycle, however, supporting evidence for the ascent mechanism of the paralarvae and the descent of the sub-adults is still required.

Along-shelf movements of ommastrephid squid and their associated fisheries are well documented (see Plates 2–8). These current-assisted migrations are directional, and carry the growing juvenile squid progressively further from the areas of hatching. Individuals of *Todarodes pacificus*, *Illex illecebrosus* and *Illex argentinus* can be found maturing along their migration routes, but no naturally spawned egg masses have been found, although captive individuals of *T. pacificus* have been observed to mate and spawn (Bower & Sakurai 1996). Certainly, such fragile spawn masses floating in mid-water are likely to be destroyed rather than captured by nets, but their complete absence in samples also leads to the assumption that generally there must be a return migration of maturing adults to their natal breeding area, and that spawning occurs over a relatively restricted geographic area. Spawning in these offshore ommastrephid squid probably occurs close to the bottom of the shelf and continental slope and along the offshore side of western and eastern boundary currents (Nigmatullin & Laptikhovsky 1994).

(a) Loliginid squid



(b) Ommastrephid squid

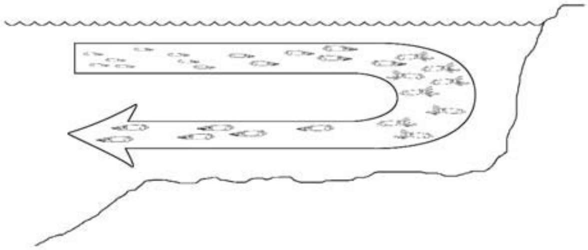


Fig. 11.4 Contrasting patterns of occupation of the coastal shelf, (a) by loliginid squid, resident and breeding, and (b) by ommastrephid squid in migratory excursions.

11.9 Excursions over the shelf: feeding and maturation

Although loliginid squid are the characteristic residents of a shelf waters, many of the major fisheries for ommastrephid squid species are conducted over the continental shelf in water less than 200 m deep (Fig. 11.4). Exploited by nets or by mechanised jigging (see Chapter 16), the rich feeding grounds of the shelf aggregate the squid into massive shoals accessible to large-scale fishing fleets. Details of the migratory routes, and locations of shoals sub-divide populations such as *Todarodes pacificus* into several major fished populations (Okutani 1983) varying in abundance and location from year to year in response to oceanographic changes.

Sporadic appearances of some species on the shelf also provide evidence that there may be substantial populations of ommastrephid squid resident and breeding offshore and not usually available to fishing. For example, *Todarodes sagittatus*, an ommastrephid known to be distributed throughout the northeast Atlantic, is occasionally present over the shelf in very large numbers. After historically sporadic catches in Norway, falling to zero in 1972–1977, the species became abundant in the late summer and autumn over the narrow shelf of Norway and in the coastal fjords during the 1980s (Wiborg 1986; Sundet 1985). In these years, the species provided commercial fisheries with catches up to 15 000 tonnes before disappearing again almost completely. It is notable that those animals caught were almost entirely sub-adults, migrating in pursuit of fish prey, before returning to deep water off the shelf for spawning. Fully mature females of *T. sagittatus* were discovered at 1200 m on the Hebrides slope off Shetland (Boyle *et al.* 1998). Examination by Lordan *et al.* (2001) of bycatches of *T. sagittatus* over several years from commercial and research trawls confirmed the idea of an ontogenetic bathymetric migration, with the larger mature squid caught in waters over 500 m deep. The potential fecundity of mature females ranged from 200 000 to 500 000 eggs, and sub-adult and adult growth rates were estimated at 1.8 mm per day.

Further evidence for the continuous presence of *Todarodes sagittatus* off the shelf arises indirectly from their presence in the gut contents of long-finned pilot whales killed in the Faroes Islands. Beaks of this squid are the most abundant prey item found in the gut even in years when they are not present in coastal waters (Desportes & Mouritsen 1993). *T. sagittatus* and other ommastrephid species such as *Illex coindetii* and *Todaropsis eblanae* are periodically abundant in coastal waters of the northeast Atlantic off Scotland, Ireland and Spain, and are subject to opportunistic fisheries (Joy 1990; Gonzalez *et al.* 1994; Lordan *et al.* 1998b), but the biological/oceanographic changes resulting in these wide fluctuations of squid availability in the northeast Atlantic are still not understood.

Chapter 12

Oceanic and deep-sea species

Summary: The oceanic and deep-sea environment, owing to its great scale and extent, encompasses the greatest diversity at the family level and total biomass of cephalopods. Large populations of migratory ommastrephids are characteristic of the productive shelf-break oceanic boundary currents and upwelling systems. Available as major fisheries and to surface predators in the epipelagic zone (<200 m depth) where they are important predators on fish, crustacea and other cephalopods, they normally range throughout the mesopelagic (<1000 m), generally breeding at depth through the spawning of large gelatinous neutrally buoyant egg masses. Specialised forms of octopus (*Argonauta*) and cuttlefish (*Spirula*) are world-wide distributed in the epipelagic zone of tropical and sub-tropical waters. All the squid families are represented in the oceanic and deep-sea environment, many of them having characteristic depth-range distributions into the bathypelagic (<3000 m) and abyssal (3000–6000 m) zones. The greatest abundance and diversity of pelagic forms is probably found in the depth range 500–1500 m. Many species undergo diel or seasonal vertical migrations, or may differ in depth distribution in different geographic regions. Typically, these mid-water squid have bodies that are more flaccid than coastal and epipelagic forms, resulting from retention of ammonium chloride in their tissues to achieve neutral buoyancy. They are believed to be less active animals, obtaining food by passive hunting and to be mostly planktonic and micro-nektonic predators. A great variety of luminescent organs and tissues are present based on endogenous or exogenous (symbiotic bacteria) production of light. Distinctively, the cirromorph octopuses appear on or close to the bottom, and also range in depth from the upper shelf down to bathyal depths. They have paired fins for locomotion and two rows of cirri flanking the suckers of each arm that are supposed to provide specialized feeding organs. A widely dispersed and diverse fauna of octopuses, both cirrate and incirrate forms (sub-orders Cirrina and Incirrina), live in epibenthic association with the bottom. Locomotion is characteristically by slow pulsations of the arms and web, or rhythmic ‘sculling’ with the paired fins. Deep-diving submersibles and ROVs are providing new insights into the behaviour and biology of these finned octopuses. Life cycle information is lacking for most deep-water species. A few estimates of growth rate and age at maturity suggest that growth is not significantly slower than in neritic species, and lifespan is not significantly longer. A greater variety of breeding mechanisms is described, including pelagic brooding of egg masses by squid (family Gonatidae) and sequential production of single eggs (families Cirroteuthidae, Opisthoteuthidae), described as continuous breeding. A reduction of muscle tissue and loss of tentacles are common in deep-water post-spawning squid, whose buoyant gelatinous bodies may rise towards the surface and become available to predators.

The major areas of the open ocean, from the surface layers to abyssal depths of about 6000 m deep, form the most extensive global habitat for cephalopods. Here we find:

- the greatest biological diversity of cephalopods (implied by the number of endemic families and genera, with small numbers of species, mostly of oegopsid squid);
- the most extensive areas of geographical distribution of individual species;
- the major bulk of cephalopod biomass (estimated from scaling up population data to ocean dimensions);
- a range of special morphological and physiological adaptations (to the deep-sea environment, including luminescence, neutral buoyancy, feeding mechanisms and reproductive differences).

12.1 Habitat

The oceanic and deep-water habitat is not a continuous volume of water. Primary sub-divisions or biomes can be recognised based on the large-scale oceanography and regional differences in the global climate, which in turn influence the biodiversity of marine life and the productive characteristics of the upper 1000 m. Further subdivision of the primary oceanic biomes is necessary to usefully describe the conditions defining the biota of different regions. These regional seas and provinces differ widely in geographic scale, their boundaries may be indistinct and vary over time, and faunal exchanges take place between them. Nevertheless, it is argued that provinces in the marine environment with characteristic biota are recognisable and are the basis for an *Ecological Geography of the Sea* (Longhurst 1998).

The sea-surface layers that define the characteristics of oceanic regional geography differ chiefly in their current patterns, temperature, nutrient supply and the associated biota. The currents are primarily wind-driven and closely linked to the major wind systems of the global climate, but the direction of water movement is modified by the eastward rotation of the Earth, which deflects currents to the right in the northern hemisphere (clockwise) and to the left in the southern hemisphere (anticlockwise). Where these large-scale circulation patterns are constrained against the continental margins, powerful western boundary currents are formed, flowing northwards in the northern hemisphere (Kuroshio Current, Gulf Stream) and southwards in the southern hemisphere (Brazil Current). These high-energy current systems, which are major causes of water transport and mixing, are regions of variability and production in the pelagic ecosystem by generating eddies of water along their meandering course and pinching off warm-core and cold-core rings. Remotely sensed sea-surface temperature or ocean colour (chlorophyll) images of the Gulf Stream clearly visualise the process, showing warm-core rings forming and moving onto the US/Canadian Shelf, while along the oceanic margin of the current, rings of relatively cold shelf water are spun away. The turning motion of mesoscale oceanic rings and eddies (10–100 km diameter) causes localised upwellings (divergence, clockwise rotation) and downwellings (convergence, anticlockwise rotation). These circulation effects give rise to vertical mixing of water, either enhancing (upwelling) or depressing (downwelling) local biological productivity, and contributing significant environmental variability (Angel 1997).

Each of the western boundary current systems supports major cephalopod populations and dependent fisheries (see Chapter 18):

- Kuroshio Current – *Todarodes pacificus* (family Ommastrephidae);
- Brazil Current – *Illex argentinus* (family Ommastrephidae);
- Gulf Stream – *Illex illecebrosus* (family Ommastrephidae);
- Arabian Sea – *Sthenoteuthis oualaniensis* (family Ommastrephidae).

In temperate regions generally (>40° latitude), the nutrient content of the euphotic surface layer is renewed annually from lower layers by seasonal mixing. In tropical and subtropical regions, however, thermal stratification of the water column is more or less stable and the re-supply of nutrients to the surface occurs primarily through vertical mixing in distinct zones of regional upwelling. These upwellings are associated with the trade winds blowing towards the equator, pushing surface water offshore, to be replaced by cooler water from below. Angel (1997) lists the five regions of the world where powerful coastal upwellings bring nutrients to the surface to create zones of high productivity which fuel the food chain of secondary production: along the Peru/Chile coast; in the California Current regions; off the coast of Mauretania (northwest Africa); in the Benguela Current region off the coasts of Namibia and southwest Africa; in the northwest Arabian Sea. Together with important areas along the equator in the central and eastern Pacific and eastern Atlantic, and the continuous supply of cold nutrient water south of the Antarctic Polar Front, these eastern boundary current systems and large-scale coastal upwelling features are the main engines of productivity in the ocean. In contrast, the central areas of the main ocean gyres are relatively nutrient-depleted, generating lower primary productivity and supporting a smaller assemblage of secondary producers and their predators.

The eastern boundary currents, the circumpolar current of the Southern Ocean and major upwelling systems also support major populations of fished cephalopods (see Chapter 18):

- Peru Current – *Dosidicus gigas* (family Ommastrephidae);
- California Current – *Loligo opalescens* (family Loliginidae);
- Canaries Current – *Octopus vulgaris* (family Octopodidae);
- Antarctic Circumpolar Current – *Nototodarus sloanii*, *N. gouldi*, *Martialia hyadesi* (family Ommastrephidae).

Cephalopods do not consume phytoplankton, but the overall distribution and biomass of the epipelagic forms is linked to these broad features of ocean productivity through the flow of energy and material into the great range of secondary producers and predators that form their prey.

The oceanic cephalopod fauna consists mainly of oegopsid squid (e.g. Vecchione & Pohle 2002) – a great assemblage of families and genera, the majority of them with five or fewer described species (see Appendices A and B). The reviews by Clarke (1966) and Nesis (1987) remain almost the sole attempts at a comprehensive treatment, although families such as the Gonatidae (Nesis 1997), Histioteuthidae (Voss, N. 1969) and Cranchiidae (Voss N. 1980, 1988a) are subjects of specialised monographs. Apart from the oegopsids, the pelagic ocean fauna includes the living nautiluses; specialised pelagic forms such as the sepiolid *Spirula*, the octopus *Argonauta*, and *Vampyroteuthis infernalis*, the vampire squid (order Vampyromorphida, family Vampyroteuthidae). On the lower continental slope and deep sea bottom there is a specialised fauna of both cirromorph (suborder Cirrina) and incirrate (suborder Incirrina) octopuses. A compilation of the depth distributions of representative oceanic genera is shown in Fig. 12.2.

12.1.1 Environmental changes with depth

Light penetration diminishes rapidly with depth. The euphotic zone, where light penetration is sufficient for carbon fixation by photosynthesis to exceed losses from respiration and result in primary production, may be as deep as 80 m in the open ocean where there is little absorption or scattering of light. Below that, only the blue–green

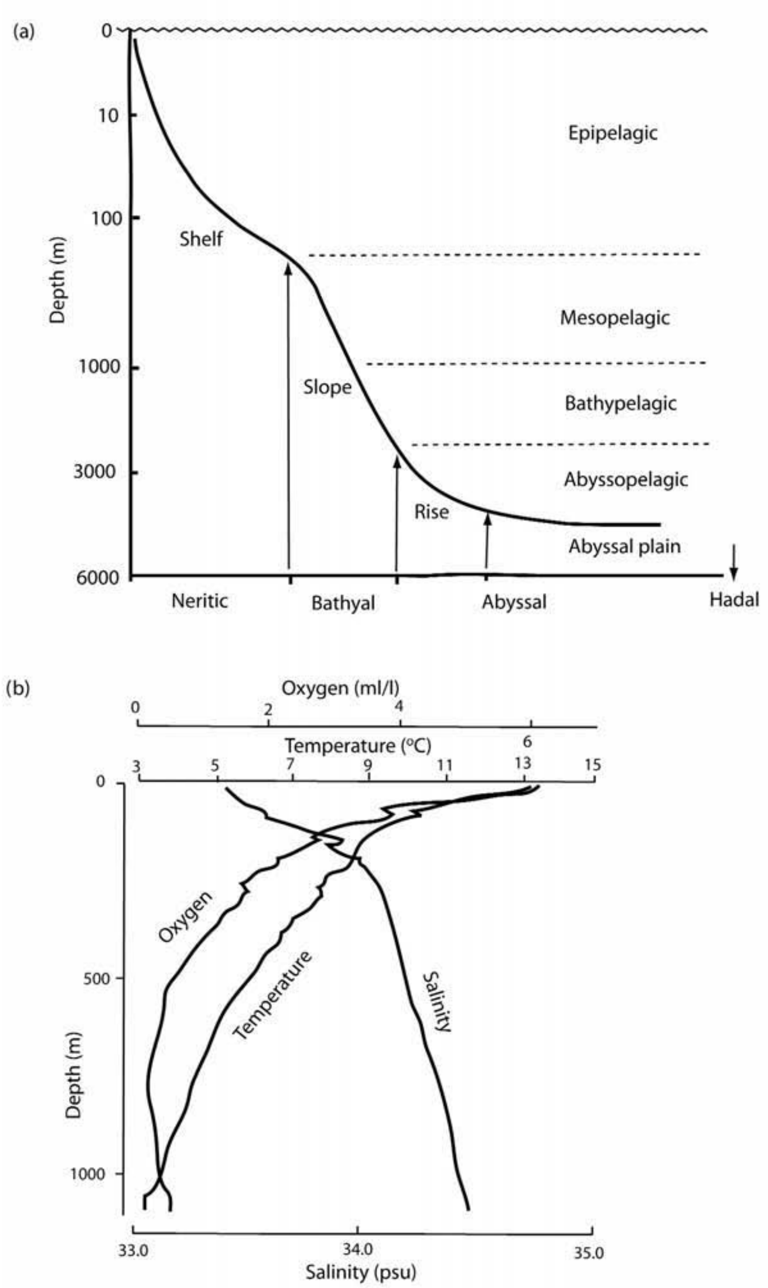


Fig. 12.1 (a) Schematic representation of the pelagic and benthic zonation in the ocean and the associated terminology (after Angel 1997). (b) Depth profiles of temperature, salinity and oxygen concentration in the Monterey Canyon, California, over the vertical distribution range of the squid *Gonatus onyx* (after Hunt & Seibel 2000).

wavelengths penetrate, possibly to 1000 m in the very clearest water. The intensity and direction of light striking organisms in the water column, i.e. the proportion coming from the surface compared with that which is back-scattered from below, is an important factor influencing their visibility to predators. In common with the other major groups of mesopelagic nekton, cephalopods adopt bioluminescent sources in a variety of forms, especially for defensive countershading against down-welling illumination from the surface (Young & Roper 1977; Young *et al.* 1979a). Generally, the cephalopods of the dark zone retain large functional eyes, although evidence for the simplification and reduction of the eyes occurs in the blind octopus *Cirrothauma* (family Cirroteuthidae, Aldred *et al.* 1978).

Hydrostatic pressure in the sea is a more or less linear function with depth. It is a function of the weight per unit area of the overlying water at a given depth plus the atmospheric pressure at the surface. Although climatic changes in atmospheric pressure are important influences on weather patterns, and affect the tidal range at the ocean margins, below the surface the effect is marginal and rapidly lost at depth. Water itself is only very slightly compressible (surface water with a density of 1028.1 kg/m^3 at 0°C will increase in density to 1028.6 kg/m^3 if lowered to 100 m depth without changing its temperature (Angel 1997). The main influences on seawater density are its temperature and its salinity; these properties define the character of water masses of different origin, their effect on its density in turn tending to cause layering or stratification of the ocean. The value of gas spaces within animals for buoyancy control rapidly decreases with depth because of their relatively high compressibility, and most of the mid-water squid appear to maintain near neutral buoyancy by matching their average density to that of the seawater using retention of lighter fluids (Denton & Gilpin-Brown 1973; Denton 1974; Voight *et al.* 1994).

The presence of dissolved gases in seawater is critically important to its capacity to support life. The chemical interactions between gases in solution, with the seawater itself, and their exchanges with gases in the atmosphere is a complex area of oceanography. The gaseous equilibria established in any particular set of physical conditions are further modified by surface transport between geographical regions and by vertical movements of water masses. The partial pressures of gases in the atmosphere decrease at lower temperatures, but their solubilities in seawater increase. The cold surface waters of polar regions dissolve more carbon dioxide and oxygen than those of the tropics. Dense cold water at the polar front then sinks to deeper levels, contributing to the deep ocean bottom water, supplying dissolved oxygen for life in the deepest zones and providing a sink of carbon dioxide. The respiration of organisms at depth in the absence of light and photosynthesis, coupled with the increased dissolution of calcium carbonate from skeletons and shells due to increased hydrostatic pressure and reduced temperature, results in a substantial elevation of carbon dioxide partial pressures (Angel 1997). The major oceanographic upwelling systems return much of this carbon dioxide production to the surface, where at higher temperatures its solubility is decreased and the gas is vented to the atmosphere.

At depth, the partial pressures of dissolved gases decrease and their solubility increases. For organisms at depth, this means that the extraction of oxygen for respiration and carbon dioxide for skeleton and shell formation requires more energy. At depths below the photic zone, where life is dependent on energy and material inputs falling from above (apart from the restricted zones of hydrothermal inputs at deep-sea vents), the habitat is one of generally lower productivity and standing biomass density. Comparative estimates of the metabolism of cephalopods living at depth shows a general decline in metabolic rates (Seibel *et al.* 1997), apparently resulting from a lowered availability of oxygen and weaker demands for energetic behaviour (Childress & Seibel 1998; Seibel *et al.* 2000b; Seibel & Childress 1996, 2000). Despite these lowered metabolic demands, at least one cephalopod, *Vampyroteuthis infernalis*, has adapted to life in the oxygen minimum zone by the evolution of haemocyanin molecules with a considerably elevated affinity for oxygen (Seibel *et al.* 1999). Through the increased oxygen affinity of the blood, coupled with a tolerance of prolonged pauses in ventilation and circulation, even *Nautilus pompilius*, a representative of the earliest cephalopods, is able to survive periods of oxygen deficit or hypoxia (Boutilier *et al.* 1996).

Vertical gradients in the physical oceanic environment are strong (Fig. 12.1b), relatively stable and accompanied by marked discontinuities in the fauna. Below the wind-mixed upper layers, which are relatively consistent in temperature, salinity, and nutrient and plankton distribution, the vertical structure of the ocean is characterised by water layers of differing density, often with sharp gradients between the horizontal layers. At tropical latitudes, stratification is mainly influenced by the depth of the temperature gradient (thermocline) below the mixed layer, while at higher latitudes, discontinuities in salinity (haloclines) dominate (Angel 1997). The fauna of the open ocean is broadly stratified into biological zones consequent on these physical gradients and boundaries. Cephalopods are components of the faunal assemblages at all depths, although there are many examples of daily inter-zonal vertical migrators through the upper 1000 m (Nesis 1993a).

The epipelagic zone is usually considered to extend to 200–250 m in depth and includes the euphotic zone and the seasonal pycnocline (Angel 1997). Predominating here are the oceanic ommastrephid squid. Those of genera such as *Sthenoteuthis*, *Ommastrephes*, *Martialia* and *Dosidicus* have a more ‘oceanic’ distribution and life-cycle strategy (Nigmatullin & Laptikhovsky 1994) than the ‘offshore’ types discussed in Chapter 11. These ommastrephid populations are present and able to utilise the water column down to at least 1000 m. In the unique frontal areas between the Southern Ocean (surrounding the Antarctic polar regions) and the oceans to the north, it is considered that the ommastrephid squid effectively occupy the ecological niche normally associated with fish in the epipelagic zone (Rodhouse & White 1995). Other cephalopod types, such as the pelagic octopus *Argonauta*, are more or less restricted to the epipelagic surface layers.

The mesopelagic zone extends down to 1000 m, which is approximately the maximum depth at which light from the surface ceases to be a direct influence on organisms. The mesopelagic zone is sometimes divided into sub-zones on the basis of the distribution of characteristic fish and crustacea (*shallow*, reflective-sided fish and half red/transparent crustaceans; *deep*, non-reflective fish and totally red crustaceans). Many cephalopod genera that are characteristic of the mesopelagic (e.g. *Histioteuthis*, *Gonatus*, *Architeuthis*) are not so readily zoned by depth, and may migrate into the surface layers at night (e.g. *Watasenia*). Bathypelagic cephalopods (e.g. *Vampyroteuthis*, *Lycoteuthis*) extend to depths of nearly 3000 m, below which there is a sharp decline in

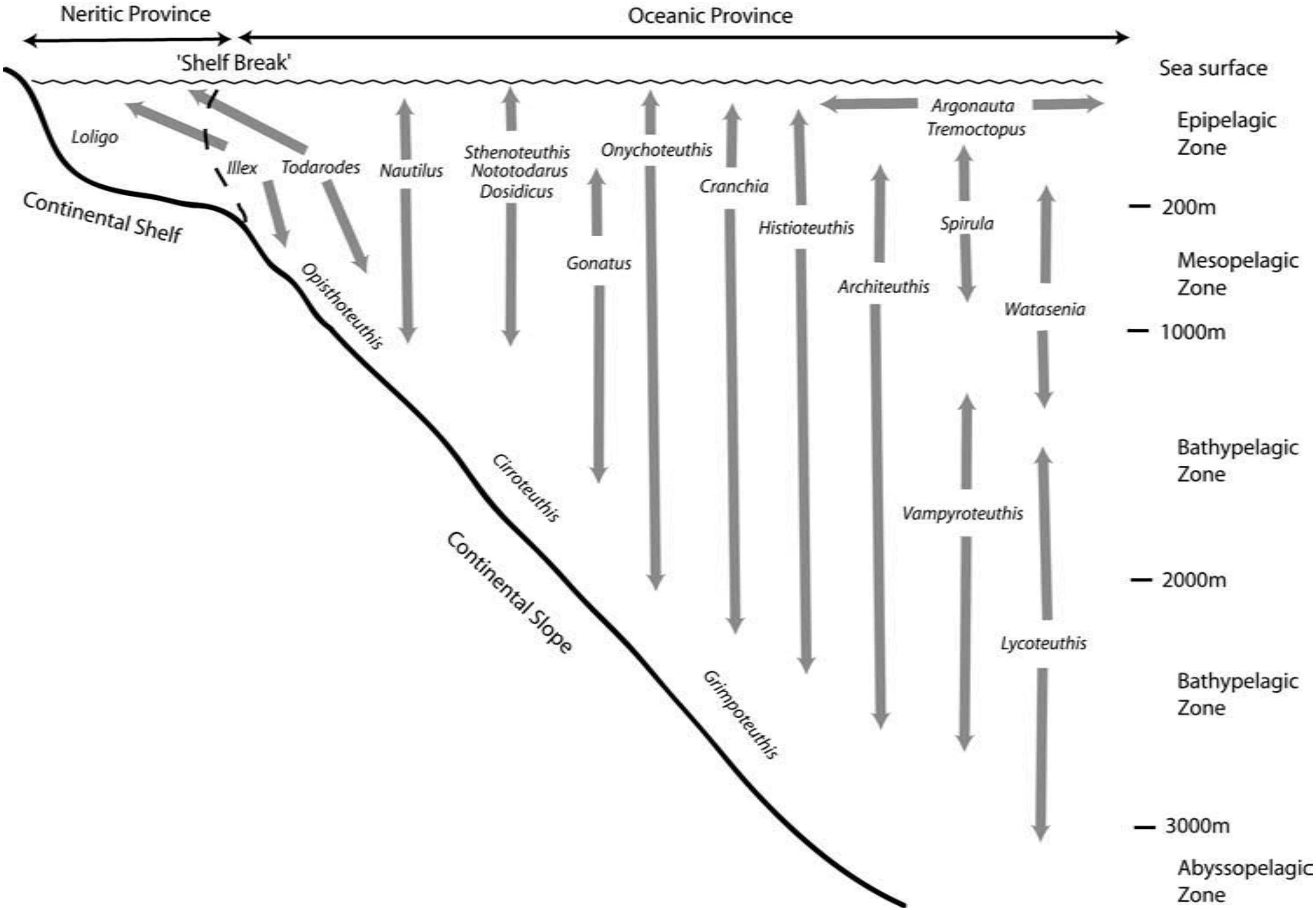


Fig. 12.2 Distribution with habitat and depth of selected cephalopod genera characteristic of the oceanic and deep-sea realms (not to scale). Although oceanic in life style and breeding at mid-water depths, squid of the family Ommastrephidae in particular exploit the upwellings and boundary currents at the shelf break and make periodic excursions over the shelf itself.

the abundance and numbers of species. Sepiolids also are associated with the bottom, and in the northeast Atlantic may be the most abundant group at depths of 500–1500 m (Collins *et al.* 2001). A small number of cephalopod species, such as those of the cirromorph octopus genera *Cirrothauma* and *Grimpoteuthis*, are known to be present on or close to the bottom at abyssal depths (<6000 m).

The shelf break, marking the edge of the continental margin at approximately 200 m below the sea surface, serves to demarcate the distribution of those coastal or neritic cephalopods which are dependent on the bottom for spawning (Fig. 12.2). It is by no means an absolute boundary, with many of the coastal forms extending down into the upper shelf and overlapping in depth range with typical deep-water forms such as the cirromorph octopuses (see Chapter 11).

12.2 Adaptations to the oceanic habitat

12.2.1 Buoyancy

In common with fish and other animals that colonise the water column, cephalopods have evolved mechanisms to offset their density in seawater and the tendency to sink. The use of gas spaces for buoyancy is efficient in aquatic animals living close to the surface because the density of gas at normal pressures, being so much lower than the surrounding fluid, contributes a considerable buoyancy gain for the space occupied. However, at deeper levels, where hydrostatic pressure is proportionately increased, it is increasingly expensive energetically for fish to secrete and maintain gas volumes at high pressure to keep the swim-bladder inflated. Considerable metabolic effort is also required to maintain the volume of the gas space if the fish migrates vertically owing to the rapid changes in hydrostatic pressure. Most fish living at depth, or actively swimming through significant vertical distances, have abandoned gas-filled buoyancy mechanisms in favour of other means.

Among cephalopods, only the nautiluses, with their heavy external calcareous shell, the cuttlefish *Sepia* and the pelagic sepiolid *Spirula* retain a gas-filled space as a variable buoyancy mechanism (but note the external gas bubbles retained by some pelagic octopuses such as *Argonauta* and *Ocythoe*). The buoyancy mechanism of these cephalopods is quite different from that of fish because the rigid shell, sub-divided into chambers, encloses the gas in an incompressible space. Effectively, the volume of the gas space is maintained independently of depth; small adjustments to its volume and the density of the animal in seawater are made by controlling the fluid component within the shell space. This is achieved by maintaining an osmotic pressure difference across the tissues sealing the shell by the active transport of salts. The osmotic differential created opposes the hydrostatic pressure, tending to force fluid into the shell space and allowing the volume of the gas to be maintained at a pressure of about 0.6–0.8 bar. Although *Sepia* is limited in distribution to coastal waters of the continental shelf, both *Nautilus* and *Spirula* which live over deep water are capable of maintaining neutral buoyancy through vertical migrations of the order of 600 m. Some introduction to these gas-filled buoyancy structures is given in Chapters 2 and 4.

Apart from the three genera mentioned above, none of the living cephalopods maintain a shell remnant which is sufficient to enclose gas spaces, but the problem of maintaining their station in the water column remains. Many of those squid genera which have colonised deep water sequester large volumes of fluid rich in ammonium chloride to reduce their density, a phenomenon first described by Denton *et al.* (1958) and reviewed by Voight *et al.* (1994). When samples of the coelomic fluid from three species of mid-water squid family Cranchiidae (*Verrilliteuthis hyperborea*, *Galliteuthis armata* and *Heliochranchia pfefferi*) were analysed, Denton and colleagues showed that the clear coelomic fluid had a specific gravity of 1.010–1.012. Because these squid were living in seawater with a specific gravity of 1.026, it was calculated that there was sufficient fluid to provide neutral buoyancy, and that the bitter taste reported was due to a high concentration of ammonium chloride (<480 mM ammonium ion).

These observations have been extended to show that the retention of ammonium chloride in the tissues is a common feature of oceanic squid. Representatives of at least 16 of the 26 families of living teuthoids tested achieve neutral buoyancy in this way; the remaining families contain squids denser than seawater, and at least three families (Neoteuthidae, Enoploteuthidae, Onychoteuthidae) contain both buoyant and non-buoyant types of squid.

The retention of ammonium chloride in squid tissues is achieved at the expense of muscularity. Squid that have elevated levels of ammonium chloride have a flaccid gelatinous feel to them, and two distinct modes of ammonium accumulation are present. In the majority (representatives of 15 families; Voight *et al.* 1994) ammonia in the form of ammonium chloride (NH_4Cl) is retained in fluid compartments and in the muscles themselves. Examined in histological section, the tissues of the mantle and arms are expanded into a loose reticulated appearance, and these reticulations form the compartments for fluid retention. It is this histological evidence that in turn may be used to recognise the ammoniacal types (Clarke *et al.* 1979). Exceptionally, squids of the family Cranchiidae develop a very expanded coelomic chamber (Fig. 12.3) fused to a transverse membrane dividing the mantle cavity. These globular, predominantly mid-water squids are present in all oceans (with the possible exception of the Arctic; Nesis 2001) and are well represented in most pelagic habitats. There are at least 13 genera (Voss & Voss 1983) and 30 species (Nesis 1987), which are considered by Voss N. (1988b) to represent the most successful radiation of modern pelagic cephalopods.

As is so commonly the case with biological systems, there is a trade-off between the evolution of specialisms for one purpose and their effect on other aspects of body function. In this case, the weak and flaccid bodies of the mid-water squid must limit their ability to move and tackle other animals, thus setting new constraints on the typical cephalopod features of high activity, rapid locomotion and predatory attack behaviour. All of these mid-water forms, however, appear to remain exclusively predators, developing in compensation their capacity for passive hunting. Hanging motionless and neutrally buoyant in complete darkness, with eyes relatively even larger than those of their coastal relatives and presumably acutely able to detect luminescence from ambient animals, the wide spread of the arms and web operate to capture and gather passing prey (see Chapter 14).

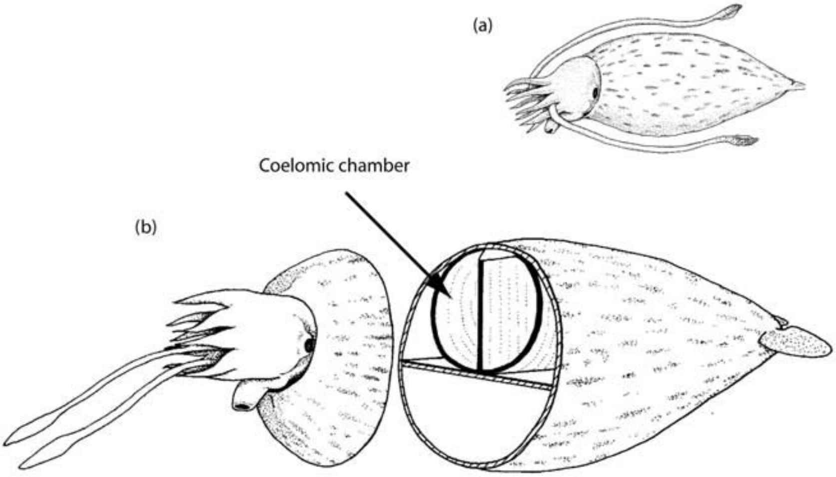
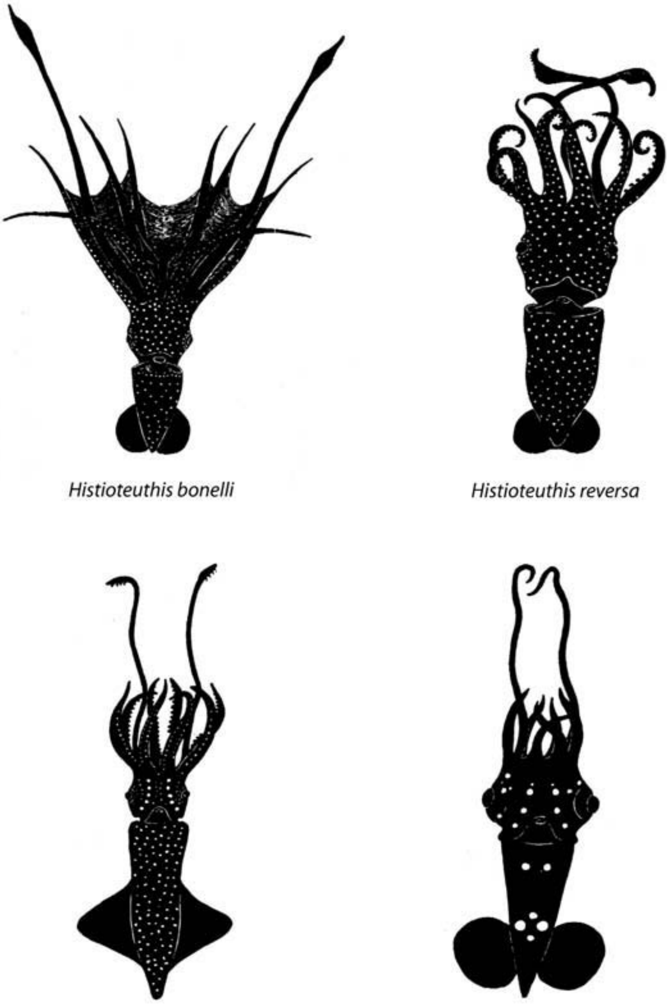


Fig. 12.3 (a) Globular body form of the mid-water squid *Heliocranchia pfefferi*, which is typical of the family Cranchiidae. (b) Schematic section of the body of the cranchid squid *Cranchia scabra* to show the large coelomic chamber containing ammonium chloride for buoyancy (after Clarke 1962c).

12.2.2 Luminescence

Many cephalopods have the capacity to produce light. Contained in luminescent organs (photophores) ranged in patterns on the body or released as luminescent clouds of material into the surrounding water, displayed as steady illumination or controlled in flashing luminescent displays, these light-generating capabilities are particularly well-developed in, although not restricted to, the mesopelagic and bathypelagic squid (Fig. 12.4).

The biochemical basis for luminescence in cephalopods appears to be the same generalised luciferin–luciferinase system of substrate and enzyme found in fish and other light-producing species. Cephalopods are able to produce these luminescent sources from intrinsic systems (self-generated), and also to utilise pockets of symbiotic bacteria to generate them. Herring *et al.* (1981) compare and contrast the light organs of the coastal sepiolids *Sepiola atlantica* and *S. robusta* with those of the oceanic sepiolid *Spirula spirula*. In *Sepiola*, the luminescence emanates from paired bodies lying in the mantle cavity, which are partially embedded in the ventral surfaces of the ink sac. Living *Sepiola* are observed to luminesce steadily, appearing blue–green to the dark-adapted eye. The light is directed ventrally, and is not visible from a dorsal or dorso–lateral view. In *Sepiola*, the organs themselves are yellowish coloured pockets containing a bacterial species identified as *Photobacterium fischeri*. The intensity of the emitted light in *Sepiola* appears to be regulated and increased in response to brief illumination of the animal. In contrast, there is apparently no involvement of bacteria in light emitted from *Spirula* from a light organ with a highly laminate structure which is quite unlike the photocytes of other cephalopods (Fig. 12.5). The light organ is a silvery bead-like spot, set in the body wall between the fins. The illumination produced is described as steady and long-lasting, but is also capable of up to a 10-times increase in intensity for a few seconds when the animal is handled.



Histioteuthis bonelli *Histioteuthis reversa*

Abraliopsis morisii *Pterygioteuthis giardi*

Fig. 12.4 Distribution of photophores on a variety of deep-water squid species (after Marshall 1954).

Another well-known symbiotic luminescent association relates the coastal sepiolid *Euprymna scolopes* with the bacterium *Vibrio fischeri* (McFall-Ngai 1994; Dunlap *et al.* 1995). Culture of *E. scolopes* in aquarium conditions in groups with and without the bacterium showed that growth, development and reproduction in both groups was similar (Claes & Dunlap 2000). There were no obvious morphometric or histological differences between the colonised and uncolonised individuals, as suggested in other species (Diono & McFall-Ngai 1995), except for changes in the epithelial tissues actually in contact with the bacteria. Notably, there are pockets of symbiotic bacteria associated with the reproductive system (accessory nidamental glands) in several species of non-luminescent cephalopods (Bloodgood 1977) where the proliferation of the colonies coincides with the onset of reproductive maturity (Lum-Kong 1992). These associations raise many interesting questions about the routes of acquisition and

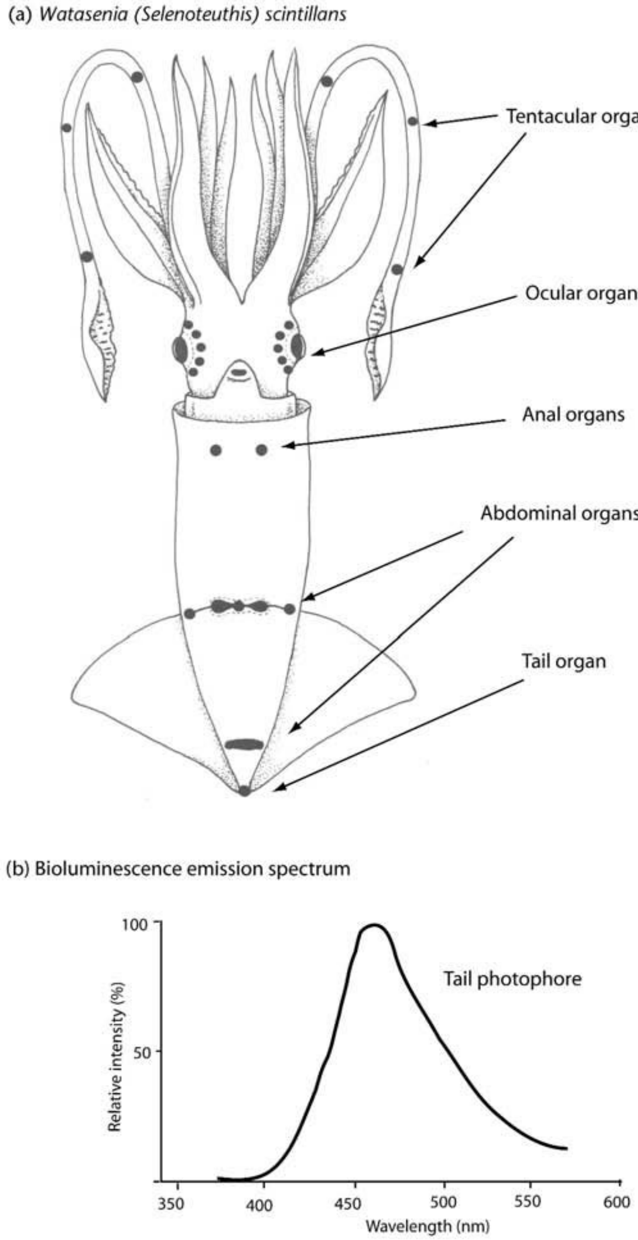


Fig. 12.5 (a) Distribution of luminescent organs in a male *Selenoteuthis scintillans* (family Lycoteuthidae). (b) The bioluminescence emission spectrum of the tail photophore. The various photophore types have different microscopical organisation (after Herring *et al*. 1985).

the physiological links between the cephalopod and the symbiont (Barbieri *et al.* 2001; Fidopiasris *et al.* 1998; Foster *et al.* 2002; Nishiguchi 2001, 2002; Nishiguchi *et al.* 2004).

In his review of the occurrence of light organs in cephalopods, Herring (1977) lists 71 genera containing luminous species from 19 out of the 31 families included in the survey.

Descriptive details have been provided for numerous species, such as *Bathothauma lyromma* (Dilly 1978; Aldred 1974), *Heteroteuthis dispar* (Dilly & Herring 1978), *Histioteuthis macrohista* (Dilly & Herring 1981), *Cirrothauma murrayi* (Aldred *et al.* 1982), *Pyroteuthis margaritifera* (Butcher *et al.* 1982), *Selenoteuthis scintillans* (Herring *et al.* 1985), *Japetella diaphana* (Herring *et al.* 1987), *Vampyroteuthis infernalis* (Herring *et al.* 1994), and *Stauroteuthis syrtensis* (Johnsen *et al.* 1998), from a diversity of families and illustrating considerable variety in anatomical arrangements. Photophore morphology within a single species may be very specific to different parts of the body and produce spontaneous luminescence or fluorescence (when illuminated or chemically treated) of characteristic emission spectra (Fig. 12.5). Some, like the mesopelagic sepiolids *Heteroteuthis* spp., even release a cloud of luminescent particles and mucus. It is also the case that cephalopod tissues (kidney, blood, digestive gland and renal fluid) from a range of species that are non-bioluminescent *in vivo* will luminesce when homogenised or even simply exposed to air (Young *et al.* 1979a).

In common with most aspects of the physiology of specialised deep-sea organs, there is little first-hand knowledge of the function and ecological meaning of photophore displays. Descriptions of the morphology and distribution of photophores in many types of mid-water cephalopods suggest the significance of this capability in the lives of these animals. A principal function for the photophores distributed over the ventral surface of mid-water species is to provide bioluminescent counter-shading to match the down-welling illumination from above and prevent the silhouette of the animal being visible to predators against the surface luminosity (Young & Roper 1977; Young 1975, 1977; Herring *et al.* 2002). Although the positioning of the photophore pattern is fixed as a species-characteristic pattern, it has been discovered that specialised photoreceptors within the orbit (intra-ocular) of *Abraliopsis* detect the intensity of the down-welling light, leading to active variation of the intensity of light production from the photophores (Young & Roper 1977; Young *et al.* 1979b).

12.2.3 Vertical migration

The general difficulties and uncertainties in compiling data on the depth ranges of cephalopods are further complicated by a real biological variation in their vertical distribution in the water column. The depth ranges of some species vary substantially in different parts of the geographical range. *Illex coindetii*, for example, with an overall depth range from the surface to 1000 m (Nesis 1987), is recorded to be most abundant at 180–450 m in Caribbean waters, 200–600 m in the west Atlantic, 150–300 m in the east Atlantic and 60–400 m in the Mediterranean.

Many mid-water squid species are considered to undergo substantial diel vertical migrations. Such migrations, deeper during the day and rising towards the surface each night, may be inferred from comparative trawling at depth with opening/closing nets at different times of the day (Roper 1977; Clarke & Lu 1974; Clarke 1975) for species of Enoploteuthidae, such as *Pyroteuthis margaritifer* and a *Pterygioteuthis giardi*, Bathyteuthidae, *Bathyteuthis abyssicola* and the pelagic octopod *Japatella diaphana* (Bolitaenidae). Direct observations on the oceanic *Ommastrephes bartrami* (Ommastrephidae) in which individuals were tracked with ultrasonic transmitters

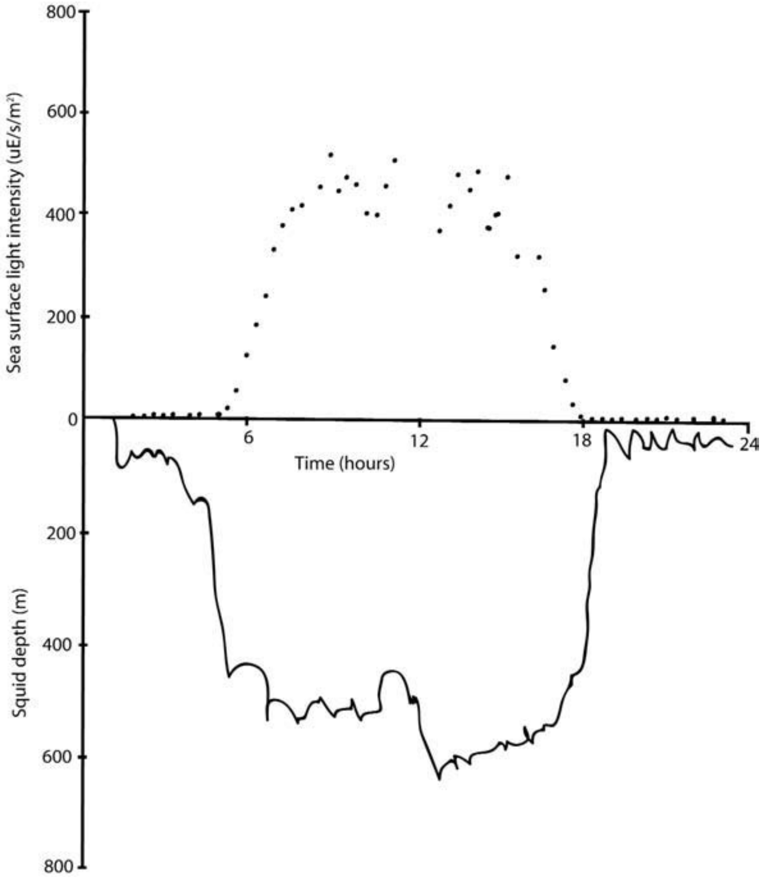


Fig. 12.6 Depth distribution of a single squid, *Ommastrephes bartrami*, tagged with an ultrasonic transmitter in relation to changes in light intensity at the sea surface over a 24-h period (after Nakamura 1993).

(Nakamura 1993) showed them swimming close to the surface, at 40–70 m depth, at night until about an hour before sunrise, when they descended to 400–700 m during the day. The subsequent ascent began at about sunset. There was a significant trend in falling temperature and salinity over this depth range, but the implication is that the tagged squid was tracking the depth profile of the changing isolumes (Fig. 12.6), although the authors report some inconsistencies in this interpretation. The general pattern of nocturnal ascent in oceanic cephalopods is supported by large-scales studies such as that of Young R.E. (1978), in which vertical distribution data were obtained for 47 species of pelagic cephalopod off Hawaii. Peaks of species richness occurred at 500–800 m during the day, rising to less than 300 m at night. Approximately 60% of the species underwent diurnal migration, with over 80% of the individuals occurring in the upper 250 m at night.

Patterns of diurnal vertical migration in oceanic squid species clearly influence their availability as prey to surface-living and shallow-diving predators. The frequent occurrence of many deep-water species in the diet of albatrosses has led to several speculative alternative explanations about how this can arise (Croxall & Prince 1994).

Albatrosses are capable of catching live prey which are close to the surface at night time, and some species operate effectively as scavengers on regurgitations from squid-eating cetaceans. Whether they feed on the floating carcasses of squid resulting from post-spawning mortality is still unclear.

The habit of spawning large gelatinous egg masses at depth while floating at an isopycnic surface (between water layers of different density) seems to be normal for most of the family Ommastrephidae (Fig. 11.3; Bakun & Csirke 1998; Sakurai *et al.* 2000). The consequence is that the hatchlings rise to the surface waters while growing and feeding, and this is followed by an ontogenetic descent, growth and maturation of the sub-adults to breed at depth. In addition to the vertical movements of adults through this depth range, there is clearly a component of distribution with depth of different ontogenetic stages. Unusually, some squid of the families Enoploteuthidae and Brachioteuthidae release their eggs directly into the plankton as masses of individual eggs that subsequently hatch into larval forms (Young *et al.* 1985; Young 1985) before ontogenetic descent to the adult depth range.

The enoploteuthid squid *Watasenia scintillans*, the Japanese firefly squid, is famous for its mass annual migrations into shallow water to breed in great numbers (Hayashi 1993). Normally distributed from 225 m down to 1225 m in the Sea of Japan, millions of these spectacularly luminescent squid migrate into shallow bays to breed in spring, where they are an important commercially fished catch in shore-based nets set at night, and also become available to a range of coastal demersal fish (Fig. 12.7).

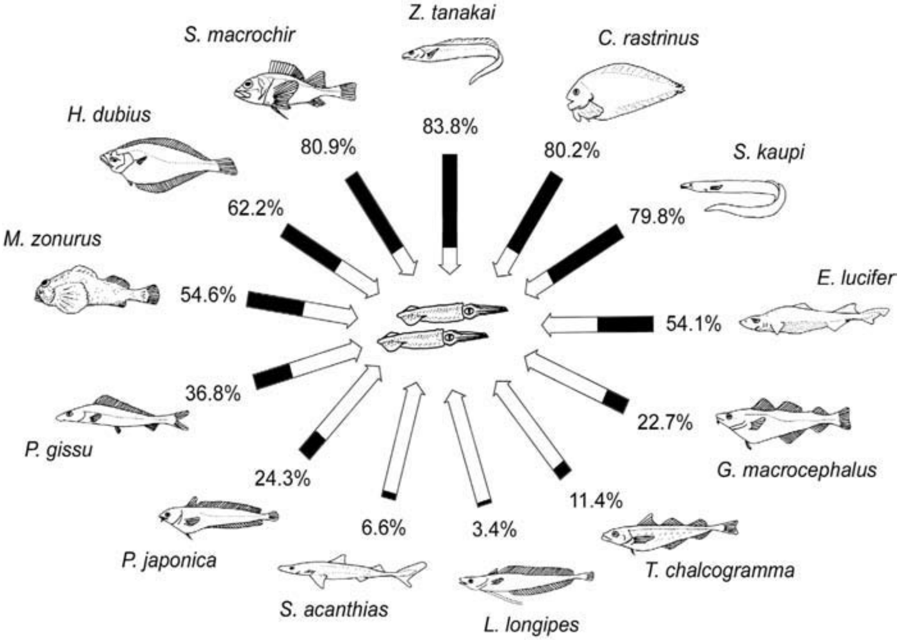


Fig. 12.7 *Watasenia scintillans*: relative contribution to the diet of a range of demersal fishes off Sendai Bay, North Japan (after Yamamura *et al.* 1993).

12.2.4 Feeding

Mesopelagic and bathypelagic squid generally have less muscular, gelatinous and flaccid bodies. Although there is little direct evidence of their feeding habits, the body form suggests a much less active lifestyle. Many of these squid probably rely on passive hunting, i.e. drifting with arms extended, or slow stalk and capture techniques to catch pelagic prey. Examination of the gut contents of the deep-sea cirrate octopuses suggests a mainly microcarnivorous habit, using the spread arms and web to capture small organisms in the water column or from the surface of the sediment (see Chapter 14).

Shchetinnikov (1992) describes several ontogenetic stages in the diet composition of the epipelagic oceanic ommastrephid *Sthenoteuthis oualaniensis*, graded by the size spectrum of the prey. At stage I (4–10 cm mantle length), the squid are epipelagic micronekton and plankton feeders; at stage II (10–15 cm mantle length) they feed on planktonic crustacea, fish larvae and myctophid fishes; at stage III (adults, 15–36.5 cm mantle length), the main diet becomes myctophid fish with a noticeable increase in the proportion of cephalopods, including evidence for cannibalism.

12.2.5 Reproduction

The main themes of cephalopod reproduction have been established almost exclusively from studies on the coastal forms. There is a remarkably consistent pattern of growth and reproduction during a single breeding season, followed by post-spawning senescence and death (see Chapters 9 and 10). In the epipelagic oceanic realms, members of the family Ommastrephidae are almost as well known from the numerous population studies on fished species. These powerful muscular migratory squids conform to the general pattern of growth and reproduction established for the neritic species, with the principal exception of the release of pelagic egg masses in deep water at isopycnic surfaces (Fig. 11.3). In addition to the Ommastrephidae, reproductive information is known for species from several oceanic families, particularly the Gonatidae, Histioteuthidae (Laptikhovsky 2001b) and Onychoteuthidae, but the information is simply insufficient, in terms of numbers of species and individuals, to draw general conclusions with reasonable certainty. Rather than speculate on the general features of reproduction in the oceanic deep habitats, we note some aspects of the reproductive process which are well established, and which may contrast with the general patterns of the coastal forms.

12.2.5.1 Brooding of pelagic eggs

The pelagic octopuses are noted for the retention of the egg mass by the female, and carrying it throughout the incubation period of the embryo until hatching. The paper nautilus, in fact, has a calcareous brood chamber secreted by the specialised dorsal arms of the epipelagic female *Argonauta* (family Argonautidae) to which the eggs are attached and which shelters the body of the adult. In other epipelagic octopuses (family Tremoctopodidae), the eggs are carried by the basal part of the arms as they are in the meso- and bathypelagic octopus families (families Vitrellodellidae, Bolitaenidae). Uniquely, in *Ocythoe tuberculata* (family Ocythoidae), the eggs are brooded in the enlarged oviducts of the female, from which the hatched larvae are extruded.

Evidence from some deep-sea squids (family Gonatidae) suggests that the spawned egg mass is held within the arms of the female and trailed behind while swimming for the duration of egg incubation. First reported as an unknown species in shallow water in the Sea of Okhotsk (Okutani *et al.* 1995), squid paralarvae were observed emerging from the eggs as the squid swam. Squid, *Gonatus fabricii*, caught with a pelagic trawl in the Norwegian Sea at depths down to 1100 m, were found to be mixed with many fragments of egg mass of the same species which appeared to have spawned naturally (Bjørke *et al.* 1997). Further collections of post-spawning adults of *Gonatus onyx*, together with maturing eggs and hatchlings at depths between 1250 and 1750 m off southern California (Seibel *et al.* 2000a), has led to an inference of a general reproductive strategy of deep-water spawning and egg care in the Gonatidae. The post-spawning mortality of *Gonatus* breeding at depth after 2 years led Bjørke & Gjosaeter (1998) to estimate a total of 20 million tonnes of biomass from this source being potentially available to predators.

Notably, observations from deep-sea submersibles confirm earlier suggestions (Young 1972) by revealing that octopuses of the genera *Graneledone* and *Benthoctopus* also brood their benthic egg deposits at depths of 2600 m, apparently throughout development (Voight 2000b; Voight & Grehan 2000; Laptikhovsky 2001a).

12.2.5.2 Release of single eggs

A distinctive feature of the breeding of deep-water cirromorph octopuses is the continuous production of single large eggs. Described in detail for *Opisthoteuthis agassizi* by Villanueva (1992a), the key features are that both males and females mature over a very wide range of body size, and that from the first point of maturity, females are always found with a single egg ready for release. The implication of this finding was that they were capable of breeding over the majority of their life-time, a condition he described as continuous spawning. The same pattern is found in other cirromorph octopuses (*Opisthoteuthis massyae*, Boyle & Daly 2000), leading Rocha *et al.* (2001) to identify ‘continuous spawning’ as an established cephalopod strategy. Whether this pattern of reproduction really is a characteristic of the cirromorph octopods as a group, or is an adaptation to special conditions of bathybenthic life, is yet to be explored. Single eggs of some oegopsid squid (families Enoploteuthidae, Brachioteuthidae) are also commonly found in near-surface plankton in the tropics (Young *et al.* 1985), but there is no supporting information as to whether this is a usual route to completion of the life cycle, in contrast to the brooding behaviour of gonatids described above.

12.2.5.3 Duration of the embryonic phase

No direct information on the normal duration of the embryonic phase in deep-sea and oceanic species is available. Nesis (1999) points out that the duration of embryonic development in poikilothermic animals depends on the two key parameters of temperature and egg size (quantity of yolk). Mathematical formulae relating these two variables, derived by Laptikhovsky (1999) and supported by limited rearing data at low temperatures, give estimates of extended periods of development. Large-egged species such as the finned octopods *Cirroteuthis muelleri* and *Opisthoteuthis* spp. could take 20–32 months to hatch, and the Antarctic *Cirroctopus glacialis* and *Megeledone semoi* from 30 to 42 months. This method also suggests that development time in the relatively large-egged gonatid squid *Gonatus fabricii*, *G. onyx* and *Berryteuthis magister* may be 12–16 weeks, causing Nesis (1999) to doubt the reality of pelagic egg-brooding by the female.

12.2.5.4 Seasonality

All that has been learnt about the coastal cephalopods suggests that seasonality, i.e. some degree of phasing of reproductive activity with an annual cycle, is normal. In the oceanic environment this is also true for the epipelagic and shelf-break ommastrephids that follow major seasonal changes in population distribution (migrations) for feeding and breeding (see Chapters 11 and 18). For most meso- and bathypelagic species, evidence for seasonality is much less certain. For some (e.g. *Watasenia scintillans*, family Enoploteuthidae) there are distinct patterns of on-shore migration for seasonal breeding (Hayashi 1993), but for the bulk of deep-water species there are simply no data.

Studies in most deep-sea organisms have generally established that seasonality in the deep sea is at a low level or absent (Gage & Tyler 1991). However, interest in carbon cycling in the oceans has shown that an annual variation in the fall of phytoplankton and other production from the surface does impose a low level of seasonality on this otherwise constant environment. Little direct information is available for deep-water cephalopods, although for the benthic octopus *Opisthoteuthis massyae* (800–1300 m, Daly *et al.* 1998), no significant differences in the incidence of reproductive individuals in the population were found over an annual cycle.

12.2.5.5 Tissue degeneration in spawning animals

The loss of tone in somatic muscle tissue is often associated with sexual maturity and spawning in cephalopods, leading to suggestions that it is mobilised as a source of material and energy for reproduction (see Chapter 9). In a number of deep-water squid species, the bodies of the mature and spent animals may be quite gelatinous, with a great loss of muscle tissue and complete loss of the tentacles. Common among members of the families Onychoteuthidae, Gonatidae, Histioteuthidae and Cranchiidae, meso- and bathypelagic species in which spawning occurs at depths of 500–2500 m, is the finding that after spawning the spent gelatinous animals lose neutral buoyancy and rise to the surface, where they become accessible to seabirds and other surface predators (Jackson & Mladenov 1994; Nesis 1993c, 1996; Nesis *et al.* 1998; Cherel & Weimerskirch 1999).

12.3 The oceanic pelagic habitat

The amount and quality of verifiable scientific information on the majority of deep-water and oceanic cephalopod species is poor. Collections made from scientific cruises are invariably preserved and are often only worked up years later, if at all. Uncertainties surrounding the deep-sea fauna arise for many reasons:

- real difficulties of species identification in the oceanic habitat;
- the extreme dearth of observations on living animals, which has only recently improved with the use of underwater video;
- the poor capabilities of most biological collecting gear operated at sea and its probable selectivity, as suggested by predator diet comparisons;
- the highly dispersed distributions of most of the macrofauna;
- the absence of linear studies on key processes such as growth and reproduction;
- the sheer scale of the oceanic environment compared with the density and frequency of biological samples;
- the technical difficulties of reaching the greatest depths.

Knowledge of the oceanic and deep-water cephalopod fauna will hardly support a cohesive descriptive account, and is far from any quantitative approach. Guided by Nesis (1996), who laments of the oceanic cephalopod fauna '. . . I do not see any other way to bring nearer to obscure truth than to collect dispersed, fragmentary, anecdotal, and in some cases unproven observations . . .', we have chosen to bring together a natural history of some selected species, loosely grouped by habitat zone, but without any attempt at community ecology. The terminology used in describing oceanic depth zones (see Fig. 12.1) is conventionally applied, but diurnal migrations and regional differences in depth distribution considerably overlap the zone boundaries in many cases. It is also the case that squid families may include species with widely different depth distributions, and therefore grouping families into depth zones is only an indication of the modal distribution of their species. A further problem with the maximum depth ranges quoted for some species is that they arise from non-closing nets, and will exaggerate the actual depth range of the specimens caught. The oceanic epipelagic paper nautilus, *Argonauta*, produces a fragile calcareous brood chamber for the eggs (Fig. 12.8). These 'shells', like the true cephalopod shells of *Nautilus*, *Sepia* and *Spirula*, float and drift over great distances, adding further doubt over the distribution range of the living species. Appendix B provides a synopsis of cephalopod families in which the habitat characteristics and depth ranges of the genera mentioned in this book are given.

The distributions of many oceanic species are implied from scattered collections of adults, juveniles or eggs (Fig. 12.9) and the potential remains for completely new discoveries of large oceanic cephalopods. Aside from the continuing saga of strandings of giant squid *Architeuthis*, the recognition of previously undescribed species of large squid from submersible observations (Vecchione *et al.* 2001a) vividly illustrates the possibilities.

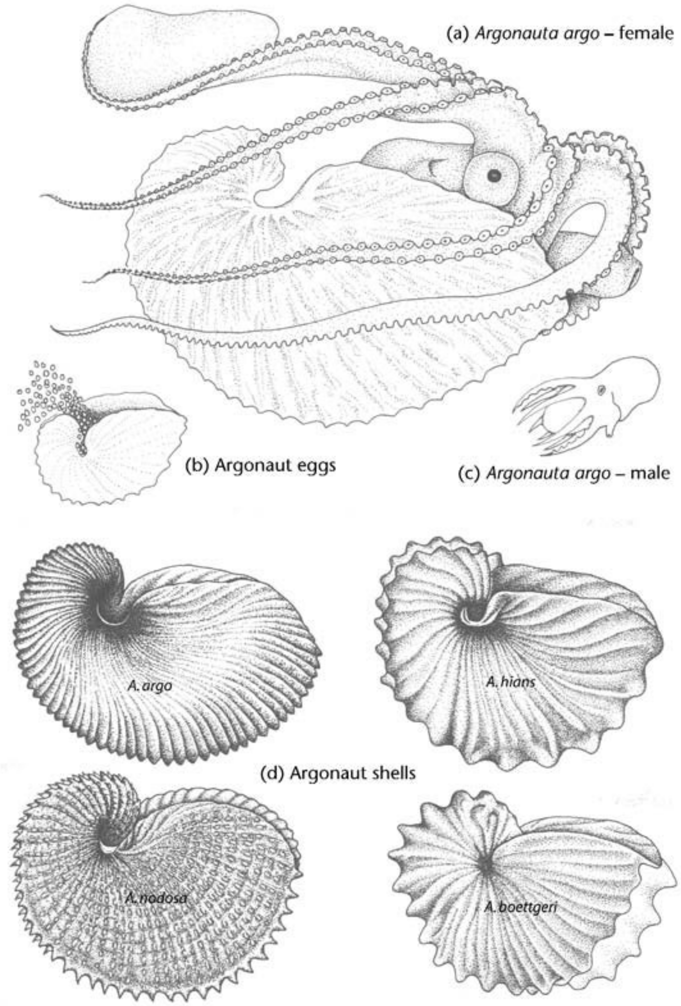


Fig. 12.8 *Argonauta argo*. (a) Female within the shell (egg case or brood chamber) showing the modified arm used to secrete the shell. (b) Eggs within the shell. (c) Male to the same scale as the female (after Voss & Williamson 1971). (d) Shells of several species of paper nautilus (after Nesis 1987).

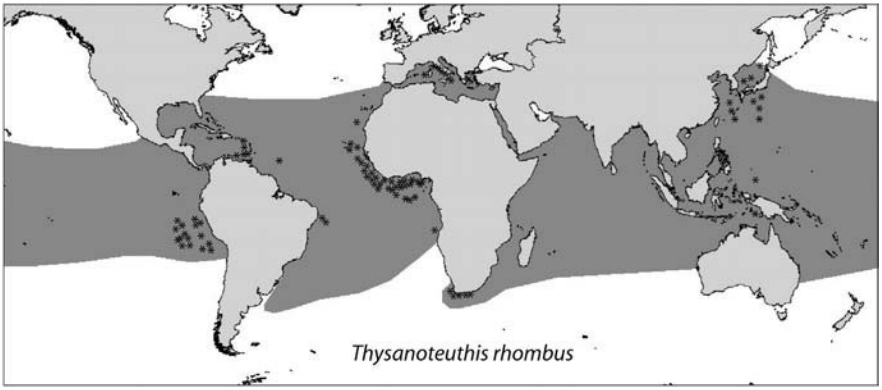


Fig. 12.9 *Thysanoteuthis rhombus*. The estimated global species range based on scattered locations of captures of adults, juveniles and egg masses, shown approximately by the data points marked with an asterisk (after Nigmatullin & Arkhipkin 1996).

Box 12.1 The search for the giant squid *Architeuthis*

Giant squid of the genus *Architeuthis*, the only members of the family Architeuthidae, are certainly the main models for the sea monsters of myth and legend. Early descriptions of encounters between mariners and isolated giant squid have given rise to many exaggerated historical accounts of the size of these animals (Ellis 1998), but students of science fiction will recognise many cephalopod features (beaks, suckers and slime, large size and predatory) among the characteristics of modern science fiction monsters!

Scientific knowledge of these animals is largely limited to the examination of infrequent single specimens found in surface waters and cast up on beaches (Fig. 12.1.1). Although these are smaller than descriptions suggest is possible, it is certain that a body mass of 450 kg, mantle length ≈2 m and overall lengths (including tentacles) of 15 m are achieved. Despite very significant investments in dedicated research cruises, no healthy living specimens have been caught for scientific research, or observed by underwater video or from ROV. Consequently, nothing definite is known about their habitat or population biology.

Fig. 12.1.1 A small *Architeuthis* stranded on the Aberdeenshire coast in 1998 (photograph courtesy Martin Collins).

It is presumed that these are largely mesopelagic animals (500–1000 m depth), widely distributed throughout all ocean basins, and feeding on fish and crustaceans. Although they are powerful muscular squid, they also have a high content of ammonium chloride which reduces their density in seawater. The history of whaling provides several accounts of sperm whales surfacing with giant squid in their jaws (Fig. 12.1.2). *Architeuthis* beaks are known from the stomachs of sperm whales, which are probably one of the only natural predators on adult giant squid.

Fig. 12.1.2 Interactions between giant squid and sperm whales depicted on postage stamps.

Table 12.1 Estimates of adult size (mantle length, mm) and approximate age (months or days) for selected oceanic and deep-sea cephalopods.

Species	Family	Size/age data	Source
Watasenia scintillans	Enoploteuthidae	F 61 mm, 12/13 months M 50 mm, 11/12 months	Hayashi 1993
Berryteuthis magister	Gonatidae	F 190–210 mm, 36 months M 180–240 mm, 36 months	Natsukari *et al.* 1993
Enoploteuthis leptura	Enoploteuthidae	F/M 80–100 mm, 6 months	Arkhipkin 1994
Onychoteuthis banksi	Onychoteuthidae	F 80–148 mm, 200–260 days M 70–117 mm, 160–232 days	Arkhipkin & Nigmatullin 1997
Sthenoteuthis pteropus	Ommastrephidae	F/M 320–600 mm F 12 months M 10/11 months	Arkhipkin & Mikheev 1992
Sthenoteuthis oualaniensis (giant form)	Ommastrephidae	F 500–650 mm, 13/14 months M 230–320 mm, 12 months	Nesis 1983
Cranchia scabra	Cranchiidae	F/M 120–130 mm Immature 4/5 months	Arkhipkin 1996
Liocranchia reinhardti	Cranchiidae	F/M 179–200 mm Immature 4/5 months	Arkhipkin 1996

F, female; M, male.

12.3.1 Age and growth in the oceanic and deep-sea cephalopods

Chapter 13 questions the extent to which the oceanic and deep-sea species resemble their coastal relatives in the key features of growth, and age to reproductive maturity and subsequent death. Whether the generalisations and assumptions of high growth and early death apply in the deep-sea environment of relatively low food availability and temperature is critical to the extrapolations that can be made about the probable standing crop biomass of cephalopods and their annual production.

Despite the low temperature and apparently low productivity of the meso- and bathypelagic environment, the available estimates of growth in squids are not dramatically lower than those of coastal species of comparable size (Table 12.1).

12.4 Benthos of the slope and deep sea

12.4.1 The upper slope

Despite the 'overlaps' of the neritic fauna of the shelf, over the shelf-break at about 200 m, and on down the continental slope to some hundreds of metres depth that were noted in Chapter 11, there is a distinctive change in the composition of the cephalopod fauna at this boundary.

12.4.2 Benthic and epibenthic octopuses (suborder Incirrina)

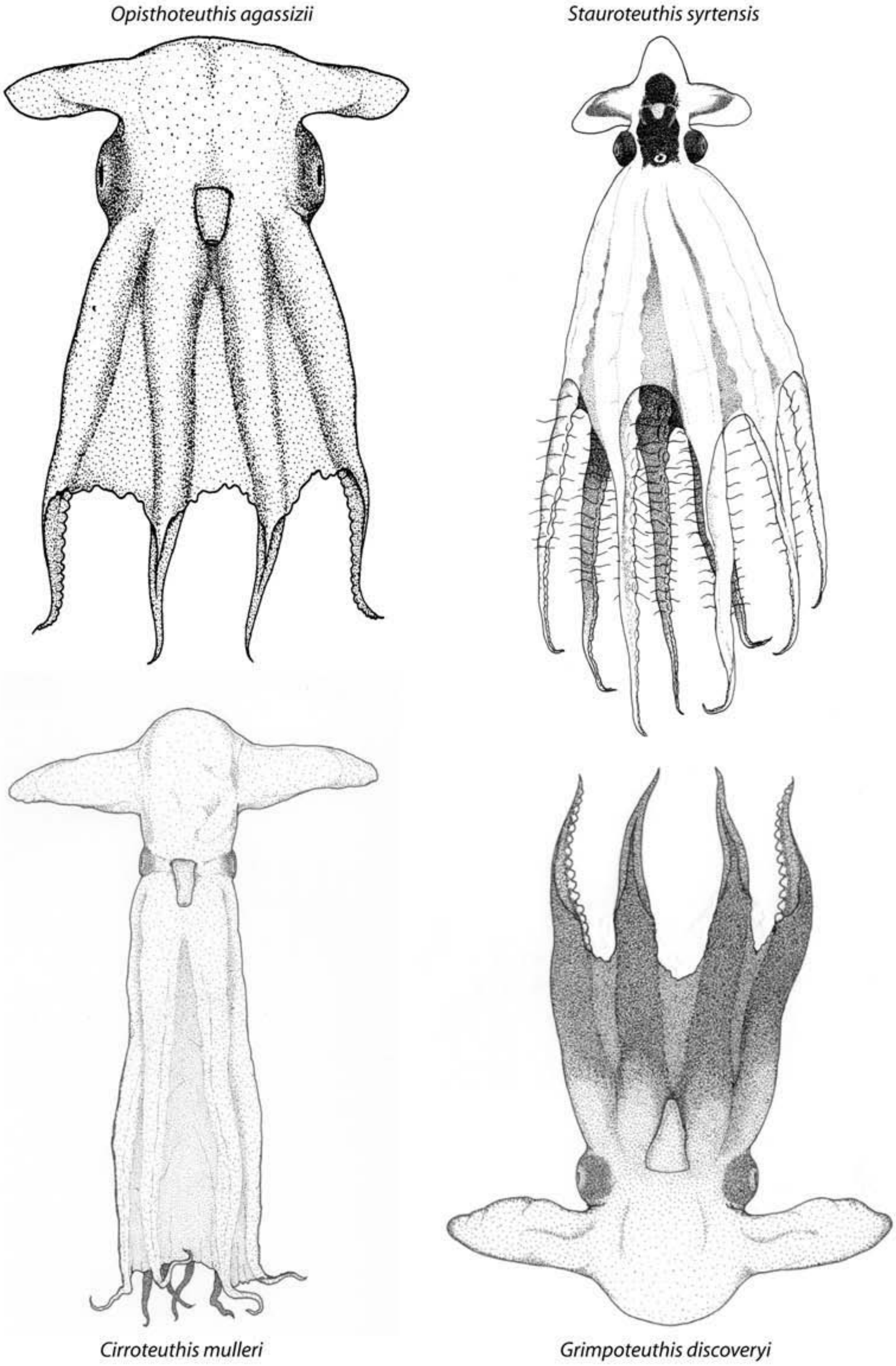
In her overview of shallow-water octopus biogeography, Voight (1998) includes 93 species of the family Octopodidae (suborder Incirrina), some of which have distributions down to 800 m. Octopus species from this and other incirrate octopus families

(Alloposidae, Amphitretidae, Idioctopodidae) have continuous depth distribution ranges from the littoral to bathyal–benthic zones (<2000–3000 m), and include species of *Alloposus* (*Haliphron*), *Bathypolypus*, *Danoctopus*, *Graneledone*, *Octopus*, *Scaeurgus* and *Pareledone* (e.g. González & Sanchez 2002; Quetglas *et al.* 2000). Molecular approaches applied to the deep-water Southern Ocean octopuses (Allcock & Piertney 2002) shows that several genera are polyphyletic, including the endemic genus *Pareledone*. For these deep-water forms especially, for which there is relatively little conventional museum material available to systematists and almost no biological knowledge, molecular systematics can be expected to have a significant impact on current ideas of their classification.

Virtually nothing is known concerning any special adaptations of these octopuses to occupy such a wide depth range, operate at low-temperatures in permanent darkness, and grow and reproduce in such a relatively low productivity environment. Some are flaccid and gelatinous (*Alloposus*), while others (*Octopus*, *Pareledone*, *Bathypolypus*) resemble the muscular shallow-water forms. Study of a substantial collection of *Bathypolypus articus* from the northwest Atlantic and living on soft sediments, supported by observations of live specimens in captivity (O'Dor & Macalaster 1983), suggest an animal that feeds on benthic infauna located primarily by chemotactile senses, grows and matures more slowly than shelf species and may take nearly 4 years to complete its life cycle.

12.4.3 Cirrata – the finned octopuses (suborder Cirrina)

Characteristic of the slope and abyssal environment are the gelatinous finned octopuses of the suborder Cirrina (Fig. 12.10), defined by the double row of cirri along each arm alternately flanking the suckers, and the presence of a pair of fins in the middle or at the posterior end of the mantle. Two families are recognised (see Appendix B): the Cirroteuthidae (bell-like elongated mantle, 6 genera, 23 species) and the Opisthoteuthidae (thickened mantle and short arms, 1 genus, 11 species). Other arrangements of families are recognised (Voss G. 1988b; Nesis 1987; Voss *et al.* 1998a), and it is clear that broad agreement on the systematics and biology of these fragile and deep-water animals is still hampered by lack of access to living specimens (Vecchione *et al.* 2002a). They are typically distributed on the slope below about 200 m to depths of over 5000 m, but specimens are increasingly available caught by deep-water fishing and research trawls (Boyle *et al.* 1998; Collins *et al.* 2001), coupled with live observations caught on camera and video from research and commercial remotely operated vehicle (ROV) observations (Roper & Brundage 1972; Roper & Vecchione 1997, 2001; Vecchione & Roper 1991; Vecchione *et al.* 2002b; Villanueva *et al.* 1997). These cirrate octopods do not swim using the mantle for jet propulsion, but by a combination of a sculling action by the fins and medusoid propulsion by the arm/web complex (Vecchione & Young 1997). Females of *Opisthoteuthis* appear to become reproductively mature at a small size and to produce a continuous output of single eggs, deposited freely on the bottom, while continuing to grow (Villanueva 1992a; Boyle & Daly 2000). Gut contents also suggest a diet which largely consists of small benthic infaunal animals such as polychaetes and amphipods (Villanueva & Guerra 1991). It is



Opisthoteuthis agassizii

Stauroteuthis syrtensis

Cirroteuthis mulleri

Grimpoteuthis discoveryi

Fig. 12.10 Representative examples of cirromorph octopuses from the slope and deep-sea benthos. All ventral views, not to scale (drawings courtesy Martin Collins).

suggested by Vecchione & Young (1997) that some of the more benthopelagic forms, such as *Stauroteuthis*, may even entrap prey in a mucous web in combination with the action of their relatively long cirri. Although the earlier concepts of complete aseasonality in the dark, deep-water environment have been dispelled (Gage & Tyler 1991), the only study of the reproductive condition of a cirrate octopus from the upper shelf over an annual cycle failed to find any evidence for a seasonal change in the frequency of reproductive stages in the population (Daly *et al.* 1998).

Reports of luminescence in octopuses are rare, but it appears that at least some cirrate octopuses (*Stauroteuthis syrtensis*, family Cirroteuthidae) have light organs along each arm, apparently formed from adapted suckers (Johnsen *et al.* 1999).

12.4.4 Bathy- and abyssobenthic octopuses

The deep-sea benthic and epibenthic cephalopod fauna is typically dominated by the octopods (Voss G. 1988b). Both incirrate and cirrate forms tend to develop flaccid, gelatinous bodies and a deep web between the arms. The increasing availability of specimens from targeted scientific sampling (Collins *et al.* 2001; Collins 2003; Roeleveld *et al.* 1992) and the bycatch of deep-water trawling (Boyle *et al.* 1998) show a diverse epibenthic cephalopod fauna adapted to feeding on small benthic prey. The radula is usually reduced or lost (but present in *Graneledone*, *Benthoctopus* and some *Grimpoteuthis*). Visual information from manned submersibles and ROVs suggests that active swimming is by gentle pulsations of the web and arms (analogous to scyphozoan jellyfish) or sculling motions of the fins. The fin muscles in cirromorph octopuses are the firmest and most developed in the animal, and are firmly anchored to an internal skeletal structure considered to be a remnant of the ancestral shell. These octopods are often observed apparently motionless in the water column, or descending gently with the web widely spread giving rise to the view that parachuting down on to the bottom and covering an area equivalent to that of the spread arms and web is the normal method of feeding.

The cirromorph octopuses are distinguished by (usually) degenerate suckers along the arms, each flanked by a pair of distinctive appendages – the cirri. In the absence of live studies there is no definite information as to the use of these structures, but it is generally believed that they are feeding organs, assisting in the capture of microbenthic (and even micronektonic) prey (Collins *et al.* 2001; Vecchione & Young 1997; Villanueva & Guerra 1991) from the water or sediment surface. Despite wide areas of distribution, these bathyal octopod species are probably over-dispersed and present in low overall densities. Collins *et al.* (2001) give abundance estimates by area for several species in the northeast Atlantic which reached to 25 individuals per square kilometre.

In common with many groups of widespread deep-sea animals, cephalopods have taken advantage of the specific loci of production associated with hydrothermal vents. Voight (2000a) describes how *Graneledone boreopacifica*, a widely distributed species, was collected by submersible from the caldera wall of the Axial Volcano on the Juan de Fuca Ridge in the north Pacific at 1459 m depth. At least 30 individual gastropods and 46 individual polychaetes were identified in the gut contents; in contrast to the shelf species, the large beaks had crushed the prey and sufficient hard parts were ingested to allow ready identification. With increasing exploration of these isolated habitats, the first new species associated expressly with the hydrothermal environment has been described. This is *Vulcanoctopus hydrothermalis* from the east Pacific Rise at 2640 m deep, and it raises the possibility that a new sub-family of octopuses (Vulcanopodidae) may be justified (Gonzalez *et al.* 1998b, 2002b). Through the increased use of submersibles at these great depths, new biological and behavioural information on these animals is becoming available (Gonzalez *et al.* 2002a; Rocha *et al.* 2002).

12.5 Cephalopods of seamounts and submarine ridges

Based on extensive oceanographic campaigns by Russian and former USSR vessels, Nesis (1993a) provides the best available description of oceanic cephalopod communities associated with seamounts and submarine ridges. Seamounts and guyots (flat-topped) are undersea mountains of volcanic origin, rising from the ocean bed to within 200 m or less from the surface, and are present in all the major ocean basins. Usually distant from the continental margins, they represent a discrete oceanic habitat (Rogers 1994) with enhanced productivity and a fauna different from that of the continental shelves. In most respects these isolated habitats might be expected to be quite distinct from the coastal shelves. Nevertheless, as a consequence of their discrete formation they have provided almost the only descriptions of what may be understood as cephalopod communities. In his review, Nesis (1993a) distinguishes five main groups of cephalopod species associated with seamounts and a sixth group which avoids them.

- Bottom and near-bottom species living permanently on seamounts (Fig. 12.11), consisting principally of cuttlefish and sepiolids, loliginid squids and octopuses, and further zoned into shallow (<200 m, *Sepia* spp., *Octopus* spp., *Loligo* spp.), lower sublittoral and upper bathyal (100–800 m, *Pteroctopus* spp., *Danoctopus* spp., *Scaeurgus* spp.), and middle and lower bathyal species (500–2000 m, typically octopuses such as *Grimpoteuthis* spp., *Opisthoteuthis* spp. (sub-order Cirrina), *Benthoctopus* spp., *Bathypolypus* spp. (suborder Incirrina)).
- Near-bottom and benthopelagic species, which regularly (or at some part of their life history) rise into mid-water over the seamount, such as the micronektonic sepiolids which are diel migrators, e.g. *Sepiolina* spp. and *Stoloteuthis* spp.
- Nerito-oceanic species, i.e. paralarvae, juveniles and some sub-adults from some of the oceanic squid families (e.g. the Ancistrocheiridae, Lycoteuthidae, Onychoteuthidae, Histioteuthidae, Ommastrephidae and Pholidoteuthidae).

Then there are groupings of true pelagic forms (Fig. 12.12) which have no direct connection with the hard substrate (except possibly at spawning).

- Interzonal epi-mesopelagic animals that are passively advected by currents over the seamounts at night and descend during the day to the bottom (i.e. diel vertical migrators) if the bottom depth is shallower than their usual lower depth horizon. There are examples of many species of Enoploteuthidae, Histioteuthidae, Octopteuthidae and *Ctenopteryx sicula*.

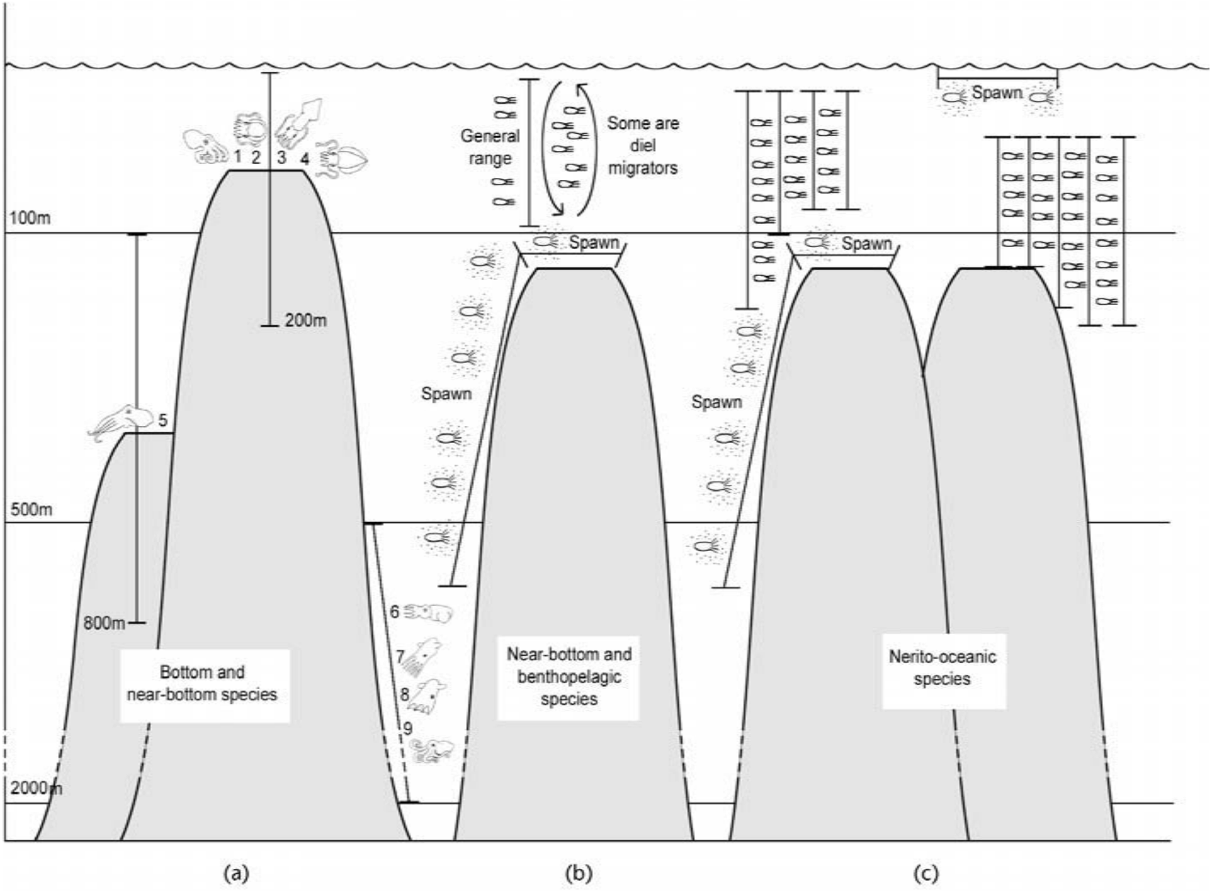


Fig. 12.11 Associations of cephalopods with oceanic seamounts and banks. (a) The permanent bottom and near-bottom shallow-water resident genera (e.g. 1, *Octopus*; 2, *Sepia*; 3, *Loligo*; 4, *Sepioteuthis*) and upper and lower bathyal slope residents (e.g. 5, *Scaeurgus*, *Pteroctopus*, *Danoctopus*; 6, *Neorossia*; 7, *Froekenia*; 8, *Grimpoteuthis*, *Opisthoteuthis*; 9, *Benthoctopus*, *Bathypolypus*). (b) Near-bottom genera (e.g. *Sepiolina*, *Stoloteuthis*), and the cycling between the benthic habitat and mesopelagic or surface waters of these bottom and near-bottom species at different life-cycle stages. (c) The associated larval and juvenile forms of some true oceanic squid families. After Nesis (1993a).

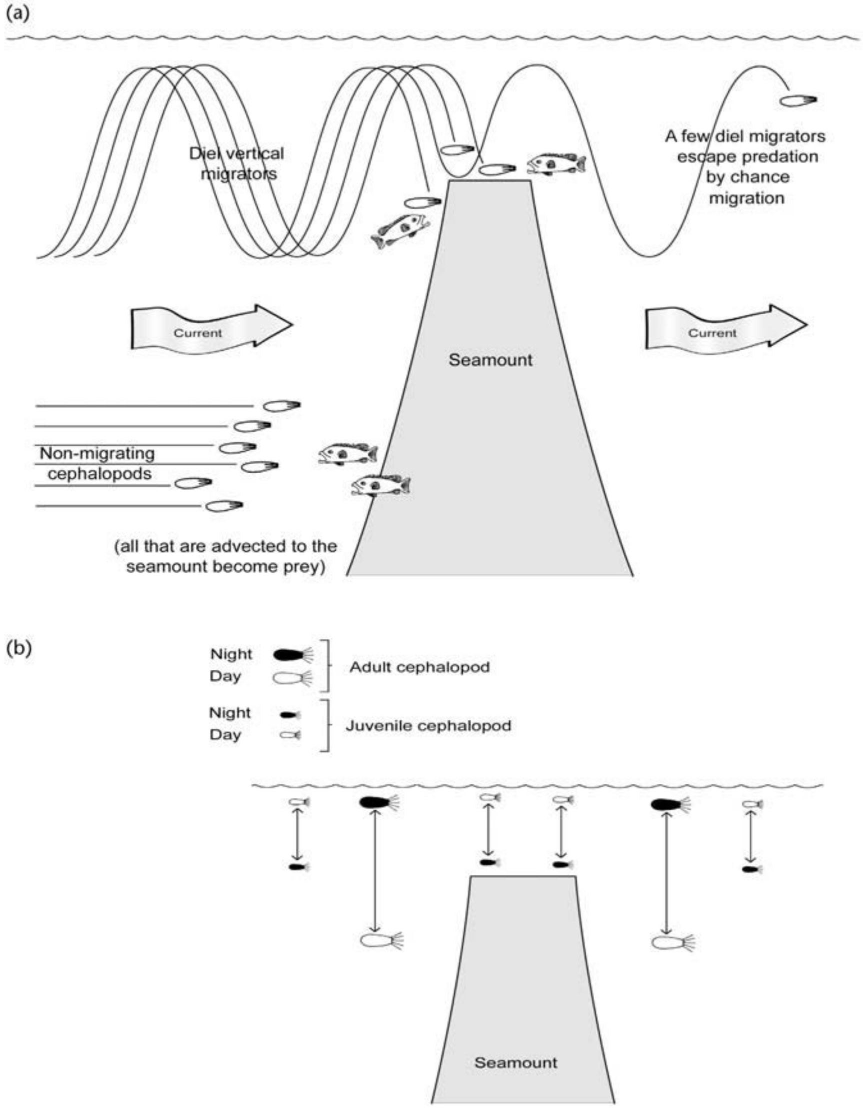


Fig. 12.12 Schematic representation. (a) Pelagic cephalopods passively advected by currents to seamounts. Two categories are represented: diel vertical migrators, descending to the bottom during the day (Enoploteuthidae, Pyroteuthidae, Histioteuthidae, etc.), and non-migrating (mostly bathypelagic) species (Chiroteuthidae, Mastigoteuthidae, Cranchiidae, *Vampyroteuthis*, *Japatella*, etc.). (b) Nektonic oceanic squids (also diurnal migrators) that avoid the waters over the summits of banks and guyots (e.g. *Ommastrephes bartrami*, *Sthenoteuthis pteropus*, *S. oulaniensis*). After Nesis (1993a).

- Non-migrating, mostly bathypelagic species living more or less always at the same depth, and which are passively advected by currents on to the tops of deep mountains or slopes of seamounts. There are many examples from Chiroteuthidae, Mastigoteuthidae, Cranchiidae, *Vampyroteuthis infernalis* and *Japatella diaphana*.
- Pelagic cephalopods that appear to actively avoid the areas over seamounts. These include large nektonic oceanic ommastrephids such as *Sthenoteuthis pteropus*, *S. oualaniensis* and *Ommastrephes bartrami*.

Chapter 13

Population ecology

Summary: No cohesive description of cephalopod population ecology is yet available. The most abundant data arise from commercial-scale fisheries catches, but problems of species identification, the spatial and temporal location of fished stocks, and the occurrence of large-scale migrations all limit their use. The general biological features of the short life cycle and uni-seasonal breeding result in little overlap of successive generations. Cephalopod populations are highly influenced by environmental conditions for growth and recruitment of the hatchling broods, and show wide inter-annual fluctuations. Size-frequency and age-frequency analyses of populations suggest that a sub-structure of microcohorts (intra-annual) is frequently present. Modelling of population ecology for fisheries purposes is confounded by a lack of consensus among workers as to the form of growth model to be applied, and also by a lack of data to define populations. Immigration and emigration effects lead to distinct biases in estimations of growth rates and mortality in many populations, but molecular markers, particularly microsatellites, may shortly offer new certainty to population definitions. The uncertainties surrounding the generality of life cycle and population models is a major factor in evaluating the reality of the estimates of cephalopod biomass and production.

The population biology of a defined group of animals includes those quantitative aspects of its biology leading to understanding changes in the scale and distribution of their numbers and biomass. It is through these changes in numbers and biomass that the effects of environmental and biotic factors on the success of the population can be measured. The timescale over which changes occur is determined by the intrinsic characteristics of growth, reproduction and death of the animals (the life cycle), the rates of change of environmental factors and the operation of biological interactions such as predation and parasitism, and encompasses seasonal, inter-annual and decadal time-scales. Because population dynamics (including changes in the geographical area of distribution) effectively tracks the relative success of a defined group, it represents the integration or outcome of all the factors affecting the animals and is properly defined as the study of their ecology (Krebs 1972).

In the case of cephalopods, we have already said something of their growth, reproduction, life cycles and the environmental factors affecting recruitment and distribution. Here we specifically discuss those features quantitatively defining the *populations* of cephalopods, populations that are rarely stable in numbers or location. A description of the population biology is essential to understanding the interactions between cephalopods and other components of the marine food-web. In this way also, any impact by fisheries exploitation can be followed and an estimation of the population available to fishing can be attempted. For cephalopods especially, the scientific study of populations and its application to fishery questions are quite inseparable. There are few objectively structured population surveys, and most of these are research survey cruises using commercial fishing gear. Most of the population data available are obtained from commercial fisheries with all the attendant bias towards data on the adult-sized population, concentration in areas and at times of high population density, and the use of relatively large-mesh nets.

Reviews of cephalopod population biology have been undertaken principally in relation to the scale of fishery resources, notably those of Amaratunga (1983, 1987), Caddy (1983a), Saville (1987) and Voss (1973, 1983). Review articles emphasising the biological features of cephalopod populations can be found in Caddy (1983b, 1991), O'Dor & Coelho (1993), Boyle & Boletzy (1996), Carvalho & Nigmatullin (1998) and Rodhouse (2001).

The techniques available for the study of population ecology are based primarily on traditional approaches such as the size frequency as measured in large samples. Size frequency analysis has been supplemented by methods of age frequency using estimates of daily age derived from incremental lines in the statolith or gladius (see Boxes 7.1 and 7.2). Conventional fishery approaches, based on the presence of populations of fishable concentrations or breeding aggregations, are also widely used, with molecular genetic markers beginning to make an impact. Despite the wealth of data about populations describing temporal and geographical changes, a cohesive view of population ecology has not yet been fully formed.

13.1 What is a population?

13.1.1 Species recognition

The initial task in describing a cephalopod population is that of species recognition. Aside from the problems of identification of rare or deep-water species, even the main fishery resources are often incompletely recorded. Over 50% of the global cephalopod annual catch of about 3–4 million tonnes is not recorded by species (Boyle & Boletzky 1996, Chapter 17), which significantly limits the uses of the data for population studies. The reasons for this lack of precision are a lack of expertise in species recognition in the fishing industry, a lack of demand for product identification by species in the trade, and the loss of data by pooling statistics into generic categories (e.g. *Loligo* sp), or families (e.g. Loliginidae) for administrative reasons. Unusually for valuable marine products, cephalopods are often traded simply as squid or octopus.

13.1.2 Species identity

Real species identity problems are current even in the most abundant and well-studied populations. Recent studies are tending to break down some of the most widespread cephalopod species and genera. The cosmopolitan *Octopus vulgaris* is probably a species group rather than a single species, with the historically designated species being restricted to a limited area of distribution (Mangold & Hochberg 1991). The cuttlefish species, *Sepia officinalis*, extends southward only to about 15°N on the north-western coast of Africa because its previously recognised subspecies (*Sepia officinalis hierredda* of tropical West Africa and *S. o. vermiculata* of South Africa and the Western Indian Ocean) are now to be recognised as distinct species (Khromov *et al.* 1998). Evidence from allozyme studies (Pérez-Losada *et al.* 1996; Guerra *et al.* 2001a) confirmed earlier suggestions (Rochebrune 1884) that further sub-division of the genus *Sepia* will be necessary.

The loliginid squid, *Sepioteuthis lessoniana*, might represent more than one species, as suggested by differences in the spawning mode within local populations in Okinawa (Segawa *et al.* 1993) and other evidence (Izuka *et al.* 1996a, b). Three main forms of the ommastrephid *Sthenoteuthis oualaniensis* in the Indian Ocean are recognised by Nesis (1993b) on the basis of population structure. For sepiolid squids of the Mediterranean, Gabel-Deickert (1995) considers the possibility of hybrid species of *Sepiola affinis*. These examples all seem to arise from the excessive aggregating by systematists of regionally known species, and potentially the current trend towards the dividing of categories will have a significant effect on considerations of biodiversity and zoogeography. Scientific advances in the definition and recognition of cephalopod species will not necessarily lead to rapid improvements in the value of fishery data unless they are generally accepted by the industry. This is because traditional species names, e.g. *Octopus vulgaris*, when assigned to catches from a particular area may attach value to the product; value which would be lost if the species name was changed.

13.1.3 Recognition of stocks

A population, as defined by Mayr (1970), is understood to mean a large group of individuals of the same species maintaining itself by reproduction in a describable geographic area or habitat. This approach ignores the precise number of individuals encompassed and the probability that smaller groups of individuals may be recognisable and comprise distinct populations or stocks. Sinclair (1988) draws attention to the difference between species having a single, or only very few, broadly distributed populations, and species containing large numbers of populations. This difference provides the criterion of the population richness of a species, where the number of observed local populations is not necessarily identical with the number of truly distinct populations. Dispersal of individuals or groups may connect local populations in an ensemble called the metapopulation, but for cephalopods there are insufficient molecular genetic data available to define local populations and to recognise movements between them for this concept to be useful (Box 13.1).

Box 13.1 Tagging and tracking

Migration and distribution

The use of identifying tags to follow the movements of individuals and populations has wide application in conventional fisheries biology. Movements of shelled nautiluses have been readily tracked with tags (Saunders & Spinoza 1979; Carlson *et al.* 1984), but other cephalopods have proved difficult to mark because the soft body does not retain a tag very well, and their short lifespan and high natural mortality reduce recapture rates to very low levels. Nevertheless, tagging of large numbers of individuals using conventional tags, usually of plastic, have yielded results for many fished species in Japanese waters, especially *Todarodes pacificus* (Nakamura 1993).

Spawning behaviour

Where intensive fishing is localised around a spawning area, movements of individual *Loligo vulgaris reynaudi* on a day-to-day basis have been interpreted from tagged animals (Sauer *et al.* 2000).

Individual growth

Large benthic octopus can carry tags over significant periods of time. They occupy limited areas of territory and can be readily re-captured to provide linear data on growth in field conditions for *Octopus vulgaris* (Domain *et al.* 2000), and on den utilisation, movement and growth in *Octopus* (*Enteroctopus*) *dofleini* (Hartwick *et al.* 1984; Robinson & Hartwick 1986). Electromagnetic tags implanted into *Octopus tetricus* and *O.maorum* have also been evaluated (Anderson & Babcock 1999).

Activity and metabolism

Advances in the miniaturisation of acoustic transmitters have allowed the implantation of ultrasonic transmitters into cephalopods (Fig. 13.1.1). Tracked by sensitive hydrophones mounted on a vessel, large squid such as *Ommastrephes bartrami* (Nakamura 1993), *Dosidicus gigas* (Yatsu *et al.* 1999) and *Loligo forbesi* (O'Dor *et al.* 1994, 1995), as well as *Nautilus* (O'Dor *et al.* 1993), have been tagged and tracked in the wild. Acoustic telemetry not only has the potential to provide detailed information on individual movement within three-dimensional space, but also to signal information about mantle movements from which the energetic costs of locomotion can be inferred.

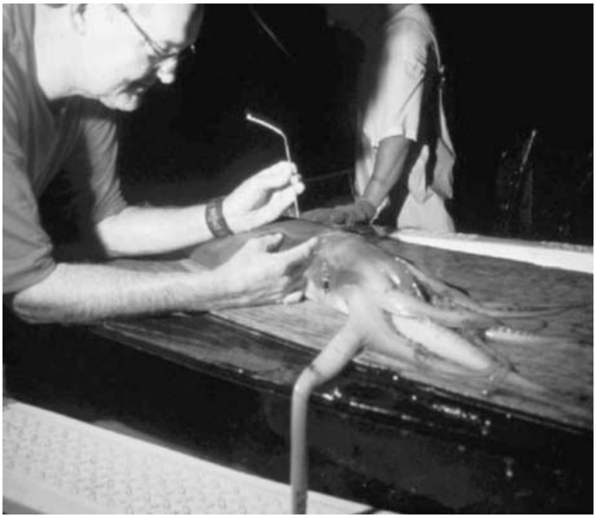


Fig. 13.1.1 Professor Frank Carey implanting an acoustic tag in a large *Loligo forbesi* in the Azores (photograph couretsy Ron O'Dor).

In practice, it is impossible to discover the number of individual members of a species inhabiting a given region of the marine habitat or a sub-division of its population, but the term 'stock' is conventionally used to refer to a subset of the population which is available to fishing in a given season or area.

The sub-division of cephalopod species into distinct populations or stocks is often made on the basis of the timing and location of breeding or the recruitment of young (Carvalho & Nigmatullin 1998). These are commonly recognised by the availability to fishing of the adult/sub-adult component. Examples of such pragmatic approaches to stocks for the purposes of fisheries assessment or management include *Todarodes pacificus* in the coastal waters of Japan (timing and strength of recruitment, Araya 1976), *Octopus vulgaris* on the Saharan Bank (geographical location of major concentrations, Bravo de Laguna 1989), *Sthenoteuthis oualaniensis* in the Indian Ocean (population size structure, Nesis 1993b; Snÿder 1998) and *Illex illecebrosus* off the northeast USA and Canada (timing and strength of breeding, Coelho & O'Dor 1993). The composition of the parasitic fauna carried by cephalopods also has potential for distinguishing between stocks or populations (Pascual & Hochberg 1996), for example between *Ommastrephes bartrami* from eastern or western North Pacific feeding grounds (Bower & Margolis 1991).

Attempts to sub-divide cephalopod populations more formally, or to define stocks on the basis of differentiation within the overall distribution of a species have had mixed results (Table 13.1). Detailed morphometric measurements, coupled with multivariate statistics, have been used to separate the Azores population of *Loligo forbesi* from the population of the European mainland (Pierce *et al.* 1994e), but morphometrics are not generally sufficiently sensitive, owing to the difficulties in taking consistent measurements from soft-bodied animals, and compensating for the effects of size variation, sample treatment or inter-worker bias (Pierce *et al.* 1994b).

The differentiation of allozymes by electrophoresis has been used successfully in some cases to recognise distinct populations (Brierley *et al.* 1993b, 1995; Brierley & Thorpe 1994; Carvalho *et al.* 1992; Carvalho & Loney 1989; Carvalho & Pitcher 1989; Katugin 1993, 1995, 1999), but is more likely to be useful at the species level and above (Yeatman & Benzie 1994; Boucher-Rodoni *et al.* 1995; Pérez-Losada *et al.* 1996).

Population markers based on DNA are at an early stage of their development and application to cephalopod populations. Shaw (2002), in his review of work in this field, charted the rapid increase in the development of microsatellite DNA markers, concluding that these molecular tools are likely to become very effective for the exploration of population structure in cephalopods. In common with those isolated from other organisms, microsatellites exhibit high levels of polymorphism even in species that show low levels of variability with other markers. Microsatellite regions are abundant and readily isolated in the species which are currently being examined. Beginning with *Loligo forbesi* (Shaw 1997), useful microsatellite markers have been isolated to more that 12 species and are beginning to be applied to ecological questions of population structuring. These cephalopod studies are at relatively such an early stage (see Shaw 2002) that questions of stock identity may grade into those of species description or even challenge the integrity of genera.

Table 13.1 Heterogeneity in cephalopod populations. Various approaches to the sub-division of cephalopod populations using criteria of: (1) geographic separation; (2) spawning characteristics; (3) recruitment pattern; (4) morphometric and meristic variation; (5) allozymes; (6) mitochondrial DNA; (7) microsatellite DNA markers; (8) behaviour/colour pattern; (9) parasite fauna, separately or in combination (+). Partially updated from Boyle & Boletzky 1996.

Species	Method	Reference
Berryteuthis magister	5	Katugin 1993, 1999
Dosidicus gigas	9	Shukhgalter & Nigmatullin 2001
Eledone cirrhosa	4	Boyle *et al.* 1988
Eledone sp.	5	Levy *et al.* 1988
Illex argentinus	5,7,4	Adcock *et al.* 1999a,b; Carvalho *et al.* 1992; Martinez *et al.* 2002
Illex coindetii	7,4,9	Dillane *et al.* 2000; Martinez *et al.* 2002; Pascual *et al*. 1996
Illex illecebrosus	1+2+3,4	Coelho & O'Dor 1993; Martinez *et al.* 2002
Loliginidae	6	Anderson 2000a, b
Loligo spp.	8	Hanlon 1988
Loligo bleekeri	5	Suzuki *et al.* 1993
Loligo chinensis	4+5	Yeatman & Benzie 1993
Loligo forbesi	5,3,4,7	Brierley *et al.* 1993b; Boyle & Ngoile 1993; Pierce *et al.* 1994d; Shaw *et al.* 1999
Loligo gahi	5,2+4+5	Carvalho & Loney 1989; Carvalho & Pitcher 1989; Vega *et al.* 2002
Loligo opalescens	4,5,5	Kashiwada & Recksiek 1978; Ally & Keck 1978; Augustyn & Grant 1988
Loligo pealei	5	Garthwaite *et al.* 1989
Loligo plei	5	Garthwaite *et al.* 1989
Loligo vulgaris	4,5	Augustyn & Grant 1988
Loligo vulgaris reynaudi	2	Augustyn *et al.* 1993
Loliguncula brevis	5	Garthwaite *et al.* 1989
Martialia hyadesi	5	Brierley *et al.* 1993a
Nototodarus sloanii sloanii	1,2,3	Kawakami & Okutani 1981, In: Okutani 1977
Nototodarus gouldi	5	Richardson 1983
Octopus spp.	8,8,4+8	Roper & Hochberg 1988; Hanlon 1988; Norman 1992b, c
Octopus vulgaris	1,7,4,6	Bravo de Laguna 1989; Greatorex *et al.* 2000; Mangold & Hochberg 1991; Soller *et al.* 2000
Ommastrephidae	5	Yokawa 1994
Ommastrephes bartrami	3,9	Dunning 1993; Bower & Margolis 1991
Pareledone turqueti	5	Allcock *et al.* 1997
Photololigo edulis	2	Natsukari *et al.* 1988
Sepia officinalis	5,7,5	Travouez & Boucher-Rodoni 1990; Perez-Losada *et al.* 1996, 2002; Shaw & Perez-Losada 2000; Sanjuan *et al.* 1996; Perez-Losada *et al.* 1999
Sepia orbignyana	5	Perez-Losada *et al.* 1996
Sepioteuthis lessoniana	2,6,8	Segawa *et al.* 1993; Izuka 1996a, b
Sthenoteuthis oualaniensis	1,2,3,4	Nesis 1993b
Sthenoteuthis pteropus	1,2	Zuev & Nikolsky 1993
Thysanoteuthis rhombii	6	Kitaura *et al.* 1998
Todarodes pacificus	1,2,3,5	Araya 1976; Katugin 2000
Todaropsis eblanae	7	Dillane *et al.* 2000

13.2 Structuring of populations – size and age

‘Population structure is a difficult concept to define, let alone determine’ (Hatanaka *et al.* 1993).

13.2.1 Annual cohorts

In cephalopod species that are fundamentally uni-seasonal breeders, the expectation is that there would be a single or main period of annual recruitment. In its simplest form this reproductive pattern should define a limited period of time over which recruitment occurs, followed by growth and maturation of the new population to breeding condition at the end of the same year. In many fishery studies this expectation is partially fulfilled, and over a few successive months a single size mode in the population may be recognised and used to describe seasonal growth. This simple pattern of uni-modal recruitment and growth has been a used many times to provide models of individual growth and population biomass of relevance to fisheries.

Unfortunately, detailed studies of most fished cephalopod populations find that the simple uni-modal population structure is difficult to recognise, or it breaks down for certain periods throughout the year. Attempts to interpret these complex multi-modal population size frequencies have been the vexed subject of numerous papers on population ecology. Various reasons are suggested to account for why a simple uni-seasonal life cycle may not result in a clear population structure showing progressive growth over time. Commonly suggested reasons for the complex population structures actually observed include:

(1) the variable duration of the breeding season, resulting in successive waves of recruitment (Arkhipkin 1993b);
(2) changing environmental conditions (especially temperature) throughout the egg development stage or recruitment period, resulting in different conditions for growth and consequent individual size in the population (Forsythe 1993);
(3) movement of component stocks into and out of an area (Boyle *et al.* 1995);
(4) differential mortality on components of the recruited population (Caddy 1991).

These complex and interacting influences on the size structure of cephalopod populations have generated a great variety of descriptive papers on different species (e.g. Perez *et al.* 2002) but have hindered the development of a simple theoretical basis for modelling population growth.

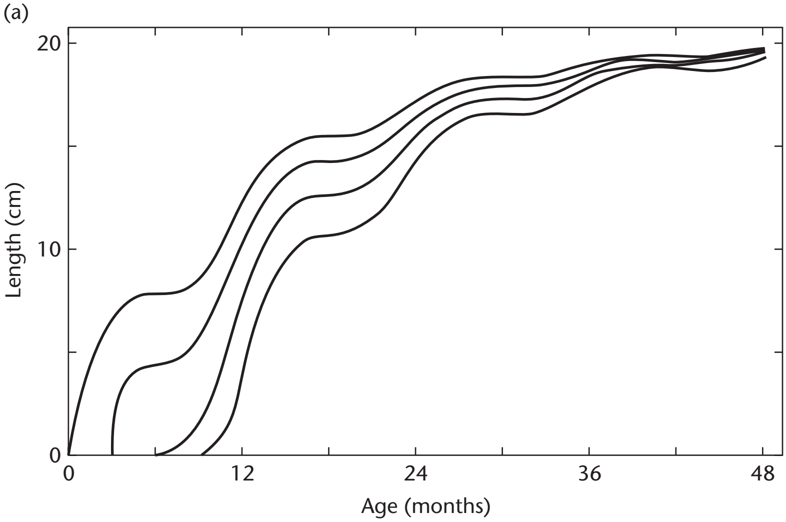
The selection by eye of size modes in the population has often been the basis for separating different cohorts. The difficulty in justifying this simple approach theoretically, and the impossibility of applying it practically in many cases, has promoted the use of statistical procedures for the formal recognition of modes such as the commonly used programmes ELEFAN™ and MIX™. These procedures are able to select modes which the show apparent growth over time, and can ignore the gaps in the size frequency pattern where these occur as breaks in the continuity of the time sequence (usually monthly samples). Some authors accept this outcome as simply reflecting the inadequate sample size, while others feel that it ignores the biological reality of tracking animals growing over periods of time (Jackson *et al.* 2000a). In populations of *Loligo gahi* in the south Atlantic, where the size frequency of the whole population is unresolved, combining data on the maturity state of animals in the sample allowed Hatfield (1996) to use proprietary software to resolve cohorts representing three annual recruitment pulses during the year.

A more fundamental theoretical problem arises with the use of statistical methods for the selection of modes that are based on assumptions that the size mode is normally distributed and that the growth form of the individual reaches an asymptotic final size. The applicability of this form of growth curve (von Bertalanffy) to cephalopods has been the subject of considerable controversy. On the one hand it is felt that there is no evidence that cephalopods individually reach final adult size, and instead that growth is interpreted as being curtailed and finally stopped by maturation and breeding and that this can occur at a wide variety of sizes (see reviews by Saville 1987; Forsythe & Van Heukelem 1987). Other authors claim that the form of the individual growth curve does not count in this regard provided that the average growth curve for the group reaches an asymptotic plateau. Pauly (1985) promotes the use of a seasonally oscillating version of the von Bertalanffy curve (consistent with his view that the age of the larger squids is consistently underestimated), and suggests that the exponential growth curve of cephalopods is consistent with a portion of a generalised von Bertalanffy model (Pauly 1998), as shown in Fig. 13.1.

13.2.2 Seasonality and recruitment

Many factors contribute to the seasonality of reproduction and recruitment. Sexual maturation of the breeding adults is usually phased to changing environmental conditions such as temperature or food availability, leading to a defined period of the year when the majority are able to breed. The same factors also serve to bring large numbers of breeding adults together as spawning aggregations, thus maximising the chance of successful breeding and promoting mixing of the gene pool. Examples of strongly seasonal breeders may be found among octopuses such as *Octopus vulgaris* and *Eledone cirrhosa*, the cuttlefish *Sepia officinalis*, loliginid squid *Loligo opalescens* and *L. forbesi*, and mid-water enoploteuthid squid *Watasenia scintillans* (Hayashi 1993). These clearly seasonal breeders frequently undergo localised migrations into shallower waters which are suitable for egg deposition and which have higher temperatures for development. In coastal cuttlefish (*Sepia officinalis*), the onset of maturity seems to be triggered by changing day length activating neuro-hormonal mechanisms which influence physiology and behaviour.

The environmental drivers of seasonal breeding do not operate consistently among related species. An intriguing case is that of the loliginid squid of the shelf off Europe and Africa. In the north, *Loligo forbesi* and *L. vulgaris* are known as 'winter breeders', maturing and spawning during November–February in conditions of shortening daylength and dropping temperatures (Pierce *et al.* 1994a). Futher south along the Atlantic coast of Africa, the closely related *L. vulgaris reynaudi* also spawns at the year end (October–December), but at a time of increasing daylength and rising temperatures coincident with the onset of the austral summer in South Africa (Augustyn 1990, 1991).



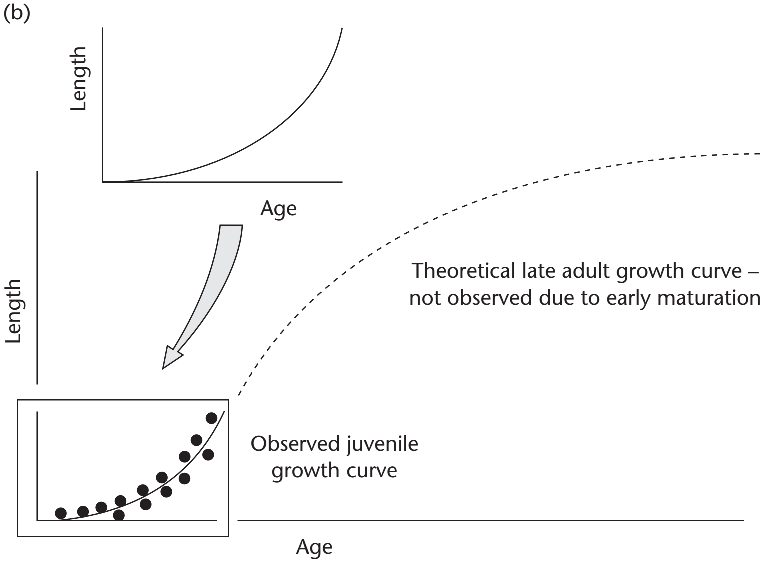


Fig. 13.1 (a) Growth curves based on a seasonally oscillating model of the von Bertalanffy growth equation in which the apparent differences in growth with time results from differences in birth-date (after Pauly 1985). Each curve uses the same set of parameters except for different values of *t* (time). (b) Schematic representation of how the 'logarithmic' phase of cephalopod growth can be interpreted as the first phase of a generalised von Bertalanffy model that has been curtailed due to paedomorphosis, i.e. early maturity at a juvenile stage (after Pauly 1998).

Seasonality in the spawning of the fertilised egg masses is only the first stage in establishing a seasonality of population recruitment and growth. The temperature at which embryonic development takes place is by far the most important influence on the duration of the incubation period and the timing of hatching (Boyle *et al.* 2001). The emergence of hatchlings to coincide with environmental conditions favourable for growth and survival is clearly extremely important. Since Cushing (1982) first coined his 'match and mis-match' concept for the timing of larval emergence, it is widely accepted that the timing of recruitment is critically important in most marine species with vulnerable small or planktonic larval stages. Species exhibiting a high degree of reproductive seasonality carry a major risk of failure to recruit should the hatchlings not coincide with optimum conditions. There would seem to be good reasons to suggest that much of the minor variability in the timing of egg-laying, and the presence of a small proportion of breeding animals at almost any time throughout the year, operates to a ensure continuity of the species if the main period of recruitment in any one year is a failure.

The basic life cycle of the coastal cephalopods therefore promotes a pattern of seasonal build-up of biomass due to growth, followed by a post-breeding crash as the population dies or is consumed by predators. There is little potential for the overlap of successive generations in the breeding population, but factors leading to extension of the breeding season, such as reduced spawning synchronicity of the population or the phasing of recruitment, will reduce the seasonal peak (Fig. 13.2).

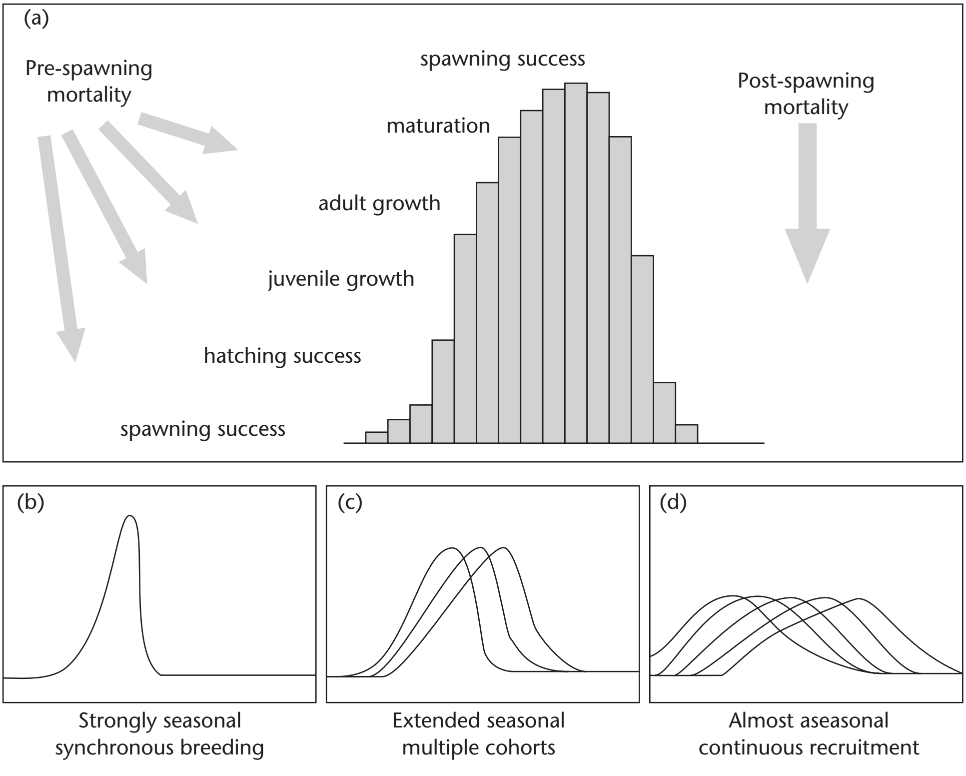


Fig. 13.2 Schematic representation of the seasonal build and crash of biomass which is typical of many neritic cephalopod populations (after Boyle & Boletzky 1996). (a) The biomass in the population (vertical axis) is determined by the relative success of the various phases of recruitment and growth, and the impact of pre-spawning mortality at each successive life-cycle stage. After breeding, post-spawning mortality resulting from endogenous factors or consumption by predators effectively eliminates the annual population. The extension of the breeding season and the progressive phasing of recruitment reduces the extremes of population scale and timing (b–d).

13.2.3 Micro-cohorts (intra-annual)

The size structure of the common cephalopod populations should be expected to be essentially simple, a single size resulting from the annual recruitment. The complexities of size structure apparent in actual population samples have usually proved difficult to interpret because the growth of size modes month-by-month cannot be tracked consistently. The introduction of routine methods for counting rings in cephalopod statoliths, and interpreting these as records of daily growth (Jereb *et al.* 1991), has provided an independent method of identifying the substructure of the population based on the timing of recruitment. These so-called 'micro-cohorts' (Caddy 1991) sub-divide what is essentially a single year-class population into its component increments of recruitment.

Where the length frequency of individuals in the fished population cannot be resolved into component micro-cohorts of recruitment, age frequency can be used (Uozumi & Shiba 1993). In a study of the Russian fishery for *Illex argentinus* off the coast of Argentina, Arkhipkin (1993b) resolved four main waves of abundance that were recruited successively in each of the three main fishing areas during the April–June fishing season. Back-calculation of the hatching date of age cohorts showed them to arise from squid generations hatched in June, July, August and September, respectively, of the previous year (Fig. 13.3). In this way the differences in recruitment strength of each micro-cohort can be linked to the environmental conditions promoting growth and survival (Arkhipkin 1994).

13.2.4 Immigration and emigration

Population analysis, either by size structure or age structure, makes a series of assumptions about the effective sampling of the population and its stability in time and place. The methodology is open to a series of errors arising from immigration and emigration in to or out of the sampled area, coupled with the bias due to the selectivity of the sampling gear. An elegant analysis of the various pitfalls of population structure studies was given by Caddy (1991). He shows how the regular recruitment of micro-cohorts into a population at different sizes may be interpreted as the spurious growth of a single cohort (Fig. 13.4a). Most moving fishing nets are also size-selective of the catch, and Caddy (1991) describes how this selectivity for the larger sizes will have the effect of reducing the apparent rate of growth of a cohort (Fig. 13.3b). Size-selective mortality from other causes (such as predation) will have similar effects, depending on whether it is selective for larger individuals (reduction in apparent cohort growth rate) or the smaller-sized animals (apparent growth rate biased upwards).

The post-spawning mortality of cephalopod adults is certain to bias the size-frequency of the population sampled during the breeding season. This tendency will lead to an apparent reduction of individual growth rates in the breeding population (by the subtraction of the larger individuals), and could be argued to give a misleading impression of attaining an asymptotic final size. Hatfield & Rodhouse (1994a) evaluated the effect of movement in to and out of the fishery for *Loligo gahi*, and concluded

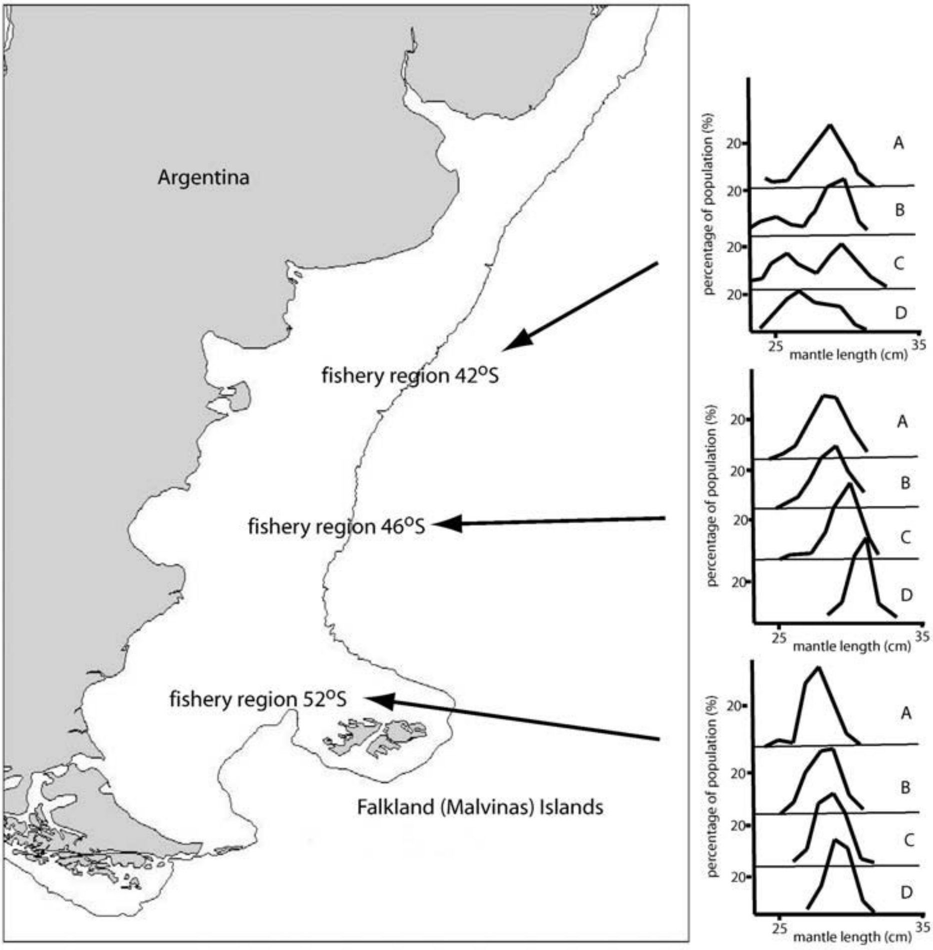
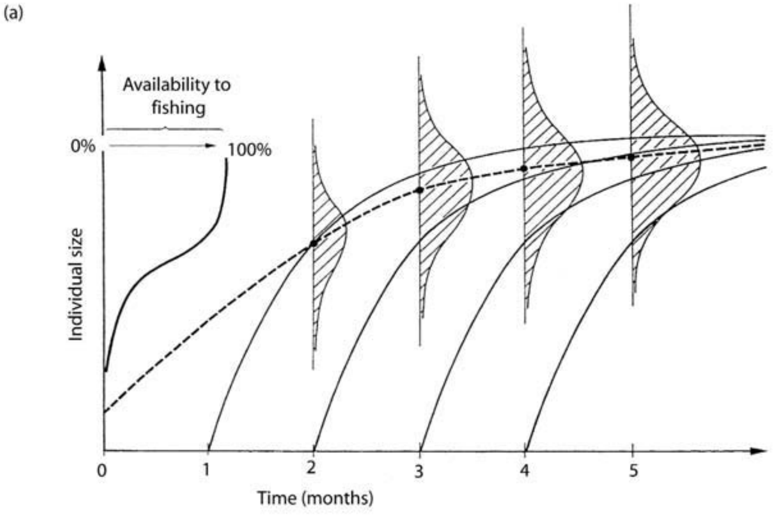


Fig. 13.3 Locations of statolith sampling (age determination) of *Illex argentinus* in three main fishery areas off Argentina. Four main waves of abundance in the fishery (A–D) resolve into generations hatched successively in June, July, August and September of the previous year (after Arkhipkin 1993b).

that there is no reservoir of older-aged individuals to buffer the population against the notorious variability of recruitment processes.

The catch rates achieved by commercial gear are one of the principal approaches available for the quantitative estimation of fished populations (see Chapter 19). The Leslie–deLury depletion model, in which declining catch per unit effort during the fishing season is extrapolated to estimate the pre-fishing population, is one of the few methods of stock assessment routinely applied to cephalopods. If, as is usually the case, the fished (sampled) area occupies only a portion of the total area of population distribution, then immigration and emigration effects will severely limit the use of this approach to modelling and the estimation of fished populations. Since age and size are frequently (but not universally) directly linked, these biases are not overcome simply by the use of age data instead of size.



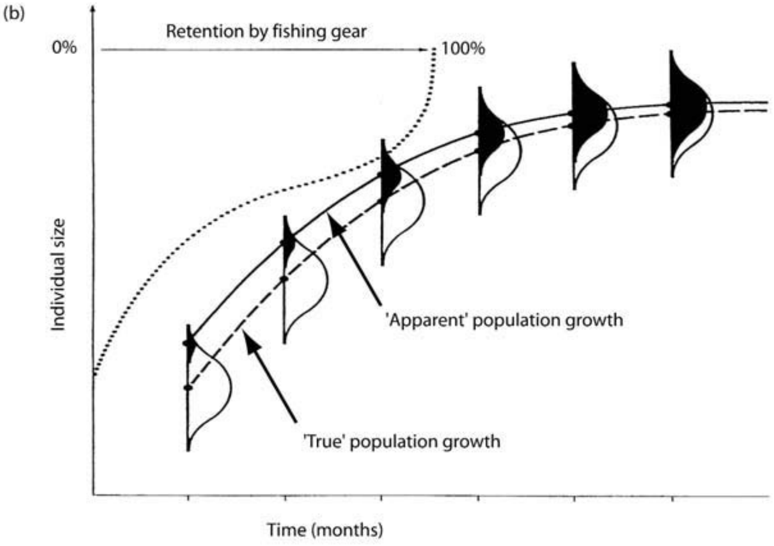


Fig. 13.4 (a) Recruitment of successive micro-cohorts of increasing size into a sampled population results in a spurious impression of cohort growth. (b) Gear selection for larger individuals will give an apparent reduction in cohort growth rate (after Caddy 1991).

13.2.5 Inter-annual variability

Records of fishery landings from most of the major commercial fisheries suggest that they commonly undergo wide inter-annual fluctuations. The causes of these shifts in abundance are not at all evident (presuming that fisheries landings can actually be used at all to represent population abundance). Since these populations are critically dependent upon annual recruitment in the year of the fishery, more than most marine resource species they are vulnerable to the success or failure of breeding and recruitment from the previous year.

Seasonality of cephalopods breeding in coastal waters, and the environmental cues that determine the time of spawning and the success of recruitment, little evidence is available to show that the inter-annual differences are due to shifts in the environmental driving forces. In the south Atlantic, the fluctuations of *Illex argentinus* and *Martialia hyadesi* have been shown to be affected by environmental variability, with teleconnections to the ENSO cycle (Waluda *et al.* 1999, 2001).

13.2.6 Longer-term trends

Despite the apparent instability of populations of these short-lived species, which are highly dependent on environmental conditions at any given time, some fisheries records show consistent trends of increases or decreases over several years. Taking account of possible changes in fishing effort and using only catch-per-unit-effort data from large fishery areas, Pierce & Boyle (2003) show that for *Loligo forbesi* in the north Atlantic, the best predictor of annual catch is the early-season temperature. Although these catches did not cycle with major environmental fluctuations (the north Atlantic oscillation, NAO) there were still consistent trends of an increase or decrease running for series of several years.

13.2.7 Population effects of fisheries

The direct effects of fishing activity on populations of cephalopods are unknown in a number of cases. Particularly serious are examples such as *Sepia pharoaonis*, in which trawling through breeding grounds along the Arabian coast and destroying the spawned egg masses has effectively eliminated the species from a large part of its original range. On a theoretical basis, Murphy & Rodhouse (1999) argue that the short lifespan of cephalopods makes them highly sensitive to the selective effects of human exploitation. Using data from *Illex argentinus* to model the potential for such effects to alter life-history characteristics, they argue that there may be a strong selection for an even earlier age of maturation and the loss of a migratory component to the population.

13.3 Biomass and production

The life-cycle and population ecology of cephalopods is directly relevant to their availability to higher predators and to commercial fishing. Their life-cycle biology (see Chapter 6), their growth and reproduction (see Chapters 7 and 9) and their role as predators (see Chapter 14) and as prey (see Chapter 15), and the differences in the neritic (see Chapter 11) and oceanic (see Chapter 12) forms are all important. Attempts to reconcile the known features of the life-cycle biology of cephalopod populations with their significance within the trophic structure of marine ecosystem lead to a wider discussion of biomass turnover and productivity in the marine environment. This train of thought gives rise to a series of unresolved general questions concerning the apparent capacity of cephalopod populations to deliver biomass to the higher marine predators. The quoted text below is from Boyle (2002).

> Rapid advances have been made in understanding key life-cycle processes of cephalopod development, feeding, growth, reproduction, and mortality – the factors underpinning cephalopod productivity; and the interactions between these biotic factors and the physical environment. They have shown that cephalopods reach large individual body sizes and are extremely fast-growing. Key aspects of their ability to achieve these high growth rates are their exclusively predatory feeding habits and high growth efficiency (food conversion). Unlike fish and other invertebrates they do not seem to attain an asymptotic adult size before reaching reproductive maturity. The coastal cephalopods breed over a short period of time and death follows shortly afterwards. They are essentially annual species in which there is little overlap of successive generations. In these circumstances, the biomass from any one species is likely to be available to predators and fisheries for only a limited period of time (Boyle 1990b).
>
> Using fisheries data alone and considering only flows of matter (catches and food consumption) between trophic levels, the primary production required to sustain total global fisheries, including the discarded by-catch, has been estimated to be about 8% of total aquatic primary productivity (Pauly & Christensen 1995). The cephalopod component of this estimate was 2.476×10^6 t (mean annual wet weight for 1988–1991), accounting for 1.88% of their estimate for the primary production removed by fisheries. Human fisheries for cephalopods have since continued to rise, reaching $>3.0 \times 10^6$ t in 1996. Extrapolation of this approach (Pauly & Christensen 1995) to include 267×10^6 t for 'removal' of adult/sub-adult cephalopods consumed by major predators (the mean annual consumption estimate for sperm whales alone) would require primary production of 2× the estimate for total global fisheries, or as much as 16% of the total for the aquatic ecosystem! This fraction may not be as unlikely as it first seems if marine mammals are harvesting deep-sea squids and fishes generally not available to human fisheries (Trites *et al.* 1997).

Can this scale of this estimated consumption by predators possibly be interpreted as biomass removal, or rapid turnover between predator and prey?

> Factors which could contribute to an over-estimation of cephalopod biomass include the possible exaggeration of their incidence in predator diets because cephalopod remains persist longer than those of other prey. Without estimates of residence time, and in the absence of good information on degradable soft tissues of prey, an over-emphasis on cephalopods in the diets is probable. It may be significant that the apparent incidence of cephalopods in the diet of stranded whales greatly exceeds that recorded in comparable animals killed by whaling (Santos *et al.* 1999).

Are the potential errors of biomass estimation from diet studies significant and can they be controlled?

> The scaling-up of limited predator and fishery data to ocean basin scales and the low carbon content (watery tissues) of many meso-pelagic cephalopods also introduces a great degree of uncertainty since this (the meso-pelagic fauna) is the largest component of the accumulated biomass estimate.

What are the uncertainties of scaling-up biomass by quantity and area, and are such extrapolations useful given the dispersed distribution of the populations and limited availability to predators?

> Life-cycle characteristics are key influences on the rate of delivery of biomass to predators. The cephalopod life-cycle paradigm is remarkably consistent across the neritic and coastal groups of octopods, sepioids (cuttlefish), loliginid squid and those epipelagic ommastrephid squid which venture on to the shelf for feeding excursions (Boyle 1983a, 1987a). These exclusively carnivorous species have high growth rates, uniseasonal reproduction and a short, endogenously determined lifespan; characteristics consistent with high biomass turnover rates or annual production/biomass ratios. For these cephalopods there is annual build and crash of biomass with little overlap of generations; the annual population results from the relative success of recruitment and the post-spawning adult biomass is available for predation without directly affecting the next generation. This pattern is most extreme when there is a short breeding season during which the whole population breeds more or less synchronously, but is mitigated in cases where there is extended duration of the breeding season, batch spawning, or trends towards the asynchronous spawning of cohorts within the population (Boyle & Boletzky 1996). These populations are subject to high variability due to environmental factors and may be considered to have a low 'inertia' leading to wide and currently unpredictable fluctuations both in location and density.

What are the key factors determining the rate of delivery of cephalopod biomass to predators?

> Large size and generous yolk provision for embryos (in the coastal species spawning benthic egg masses) and their early attainment of adult size and breeding status must reduce mortality rates in young stages. Taken together with the high incidence of cannibalism reported in many cephalopods (especially migratory species) these life-cycle characteristics will contribute to the sequestration of a high proportion of total production by a species into the adult population.

Does the short lifespan in coastal species contribute to low mortality rates in young stages and high adult biomass?

> Estimates for the individual trophic efficiency of cephalopods is unusually high, with estimates for gross conversion efficiency (weight of food consumed/somatic weight gain) estimated to range between 13% for active squid species to 69% for the more sedentary octopuses during periods of peak growth (Wells and Clarke 1996).

> This may mean that the commonly used figure of 10% for energy transfer between ecological trophic levels (Pauly & Christensen 1995) is unduly conservative.

Is the commonly used figure of 10% energy transfer between ecological trophic levels unduly conservative for coastal cephalopods?

> Life-cycle characteristics of the coastal cephalopods, therefore, suggest that biomass production can occur at high rates, and that a particularly high proportion of it may be available for consumption by predators or capture by fisheries.

Is an especially high proportion of annual production by a cephalopod species sequestered in the adult population?

> The major part of the global cephalopod biomass estimate results from inflation by area across that 85% of the marine province which is oceanic and where cephalopods may be distributed in quantity to depths of at least 600 m. Biological knowledge of the majority of oceanic pelagic forms is lacking although most systematic diversity in cephalopods is present in the meso- and bathypelagic environments. Some studies suggest the cephalopod biomass in the open sea (nektonic) to be about half that of fish (Maynard *et al.* 1975) but the mismatch between direct sampling with nets and indirect sampling from higher predators in this environment is well known (Clarke 1977 in this book). Although lower cephalopod metabolic rates at depth suggest lower productivity (Seibel *et al.* 1997), available evidence does not allow general biological conclusions. A greater range of life cycle features is probable. The slope octopus *Opisthoteuthis* (600–1400 m), for example, appears to breed continuously over the majority of its growth period (Villanueva 1992a in this book); in contrast, the mesopelagic (200–600 m) enoploteuthid squid, *Watasenia scintillans*, moves into shallow water during annual spawning aggregations which are followed by population-scale post-spawning mortality at an estimated age of only 11–13 months (Hayashi 1993).

In what respects do the characteristics of oceanic and mesopelagic cephalopod populations resemble the coastal species?

> The life cycle characteristics and ecology of the oceanic and mesopelagic cephalopod fauna, in particular, need to be established before current estimates for global cephalopod biomass can be reconciled with their biological productive capacity and that of the marine ecosystem in total. We must begin to understand whether the life cycle features established for the coastal species represent special cases, or the degree to which they may be generalised to the much greater oceanic and deepwater fauna.

Chapter 14

Cephalopods as predators

Summary: All cephalopods are carnivores, and they are all highly versatile predators. Apart from nautilus, they all take live food. The prehensile arms and tentacles of cephalopods, together with a highly evolved sensory system, allow occupation of a broad trophic niche, and migrations allow populations to exploit different production systems and prey populations. Shoaling occurs in many species, and this probably assists in the capture of prey and contributes to the impact of cephalopods on prey populations. Analysing cephalopod stomach contents is difficult because the beak bites the food into small pieces so that the hard parts of the prey, which are usually needed for identification, are often rejected, which can cause errors in estimating their diet. Despite these problems, there is a considerable amount of information on the trophic relationships of cephalopods, which has been collected using direct observations, conventional visual analysis of stomach contents, stable isotope ratios, lipid signatures and serological methods. Most cephalopods feed on small crustaceans as juveniles, and switch their diet to fish and other cephalopods as they grow larger. This is accompanied by ontogenetic changes in the allometry of the brachial crown. There is increasing evidence that myctophid fishes are an important food resource for oceanic squid. Cannibalism is probably ubiquitous in cephalopods, especially when population densities are high. Where there is predation on commercial stocks of fish and crustaceans, the effect of cephalopod feeding on recruitment may be significant. Cephalopods are trophic opportunists in marine food webs.

All living coleoid cephalopods are carnivores that capture their prey live, and they have probably been predators since their very early fossil history. The active species in particular need to feed voraciously to maintain their fast growth and metabolic rates, and they are opportunistic, versatile predators that do well in variable environments. The only cephalopod known to scavenge in the wild is the nautilus (see Chapter 4).

The short lifespan of most cephalopods, coupled with their often extensive migrations, causes their impact on prey populations to be highly seasonal. Furthermore, their effect in marine ecosystems varies from year to year, so when a strong cohort recruits into a system there is a substantial energy and nutrient flux to higher trophic levels, and fishery catches increase dramatically. It also follows that predation by a strong cohort of cephalopods on juveniles of other species can be a potential source of variability in the recruitment of the prey.

14.1 Feeding apparatus

The cephalopods possess unique adaptations for prey capture and handling, which enable them to feed opportunistically on a wide range of prey. A ring of eight arms and, in the decapods, two tentacles form the brachial crown which encircles the mouth. In the octopuses the two tentacles are absent, and in some squid, notably the Octopoteuthidae, they are lost before the animals become adults. The tentacles can be extended extremely rapidly in the initial attack on the prey (Kier 1982; Kier & Van Leeuen 1997, Kier & Curtin 2002), and the arm crown, which is effectively the functional mouth of cephalopods (Packard 1972), envelops and immobilises the victim.

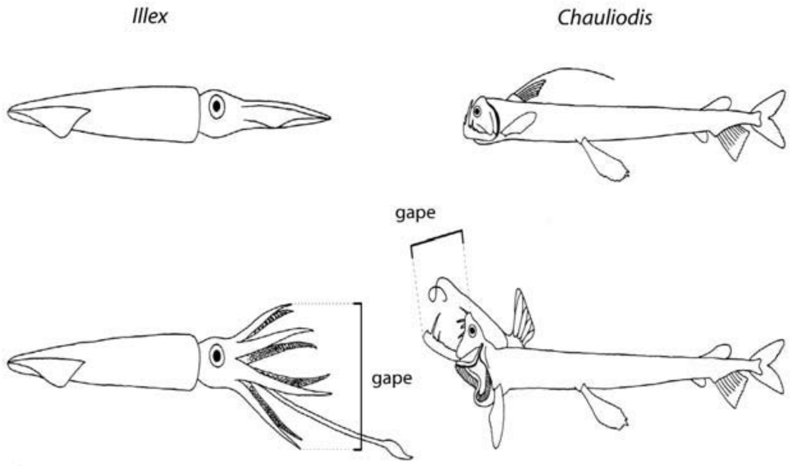


Fig. 14.1 Comparison of the span of the brachial crown of a squid (*Illex*) with the gape of the mouth of a mesopelagic fish (*Chauliodis*) of similar size, both of which feed on crustaceans and fishes (after Rodhouse & Nigmatullin 1996).

This function of the arms is helped in many species, especially the cirrate octopuses, by the presence of a web of skin between them. By comparison with the mouth of a fish, the arm crown is large and much more versatile for capturing and handling prey. In Fig. 14.1, the extended arm crown of an ommastrephid squid is compared with the gape of a mid-water fish (*Chauliodus*) of similar size which has a jaw which is adapted for handling relatively large prey items. Both the squid and the fish prey on mid-water crustaceans and fish, but it can be seen that as well as the size advantage of the squid's arm crown, it is also much better adapted for manipulating prey which may be slippery and struggling to escape.

The prehensile arms and the tentacles of cephalopods are equipped with suckers that are smooth and muscular in octopuses (Kier & Smith 1990), but which in squid possess a chitinous ring, usually furnished with small teeth that serve to prevent the sucker from slipping (Nixon & Dilly 1977) (Fig. 14.2a). In deep-sea squid of the families Onychoteuthidae, Enoploteuthidae, Pyroteuthidae, Ancistrocheiridae, Octopoteuthidae, Gonatidae and Cranchiidae, some sucker rings develop to form a chitinous hook which also prevents soft, fleshy prey such as fish and squid from slipping away (Engeser & Clarke 1988) (Fig. 14.2b). The cephalopod mouth is relatively small and contains a chitinous beak which chops up the food into small pieces before it is swallowed (Fig. 14.2c). There are species differences between the beaks of squid (Clarke 1986), and the shape of the beak is related to the area of insertion of the mandibular muscle and its mass and biting force (Kear 1994). The mouth contains a tongue-like radula (Fig. 14.2d), which in the squids is used for rasping and in the incirrate octopuses for drilling into shelled prey (Altman & Nixon 1970; Mather & Nixon 1995). In some cephalopods the posterior salivary gland, which is part of the buccal mass, produces a toxin (Ghiretti 1959) which is used to paralyse the prey when it is bitten, and which commences the process of digestion externally before it is swallowed (Nixon

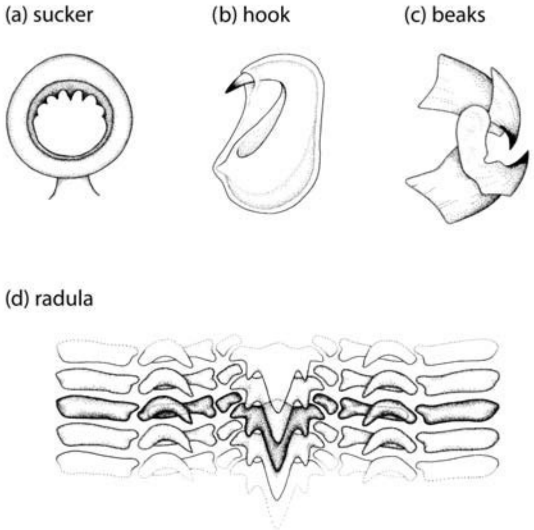


Fig. 14.2 Feeding apparatus of cephalopods. (a) Squid sucker showing teeth. (b) Tentacular hook. (c) Upper and lower beaks. (d) Section of radula showing several rows of overlapping teeth (a, c and d after Nesis 1987).

1984). Although the size of the prey fragments which can be swallowed is limited by the anatomical constraints of the oesophagus passing though the rigid cranial casing of the brain, the alimentary canal itself is adapted to cope with high feeding rates accommodating large meals in the crop (a diverticulm of the lower oesophagus). Food is digested rapidly, and absorption efficiency is high (Boucher-Rodoni *et al.* 1987). Both juveniles and adults have evolved to deal with an exclusively carnivorous diet (Boucaud-Camou & Roper 1995). The prey is located by sight using the eyes (Williamson 1995), and there is a sensory system for detecting vibration that is analagous to the lateral line in fish (Budelmann & Bleckman 1988). This is probably used to detect and locate prey in the dark and in poor visibility.

14.2 Feeding behaviour

The cephalopods display a wide variety of behavioural adaptations for feeding, from the highly active hunting of the muscular squids to the relatively passive style of the buoyant ammoniacal squid and the benthic foraging of octopuses. These different forms ambush, lure, stalk and pursue their prey, octopuses may pounce speculatively on likely patches of sand, and several cephalopod species disguise themselves as anything from pieces of seaweed to fish (Hanlon & Messenger 1996; Forsythe & Hanlon 1997).

Food resources in the oceans are seasonally variable and spatially patchy. Many cephalopod species have evolved migratory behaviour so that over their life cycle they are able to exploit production processes over large spatial scales. The major ommastrephid squid populations inhabit western boundary currents and upwelling regions, and during their life cycle they make extensive migrations within these systems, exploiting latitudinal differences in seasonal production to maintain high growth and maturation rates (Coelho 1985). The different *Illex* species spawn in tropical or subtropical regions of high productivity, and the hatchlings (rhynchoteuthions) inhabit meandering retention areas or the pole-wards flow of the boundary current (O'Dor 1993). It has been suggested that in some *Illex* species the population may subsequently split, with one portion remaining at low latitudes and another, more variable, group migrating to more productive areas in higher latitudes where, in good years, they can grow faster to a larger size. The population therefore exploits the predictable, but low productivity, low-latitude environment in the early life-cycle, and some of the stock exploits the less predictable, but more productive higher-latitude environment during the later life cycle. Some species of ommastrephids concentrate in warm core rings (Rowell *et al*. 1985; Vecchione & Roper 1986; Sugimoto & Tameishi 1992; Rodhouse *et al*. 1996), which are often areas of high productivity (Hitchcock *et al*. 1987). Once the migrating squid are ready to spawn, they usually migrate back to the spawning area. *Illex illecebrosus* has been shown to average nearly 20 km/day (Dawe *et al*. 1981) on the spawning migration, and *Ommastrephes bartrami* can cover 5–10 km/day (Araya 1983). In *Illex argentinus*, energetic considerations mean that feeding must continue during migrations, as metabolic reserves are insufficent to meet the energy cost of swimming for the times and distance needed to complete the migration (A. Clarke *et al*. 1994).

Many of the neritic cephalopods (loliginid squid, cuttlefish and octopus) spawn in shallow water, where the juveniles spend the early part of the life-cycle before migrating into deeper water as they grow larger. There is then a return to shallow water to spawn (e.g. Hatfield *et al*. 1990; Boucaud-Camou & Boismery 1991; Mangold-Wirz 1963). This life cycle means the juveniles are well placed to prey on small planktonic crustaceans that are low in the food chain and feeding on phytoplankton in the photic zone. They then find larger prey in deeper water as they grow. Some deep-water species apparently spawn in deep water and migrate upwards (Villanueva 1992b) but how these migrations relate to trophic ecology is not known. Some neritic species migrate along coastlines. *Loligo vulgaris reynaudi* migrates along the Cape Coast of South Africa (Augustyn *et al*. 1992, 1994) in search of food concentrations related to local hydrographic conditions (Roberts & Sauer 1994). They continue to feed until they are on the spawning grounds (Sauer & Lipinski 1991).

Most oceanic cephalopods make diurnal vertical migrations, enabling them to extend their foraging opportunities whilst reducing the risk from predation in the upper, well-lit layers during the hours of daylight. The vertical migrations are therefore usually upwards at dusk and downwards at dawn (Clarke & Lu 1974, 1975; Lu & Clarke 1975a, b; Piatkowski *et al*. 1994). Vertical migrations differ between species and with age and maturity. In the south Atlantic, sub-adult *Illex argentinus* forage near the bottom on the Patagonian Shelf in daytime and migrate to the surface at night. As they mature, they migrate into deeper water on the continental slope and remain near the bottom during the day, migrating upwards to depths of 200–300 m at night to feed on mesopelagic fishes, especially lantern fish (myctophids), in the deep scattering layer (Nigmatullin 1989).

Shoaling by squid is probably a behavioural adaptation to improve feeding success and reduce predation (Neill & Cullen 1974; Krause 1994), and it is a common behavioural feature of many species (Hanlon & Messenger 1996). Shoaling behaviour has a substantial influence on the predatory impact of cephalopods. Predation by shoals is patchy in space and time, and can have a potentially devastating effect on local prey densities.

14.3 Analysing cephalopod diet

There are problems with identifying the food of cephalopods because the hard parts of their prey, such as fish skeletons and crustacean integument that are usually necessary for identification, are often rejected. Selective rejection of parts tends to bias information on prey species and size, especially if the hard parts of small prey are swallowed and those of larger specimens discarded. After capture, cephalopods in net tows may feed, so their stomach contents may not reflect their natural diet. Unless only the most digested stomach contents are recorded in dietary studies, bias is caused by unnatural feeding in or near the sampling gear (Breiby & Jobling 1985). Rapid digestion means that many specimens have little or no food in the stomach, and material that has passed beyond the stomach is visually unidentifiable. Cephalopods are difficult to follow in the field, and the inshore species sometimes encountered by divers are secretive and wary, and difficult to observe feeding naturally.

Visual studies of diet have identified hard parts of prey such as fish otoliths, crustacean integument and eyes, cephalopod beaks and sucker rings. The size of some parts can be used to estimate the size of the prey, and when there are no hard parts it is sometimes possible to identify general categories from the presence or absence of fish scales and bones, and from the appearance of muscle and other tissue in the stomach contents. Paralarval diet has been visually identified in specimens as small as 2 mm ML by staining whole specimens with Alcian Blue and clearing with trypsin (Vecchione 1991a). Octopus prey has been analysed by direct observation of feeding and analysis of the hard parts of prey in middens (Mather 1991; Dodge & Scheel 1999), but this may miss some components of the diet such as fish (Cortez *et al.* 1995, 1999).

Serological analysis of cephalopod diet has been used to identify specific prey species (Grisley & Boyle 1985, 1988). This method uses antibodies from a host vertebrate injected with proteins (antigens) from a putative prey species. It tests for the presence or absence of specific prey, and was used to demonstrate that northern octopus *Eledone cirrhosa* prey on several crustacean species (Boyle *et al.* 1986), and to show that some Antarctic squid prey on Antarctic krill, *Euphausia superba* (Kear 1992). The method is too expensive to be used to identify all prey, but large numbers of samples can be screened quickly for a specific species. This method has the advantage that proteins retain antigenic sites for some time during digestion, allowing the detection of prey that cannot be recognised visually (Kear & Boyle 1992).

Naturally occurring stable isotopes of nitrogen present in animal tissues differ among species and trophic level, and so provide a way of estimating the level in the food chain. The 15N:14N ratio (δ15N) of *Loligo pealei* on Georges Bank in the western

Atlantic showed that it falls between trophic levels 3 and 4 (Fry 1988), which is similar to the level of planktivorous fish and isopods and large polychaetes in the benthos.

Lipids have been used as tracers of diet in the marine environment since the 1960s (Sargent 1976). The lipid content of the digestive gland of *Sthenoteuthis pteropus* has been used as an index to compare food availability in geographically distinct areas (Abolmasova *et al.* 1990), and has also been used to identify the major prey (myctophids) of the Southern Ocean squid *Moroteuthis ingens* (Phillips *et al.* 2001, 2003a, b). However, lipid signatures can be misleading when tracing the cephalopod prey of their predators. In oegopsid squid in particular, the most lipid-rich organ is the digestive gland, and this contains most of the lipid content of the whole squid, but here the lipid signature will be mostly of dietary origin. So the overall lipid signature of an oegopsid squid will more closely resemble its prey species. Thus, when lipids are analysed in cephalopod predators, the cephalopod prey may not be represented by a unique signature and their importance in the predator diet could be underestimated (Phillips *et al.* 2002).

14.4 The prey of cephalopods

Cephalopods are versatile opportunistic predators, and most marine phyla have been recorded in the diet of one member of the class or another (Nixon 1987). Even pelagic gelatinous forms such as cnidarians (Heeger *et al.* 1992) are consumed. The same species may feed on different diets in different geographical locations (e.g. Ivanovic & Brunetti 1994; Lipinski & Linkowski 1988), and direct observations in the field seem to confirm that when foraging, they appear to be unselective in their choice of prey type (Mather 1993).

14.4.1 Coastal and shelf cephalopods

In neritic seas, squid and cuttlefish feed primarily on crustaceans, fish and other cephalopods. A comon pattern is for juveniles to prey on crustaceans, and then switch to fish and cephalopods as they grow larger (Breiby & Jobling 1985; Le Mao 1985; Lipinski 1987; Castro & Guerra 1990; Guerra *et al.* 1991; Lipinski *et al.* 1991; Collins *et al.* 1994; Pierce *et al.* 1994c). Ommastrephid squid such as *Illex illecebrosus* feeding on surface swarms of euphausids (Nicol & O'Dor 1985) are generally considered to be pelagic predators, but recent information on benthic species in the diet of *Todarodes pacificus* caught in bottom trawls over the continental shelf (Tanaka 1993) show that they may feed in the demersal as well. Benthic organisms may be more important to neritic squid than has generally been realised, especially during daytime, when their vertical migrations take them near the seabed. The sepiolids feed almost exclusively on small mysids and shrimps. The European species *Sepietta oweniana* feeds in the hyperbenthic zone, primarily on euphausiids and pandalid shrimp (Bergström 1985).

After hatching, many octopuses are planktonic and feed on planktonic crustaceans. After a few weeks they move to the seabed, and their diet switches to benthic crustaceans and molluscs (Nixon 1985; Villanueva 1994). Squid and cuttlefish feeding on pelagic crustaceans usually ingest the exoskeleton, but most octopuses paralyse the prey with cephalotoxin and, after some limited external digestion, the flesh is eaten and the exoskeleton rejected. In some situations, *Octopus vulgaris* feed mostly on bivalve molluscs. Small bivalves are opened by pulling the shells apart, while large ones are drilled first, using the radula, and then pulled apart (McQuaid 1994). Large octopuses generally feed on large mobile prey, and they eat a larger proportion of fish and cephalopods and fewer crustaceans (Nigmatullin & Ostapenko 1976; Guerra 1978; Villanueva 1993). Octopus populations can have sufficient predatory impact to structure subtidal communities. In California, *Octopus bimaculatus* consumes gastropods, chitons, bivalves and crustaceans, and it has been recorded that over a period of 5 years, when there was an 80% reduction in octopus density, the abundance of gastropods and hermit crabs increased by about 500%. Recent observations from submersibles have revealed that some octopuses may swim up from the seabed to prey on pelagic organisms (Laidig *et al.* 1995).

14.4.2 Oceanic cephalopods

Oceanic cephalopods also feed mostly on crustaceans, fish and cephalopods (e.g. Piatkowski *et al.* 1998). Newly hatched oceanic squid typically feed on planktonic crustaceans, especially copepods (e.g. Rodhouse *et al.* 1996; Hopkins 1985). Notably also, some large benthopelagic shrimps (*Aristaeomorpha foliacea*) may themselves take juvenile cephalopods from several mesopelagic and bathyal species (Bello & Pipitone 2002). In the Gulf of Mexico, small nektonic cephalopods prey mainly on the copepod *Pleuromamma* spp. (Passarella & Hopkins 1991), probably because it is highly bioluminescent. It has been suggested that the rhynchoteuthion larvae of ommastrephid squid are suspension feeders on phytoplankton once the yolk reserves are exhausted and before effective predatory behaviour has started (O'Dor *et al.* 1985). The idea is that mucus on the mantle surface traps food particles, and cilia transport these towards the head and mouth. This is possibly why so few food remains are ever found in the stomach contents of rhynchoteuthions.

Most species switch their diet from microplanktonic prey to larger euphausiids, hyperiid amphipods, mysids and decapods as they grow. For many ommestrephid squid with distributions close to and over the continental shelf, crustaceans remain an important food source into full adult size. However, the various *Illex* species, *Nototodarus* and *Todarodes* are also opportunists and will feed on fish and cephalopods when available. Niche separation occurs between ommastrephid species with overlapping distributions, for instance where *Todarodes pacificus* and *Ommastrephes bartrami* occur in the same area, the latter feeds on fish and *T. pacificus* feeds on crustaceans (Araya 1983).

The large oceanic squid are primarily fish eaters, but they also feed on cephalopods. They prey on epipelagic fish such as mackerel and flying fish, but the lantern fishes (myctophids) are probably the most important prey for many of the larger ommastrephids over the deep ocean and at the edges of the continental shelves (Rodhouse & Nigmatullin 1996). Myctophids have also been found in the stomachs of histioteuthids (Voss *et al.* 1998b) and lycoteuthids (Voss 1962). Although myctophids are of greatest importance for the oceanic ommastrephids, they also make a significant contribution to the diet of the shelf and near-shelf forms such as the *Illex* spp. *Todarodes* spp. and *Dosidicus gigas* when they are feeding near the shelf edge.

The ecology of the oceanic mesopelagic zone is not well known, but the ommastrephid squid are obviously important predators, and also important agents for the transfer of energy and nutrients from the mesopelagic community to higher trophic levels. Several species of myctophid swim up to the sea surface at night, and they are primarily planktivores feeding mostly on copepods, small euphausiids and hyperiid amphipods (Kozlov & Tarverdieva 1989). In the open ocean much myctophid predation is by epipelagic ommastrephid squid. In the sub-Antarctic, cephalopods, especially *Martialia hyadesi*, fill the trophic niche of epipelagic fish which are apparently absent (Rodhouse & White 1995). The mesopelagic fishes form a continuous layer (the acoustic deep scattering layer) in the oceans and are very abundant. The standing stock of mesopelagics in the productive areas of the ocean can be 7–14 g/m^2 and the production 3.5–7 g/m^2/year, which is comparable with fish production on some continental shelves, which is about 5–10 g/m^2/year (1 g $\approx$ 1 kcal), so they are an abundant prey resource for oceanic cephalopods (Mann 1984).

The benthopelagic cirrate octopuses have relatively specialist feeding habits, preying largely on small epibenthic forms such as copepods and polychaetes (Vecchione 1987b; Villanueva & Guerra 1991).

14.4.3 Cannibalism

Nearly all analyses of cephalopod diets reveal some evidence of cannibalism as well as predation on other cephalopod species (e.g. Quetglas *et al.* 1999). In some studies, conspecifics have been almost the only food present in the gut contents. There are reasons why cannibalism might be overestimated, especially when the evidence comes from samples taken with fishing gear which can cause bias (Breiby & Jobling 1985). Jig fishing with lights may generate ‘feeding frenzies’ where unnatural cannibalistic behaviour may be triggered, and in trawls it is known that net-feeding can occur, which would also be a source of error. However, there is much evidence that conspecific predation is a real phenomenon. In fisheries operating with the same gear in the same area, the instance of cannibalism can be highly variable, indicating that although the fishing gear may be causing bias, there is a natural underlying process.

Cannibalism is usually most important under conditions of high population density. Also, if poor feeding conditions are met during long-distance migrations, it may provide a mechanism for survival of at least part of the shoal (O’Dor & Wells 1987). In the south Atlantic, the winter spawning population of the ommastrephid *Illex argentinus* migrates from feeding grounds near the Falkland Islands to spawn some 1000 km to the north. Prior to the migration, the squid do not possess sufficient energy reserves to fuel the whole journey so they must feed *en route* (A. Clarke *et al.* 1994). If sufficient prey are not available, cannibalism would allow some individuals to reach the spawning area.

Young cephalopods are rarely present in cephalopod populations at the same time as the adults because after spawning, most or all of the previous generation dies. This means that cannibalism usually occurs between members of the same generation, a process that has been termed intra-cohort cannibalism (Polis 1984) to distinguish it from older animals preying on young. Cannibalism in cephalopods is therefore rarely a major source of mortality in early life stages, as it can be in fish populations (Caddy 1983b), and so does not have a direct impact on recruitment. For this reason, theory predicts that cephalopod populations might fit the Beverton & Holt (1957) stock recruitment model rather than the Ricker (1975) model, because the former does not include density-dependent effects such as feeding on juvenile conspecifics. On the other hand, intra-cohort cannibalism can be extensive and so can have a major impact on natural mortality and hence population size, and is thus a factor that should be considered in stock assessments and predictions.

14.5 Ontogenetic shift in prey selection

Over the short life-span of cephalopods, feeding shifts rapidly from small to large prey. They therefore occupy a wide range of ecological niches and trophic levels during their short life cycle. Growth is frequently accompanied by migration into deeper water as the ability to capture and subdue larger prey increases (e.g. Rodhouse & Clarke 1985, 1986; Rodhouse & Piatkowski 1995).

Pelagic biomass spectra in marine ecosystems are characterised by peaks separated by one or more orders of magnitude of difference in body size, and are composed of characteristic groups of organisms (Boudreau & Dickie 1992). In one example they include, in order of increasing size, diatoms (104–106 μm^3), cyclopoid copepods (2×10^6 to $3 \times 10^7 \mu\text{m}^3$), calanoid copepods (1–50 mm^3), euphausiids (50 mm^3 to 1 cm^3) and small fish (1–10 cm^3) (Witek & Krajewska-Soltys 1989). Benthic biomass spectra may have peaks of biomass that correspond with troughs in pelagic spectra (Warwick *et al.* 1986). A cephalopod preys on species at different positions in the biomass spectrum as it grows, moving from one peak of biomass to the next (Rodhouse *et al.* 1994a; Collins & Pierce 1996).

The general shift in squid diet from crustaceans to fish as it grows is well illustrated by Breiby & Jobling's (1985) study of *Todarodes sagittatus* in Norwegian waters. However, where squid size and prey size has been studied in detail, the relationship is often blurred. Minumum prey size often changes little as the squid grows, but maximum prey size increases. Trophic niche width therefore increases with growth. For example, in *Loligo pealei* there is a marked increase in the size-range of prey as the squid grows (Vovk 1985), but little increase in the minimum prey size.

Benthic octopus species usually have a planktonic larval phase, and this strategy may have evolved in response to the discrepancy between pelagic and benthic biomass spectra, enabling them, during the planktonic phase, to feed on small crustaceans which occupy a peak in the pelagic biomass spectrum which is absent in the benthic system. During the second half of the planktonic life of *Octopus vulgaris*, prior to taking up residence on the seabed, the arms increase in length rapidly in relation to the rest of the body (Villanueva *et al.* 1995), and this is presumably an adaptation for feeding on larger organisms in the benthic biomass spectrum.

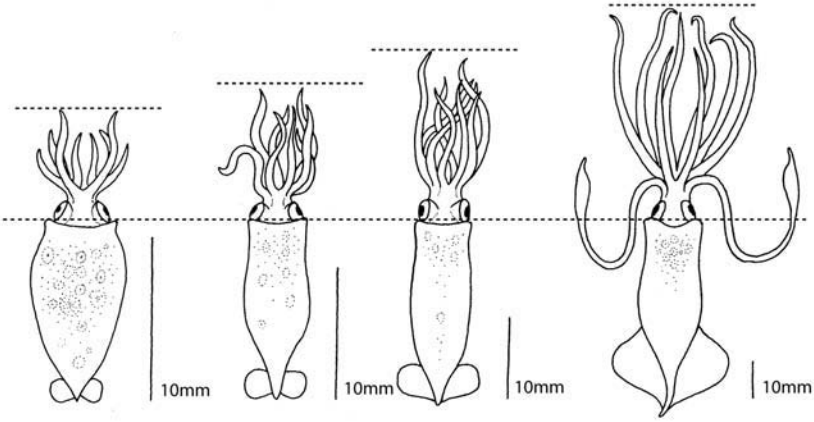


Fig. 14.3 Allometric growth of the brachial crown illustrating the relative increase in span of the arms with growth. Ontogenetic phases of growth of *Gonatus madokai* (from Kubodera & Okutani 1977).

Changes in the relative growth (allometry) of the brachial crown (arm crown) in squid (Fig. 14.3) is probably an adaptation to the structure of pelagic biomass spectra. In most squid, arm size increases in relation to overall body size during growth, especially in early life. This relatively rapid growth of the brachial crown has probably evolved in response to the need to shift predation from one peak in the biomass spectrum to the next, accommodating the transition between diets differing in body size by at least one order of magnitude (Rodhouse & Piatkowski 1995). Discontinuities often occur in the allometric growth of the brachial crown of juvenile squid (Kubodera & Okutani 1977; Vidal 1994), which suggests that relatively sudden changes in the relative size of the prey probably occur in some species during early growth.

14.6 Quantitative impact on prey populations

By combining data on stock size with information on the relative contribution of different prey types to diet, the impact of the cephalopod populations on their prey can be assessed. For example, in a study of prey consumption by *Illex illecebrosus* and *Loligo pealei* on the Eastern USA continental shelf by Maurer & Bowman (1985), crustaceans, mostly euphausiids, dominated the diet of both species in spring. In the summer and autumn, fish and squid both increased in importance, fish being relatively more important for *Loligo* and squid for *Illex*. The squid are potentially important predators of pre-recruit fish, including cod, haddock, yellowtail flounder, silver hake, butterfish, scup, mackerel, herring, menhaden and sand-lance. Cannibalism dominates the diet at certain times, but does not appear to be related to population size and probably occurs when other prey are not available. Clearly squid predation can be a factor determining recruitment success of commercially exploited stocks.

Other studies have quantified squid predation of the Patagonian Shelf (Rodhouse & Nigmatullin 1996) and in the northeast Atlantic (Pierce & Santos 1996). On the Patagonian Shelf, an average cohort of the winter-spawning population of *Illex* *argentinus* consumes a total of about 1 m tonnes of food during its lifetime, and this is mostly crustaceans (Ivanovic & Brunetti 1994). *Loligo forbesi*, in the northeast Atlantic, was estimated to consume 3000–16 000 t of food per year, including sandeels, *Trisopterus* spp. and *Merlangius merlangus*. The diet was dominated by fish, but the estimates did not include consumption by pre-recruits, which must be substantial and is probably dominated by crustaceans.

14.7 Impact on commercial stocks

Because cephalopods are predators on fish and crustaceans they are a factor influencing the natural mortality and recruitment of commercially exploited fish species and, conversely, the status of fish stocks may influence cephalopod recruitment (Dawe & Brodziak 1998). Because of the short life cycle of cephalopods, and because there are usually only one or two cohorts per year, which often undertake feeding and spawning migrations, they are likely to have an impact on prey stocks at specific times and places. Cephalopod stomach contents often contain remains of commercial fish and crustacean species (Rodhouse & Nigmatullin 1996). Fishes, clupeids, scombrids, gadoids and penaeid prawns are prevalent in the diet of a number of squid feeding on the continental shelves. Commercially exploited species of crab and lobster are attacked by octopuses, and even Antarctic krill, which supports a large fishery, is consumed by several squid species. The short life cycle compared with fish means that an individual can switch roles between prey and predator, as for instance in the *Illex*/hake predator–prey relationships in the northwest and southwest Atlantic (Caddy & Rodhouse 1998).

An excellent example of the impact of a squid population on a commercial fish stock is shown by the migration of *Dosidicus gigas* into the Gulf of California, where it changes its diet during June, July and August to the California sardine, *Sardinops sagax caerulea* (Ehrhardt, 1991). Near the bay entrance, the squid prey on myctophids, red crab and cannibalistically on other *D. gigas*. Once they migrate into the bay, they switch to post-larval penaeids and sardine until, at the peak of sardine predation, these fish contribute 80% of their total diet. There are well-documented migrations of *D. gigas* into the Gulf when up to 60 000 tonnes of sardines have been consumed and subsequent landings of sardine have been well below normal.

In another example, the trophic ecology of the gonatid squid *Berryteuthis magister* is linked to the Alaska pollack, *Theragra chalcogramma*, in the Bering Sea. The standing stock biomass of *B. magister* is on average about 640 000 tonnes, and the population feeding rate is about 7040 tonnes per day, of which some 700–1056 tonnes is *T. chalcogramma*. The total annual consumption of Alaskan pollock by this squid is therefore about 250 000–375 000 tonnes.

The predatory habits of octopuses are well known to interfere with some commercial trap fisheries for crabs and lobsters. Early records of octopus plagues (Garstang 1900; Rees & Lumby 1954) have described the resulting havoc on lobster fisheries. Fishermen will generally agree that octopus predation is of nuisance value, and studies on a limited number of cases have shown that there may be a significant quantitative effect on the catch. Ritchie (1972) estimated that in the Hokianga area of New

Zealand, predation by *Octopus maorum* on pot-caught rock lobsters (*Jasus edwardsii* and *J. verreauxi*) normally accounted for 20% of those caught, and pointed out that the impact of predation could result in greater losses of lobsters outside the traps. In western Australia, Joll (1977b) investigated the predation of *Octopus tetricus* on pot-caught rock lobsters (*Palinurus longipes cygnus*) and recommended the installation of octopus traps on the pots. Targeted dietary studies on *Eledone cirrhosa* (Boyle *et al.* 1986) have shown that the commercially valuable lobster *Nephrops norvegicus* was recognisable by specific antisera at 10% incidence in gut contents.

14.8 Global role of cephalopods as predators

The role of the commercially fished cephalopods as predators on the major marine ecosystems has been summarised by Rodhouse & Nigmatullin (1996). Data on the commercial stocks are relatively easy to obtain, but the role of the many species in meso- and benthopelagic habitats is extremely difficult to assess. Some families, including the histioteuthids, enoploteuthids, ancistrocheirids and octopoteuthids, are undoubtedly significant contributors to oceanic biomass and must have major impacts as predators, but apart from data from predators (Clarke 1980), little is known about the stock size of these forms, and virtually nothing is known about their predatory behaviour.

Using data from various sources, Rodhouse & Nigmatullin (1996) made a tentative estimate of consumption by cephalopods worldwide. Only consumption by subadults and adults was considered. Voss (1973), Clarke (1983, 1987) and Nesis (1985) have estimated the global biomass of mesopelagic squid to be 150–300 × 106 t, and Nigmatullin (1990) estimated the global stock of oceanic epipelagic squid and slope/shelf edge squid to be $30–50 \times 10^6$ and 8–15 × 106 t, respectively. No published data exist, but an estimate of the stock of sepiids and octopus on the continental shelves, based on the world catch, is about $5–10 \times 10^6$ t. The total cephalopod biomass is therefore probably about $193–375 \times 10^6$ t. The feeding rate of adult cephalopods is 1–12% body weight per day (Wells & Clarke 1996). Because mesopelagic squid, which probably have comparatively low metabolic and feeding rates, dominate the global cephalopod stock, a mean feeding rate of 3% body weight per day was assumed. The global daily consumption by cephalopods is therefore estimated to be $5.8–11.2 \times 10^6$ t. Although cephalopod populations have dramatic annual fluctuations in biomass, it was assumed that global biomass is approximately stable because the seasonal dynamics of temperate populations are approximately 6 months out of phase in the northern and southern hemispheres. This is because many abundant species spawn all the year round in the tropical regions, and in the polar regions at least some species probably have life cycles in excess of 1 year. The global consumption by cephalopods was estimated to be $2.09–4.03 \times 10^9$ tonnes per year.

Chapter 15

Cephalopods as prey

Summary: Cephalopods have a high intrinsic value as food for higher predators. They are present in a wide range of body sizes available to match predator requirements at different stages, very little of their body mass is indigestible, many are highly muscular animals rich in proteins, they rely on escape, evasion and concealment rather than offensive methods for evasion, and thus they offer little physical risk to predators. The life-cycle characteristics of cephalopods themselves suggests that a relatively high proportion of their annual production is retained in the adult population, offering a large resource of accessible biomass to higher predators. Many large fish species consume cephalopods, but there are insufficient data to estimate their quantitative significance in the diet. The role of cephalopods in the diets of many seabirds such as albatrosses, penguins, auks, petrels and terns has been carefully quantified in many cases from the residual cephalopod beaks in gut contents. Cumulative estimates of the consumption by birds over areas of ocean have been made, but how cephalopods are obtained by some birds, i.e. whether by direct predation, scavenging on regurgitations from other predators or exploiting the natural post-spawning mortality of squid, is still a matter of debate. Most seal species take cephalopods as part of their diet, and for some, like the southern elephant seal, cephalopods are the major food. Toothed whales also take large quantities of cephalopods, and sperm whales are estimated to consume 95% of their diet as squid in the open ocean and at depths down to 1000 m. Predator consumption estimates have been used to calculate the possible biomass of cephalopods available annually, and these produce very large figures when compared, for example, with the annual global fisheries catch. A number of errors and sources of bias are inherent in these estimates.

The cephalopods span much the same size range as the fishes of the worlds' oceans and provide an important source of prey to higher predators, including the marine mammals, seabirds and fish. The cephalopods range in size from paralarvae less than 1 mm to adult body sizes of 100–1000 g. Several grow much larger, and the giant squid *Architeuthis*, which is the largest living invertebrate, attains a total mass in excess of half a tonne. As far as can be determined from the fossil record, cephalopods have been the largest invertebrates in marine pelagic and benthic habitats for much of the history of life in the oceans and have been prey for higher predators at least since the Mesozoic (Sato & Tanabe 1998). The living cephalopods provide a food resource for predators ranging in size from small fish and seabirds, feeding on juveniles, to the largest bull sperm whales feeding on fully grown specimens of the largest species.

15.1 Role of cephalopods as prey

15.1.1 Intrinsic prey value

The position of the cephalopods in the biomass spectrum of the ocean is illustrated by a comparison of the mantle lengths of 62 cephalopod species with the body lengths of 76 fish species from the mesopelagic off Madeira (Fig. 15.1). This clearly shows that cephalopods available to predators match the full size-range of fish, and that at larger

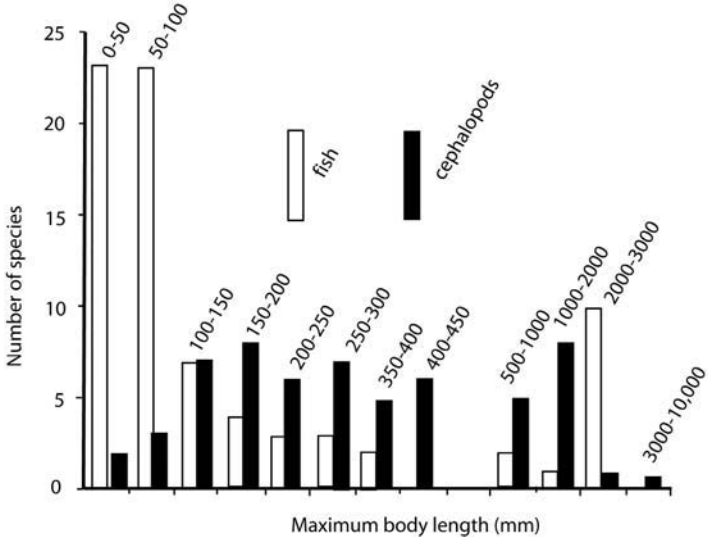


Fig. 15.1 Histogram of the maximum lengths (extracted from the literature) of 76 fish species (fork lengths) and 62 cephalopod species (standard lengths derived from mantle lengths) occurring in the mid-waters off Madeira. The fish above 1000 mm are represented by the large pelagic fish such as sharks, tunas, swordfish, billfish and sailfish (after Clarke 1996b).

sizes there are rather more cephalopod species than fish (Clarke 1996b). At small sizes (<100 mm body length), however, the numbers of fish species predominate by a considerable margin.

The indigestible hard parts of the coleoid cephalopods are confined to the beak, eye lens and gladius in squid, and the beak and eye lens, reduced internal shell and stylets in octopuses. The large cuttlebone of the sepiioids is relatively soft, easily crunched, and composed of over 50% protein, and the internal shell and stylets of octopuses are easily destroyed. Therefore, little of the cephalopod body is indigestible to the powerful digestive system of the vertebrates. The chitinous beaks present in all cephalopods are the exception; they are very resistant to digestion and erosion in the guts of higher predators and so are persistent in their guts and scats. Scientists of the *'Discovery' Investigations* and the *Falklands Islands Dependencies Survey* found numerous cephalopod beaks in the stomach contents of Antarctic vertebrate predators, especially sperm whales (Harrison-Matthews 1938), but also albatrosses, penguins and seals (Harrison-Matthews 1929a, b; Laws 1956; Stonehouse 1960; Prince & Harris 1988; Prince & Morgan 1987). Cephalopod beaks have since provided a very important tool for the study of the diet of their predators, and have contributed a wealth of information on trophic relations in the world's oceans. The beaks, especially the lower beak, can be used to identify the species, and the relationship between beak size and body weight allows the biomass represented by beaks in the gut contents of vertebrate predators to be calculated (Clarke 1980, 1986; Jackson 1995b). Knowledge of the energy requirements of vertebrate predators, the energy content of cephalopods and contributions to predators diets has allowed an estimate to be made (Clarke 1983) that some 34 million tons of cephalopods are consumed annually by seabirds, whales and seals in the Southern Ocean, while the world sperm whale population consumes up to 320 million tons per year (Clarke 1996c).

From a nutritional standpoint, most cephalopods are highly muscular and therefore rich in protein, and some species with large digestive glands (e.g. the oegopsids and gonatids) are also rich in lipids. Analysis of the tissues of a typical squid (e.g. *Illex argentinus*) has revealed that, on a fresh basis, they are composed of 78–80% water (a typical value for the soft tissues of marine invertebrates), 10–17% protein, 12% lipid and a small amount of carbohydrate (Clarke *et al.* 1994). Although the relative mass of different tissues and organs changes considerably throughout sexual maturation with the growth of the gonads and the digestive gland, the overall proximate biochemical composition does not change substantially with size and age.

The soft, unarmoured body of the cephalopods leaves them with little structural defence and they depend heavily on behavioural mechanisms to avoid predation. Selection pressure has driven the evolution of exceptional capabilities among the benthic cephalopods for cryptic colouration, and this camouflage can be changed almost instantaneously to suit a changing background. In the squid, there is a highly developed rapid-escape mechanism based on jet propulsion using the massive mantle muscle. This is served by the giant nerve fibre system, which ensures the extremely rapid transfer of signals from the highly evolved eyes, which are analogous to the vertebrate eye. Most species of cephalopod possess an ink sac (a diverticulum of the gut close to the anus) which, in response to being attacked, will release a cloud of ink that exits the mantle through the funnel and spreads to form a cloud in the water, either screening the cephalopod, distracting the predator or possibly creating a decoy.

The cephalopods do not appear to have evolved any chemical defences. The buoyant ammoniacal squid, such as the mid-water cranchids, are less muscular and presumably less strong swimmers than the non-buoyant more muscular squid. Although the buoyancy mechanism means that the coelomic cavity may contain ammonium chloride at concentrations over 300 mM/l, the buoyant squids are nevertheless consumed in large quantities by higher predators. Similarly, the octopuses are well known for their toxic salivary secretions (see Chapter 2, Box 2.2), but these are not generally defensive and have evolved to paralyse the prey and, in the case of crustaceans in the diet, to release the muscles from the carapace prior to consumption. The only exceptions may be the blue-ringed octopuses of the genus *Hapalochlaena*, from sub-tropical Australian waters; these have a bite which is highly toxic to humans and may be used for defence from natural predators. Generally though, the cephalopods produce no toxins to provide a disincentive to consumption by oceanic higher predators.

There are few direct comparisons between the relative food value of cephalopods and alternative prey, but Croxall *et al*. (1988) have been able to compare the breeding success of two related sub-Antarctic species of seabird feeding on different prey. Black-browed albatross breeding at South Georgia and foraging in the Scotia Sea depend mostly on Antarctic krill, while grey-headed albatross primarily eat squid (Prince 1980). The krill predator has a higher breeding success (as measured by hatching success and chick growth) when the food resource is available in abundance, but the krill resource has considerable inter-annual variability in standing stock (Croxall *et al.* 1999), and breeding success is reduced in years of low biomass. On the other hand, the cephalopod predator has a more consistent year-on-year breeding performance despite occasional changes in abundance (Xavier *et al.* 2003). These observations are explained by the higher energy content of Antarctic krill, which are rich in lipids, but which apparently have more variability in population biomass than the squid stocks (largely *Martialia hyadesi*), which have a lower energy density than krill and on which the grey-headed albatross depends.

In an experiment, Prince & Ricketts (1981) compared the growth rates of black-browed and grey-headed albatross chicks when transferred between nests and fed by foster parents of the other species. When fed on a predominantly krill diet by a black-browed albatross parent, the grey-headed albatross chicks grew faster than when fed by their natural parents on a predominantly squid diet. The converse was also the case, with black-browed albatross chicks growing more slowly when fed on a predominantly squid diet by the foster parents. This is explained by the much higher lipid and energy content of the natural black-browed albatross diet, Antarctic krill, which can be utilised for faster growth by the grey-headed albatross chicks when provided by the foster parent. Black-browed and grey-headed albatrosses are not good at switching prey naturally, which accounts for their inability to compensate, in terms of reproductive performance, for shortages of their primary prey species. This probably relates to their relative specialisation for different oceanic habitats. The black-browed albatross forages primarily on the continental shelf and shelf break, whereas the grey-headed albatross specialises in foraging near productive ocean frontal systems.

The generally large body size and high protein content of cephalopods, together with the lack of any physical or chemical protection from predators other than escape mechanisms, determines their intrinsic value as prey for higher predators and their significant role in many marine food webs.

15.1.2 Methods for the identification of cephalopods as prey

It was while doing pioneering work on whales that Clarke (1962a) recognised species differences in the morphology of cephalopod beaks, and the significance that they may have to studies of predator diet (Clarke 1962b). Systematising this approach and making it widely available, Clarke (1986) laid the basis for the development of the entire field of research on cephalopod predation and trophic relations among marine predators. The use of beaks for analysis of cephalopod as prey has now become widespread in oceanic ecology. This subject is summarised in Box 15.1.

Although the use of beaks from predator gut contents is the only method for identifying prey that has been used extensively to date, other methods which may have a potential for future research are serological techniques and the use of molecular genetic markers. These methods have been discussed in other chapters in relation to identifying the prey of cephalopods. Although the analysis of fatty acid signatures has been used to assess prey type in higher predators (Grahl-Neilson & Mjaavatten 1991), this may have limited use for identifying cephalopods as prey. The cephalopods have only a small amount of lipid in their tissues, apart from in the digestive gland (O'Dor & Wells 1987). In oegopsid squid, the lipid in the digestive gland largely reflects dietary lipid, so the overall lipid signature more closely resembles that of the squid's prey

Box 15.1 Beaks and their uses

The mandibles, or beaks, of cephalopods are a pair of pointed chitinous jaws lying within the buccal cavity. They are sharp-edged and capable of powerful shearing movements. In these active predators they have an important function in helping to break open prey and chop the flesh into ingestible pieces.

Cephalopods which are caught and eaten by higher predators are rapidly digested with the exception of the hard and horny beaks. In whales, seals and birds, the beaks of cephalopods consumed are retained for some time in the gut and potentially provide a historical record of the cephalopod food consumed (Fig. 15.1.1).

Details of the shape and characteristics of beaks, together with knowledge of the region from which they have been collected, can be used to identify them to family, and sometimes to genus or even species level (Fig. 15.1.2a). The various

Fig. 15.1.1 Squid beaks from the gut of a sperm whale.

(a)

Fig. 15.1.2 (a) Squid beaks sorted by family.

(b)

Fig. 15.1.2 (b) Squid beaks sorted by size.

dimensions of the beak, especially lower rostral length, show good allometric relationships with overall body size. Size measurements of the beaks in predator stomach contents allow the size of the squid eaten to be estimated (M.R. Clarke 1962a, b, 1972, 1986; Wolff 1984; Fig. 15.1.2b).

Estimation of the species composition of cephalopod food taken by predators, together with the size-frequency of individuals, has become one of the most important tools for investigating the trophic relationships of the top marine predators.

(Phillips *et al.* 2002). Thus, if lipid methods were used for dietary analysis of their predators, the squid would not be represented by a unique signature, leading to an underestimation of their role in the diet.

15.1.3 Life cycle characteristics and their bearing on population biology

The high growth rate and growth efficiency (conversion of food consumed into growth) of cephalopods mean that their populations rapidly accumulate biomass into an intermediate stage in the food chain. Their rapid attainment of maximum body size and relatively low fecundity suggests that they have low mortality during the egg, paralarval and juvenile phases of early life (Calow 1987). Coupled with the rapid and efficient incorporation of a wide range of prey resources into cephalopod biomass, this indicates that a relatively high proportion of the total production of a cohort is retained in the adult population for breeding and subsequent death (Boyle 2002).

The cephalopod biomass resource available to higher predators is in many instances strongly seasonal. This is because in many temperate and high-latitude species the short, spawn once and die life cycle means that for a substantial period of the year after the seasonal post-spawning mortality the population is represented by large numbers of small individuals with low total biomass. So for those cephalopod species with seasonal spawning events followed by catastrophic mortality, the maximum biomass of a cohort is only available for a limited period of time. This is seen in the diet of the emperor penguin, in which the proportion of prey species in the diet changes seasonally, presumably as relative abundance fluctuates (Croxall & Prince 1996). Despite the wealth of evidence from dietary studies on the scale of predation on cephalopods, there is little evidence to suggest that the population distribution and feeding patterns of predators are strongly influenced by this seasonal availability.

However, the short, semelparous life cycle of cephalopods does mean that in some circumstances the spawning aggregations can provide a dense concentration of prey for higher predators. Early reports on the breeding aggregations of *Loligo opalescens* off the California coast, a species well known for its synchronised breeding and mass post-breeding mortality, record congregations of predators becoming thoroughly gorged in the abundant supply of dying squid in the spawning grounds (Fields 1965). Subsequent to these observations, coordinated investigations on all the major components of the California Current coastal ecosystem have clearly demonstrated the central importance of *L. opalescens* to the food web, which supports higher predators including marine mammals, seabirds and large fish (Morejohn *et al.* 1978). Despite high levels of predation on the breeding squid, it is notable that there appear to be no predators that feed on the egg masses that are laid, and which are readily available and highly visible attached to the substratum. It must be assumed that there is some deterrent present in the protein and energy-rich eggs or their coating which makes them unacceptable to predators.

Elsewhere, there are further examples of a single species of cephalopod playing an apparently central role in the diet of a higher predator during the cephalopod's spawning season. In the northeast Atlantic, the movements of sperm whales (*Physeter macrocephalus*) have been linked to the seasonal breeding mortality of squid belonging to the genus *Gonatus* (the two north Atlantic species *G. fabricii* and *G. steenstrupi* cannot distinguished from their beaks). Strandings of sperm whales along the coastline of Europe analysed by Santos *et al.* (1999) were all found to be males of between about 12 and 16 m in length and some 20–25 years old. These whales all stranded in the period November–December over several years. When analysed, the stomach contents, were found to consist almost solely of cephalopod beaks, and these were overwhelmingly members of the genus *Gonatus*, but with small numbers of other oceanic cephalopods. There is substantial evidence to suggest that *Gonatus fabricii* is the most abundant squid in the Arctic and sub-Arctic waters of the north Atlantic (Bjørke 1995). It is distributed from the surface to about 2700 m, and there is an ontogenetic descent as they grow and mature. The bulk of the adult population probably lives at 600–1000 m. The population biomass of these deep-water squid is estimated to reach 1.5 million tonnes of juveniles in the surface layers, and up to 20 million tonnes of adults in the Norwegian Sea alone (Bjørke & Gjosaeter 1998). There is direct evidence that the breeding cohort of *Gonatus*, which has a 2-year lifespan, dies after spawning (Bjørke 1995; Seibel *et al.* 2000a). The size frequency of beaks in the stomach contents of the sperm whales consisted almost entirely of adult-sized *Gonatus*, suggesting that they are fed on by the whales when they aggregate to spawn, and that the abundance of this particular cephalopod resource may well account for the seasonal movements of the whales into the area (Bjørke 2001; Santos *et al.* 2002).

There are other examples of higher predators targeting spawning concentrations, such as *Loligo vulgaris reynaudi* off South Africa (Smale *et al*. 1995), and *Sepia apama* off eastern Australia (Gibson & Sefton 1995).

15.1.4 Ecological role

Although in temperate seas the availability of cephalopods to predators is usually seasonal, this is less pronounced in tropical seas where spawning is often less seasonal (Tafur *et al.* 2001), and probably also in polar seas where their lifespan seems to exceed one year in some species, so there may be multiple year classes. The availability of cephalopods as prey in marine ecosystems at all latitudes is subject to considerable inter-annual variation, and when a strong cohort passes through a system this will lead to a substantial energy and nutrient flux to higher trophic levels as well as increased catch rates in the fisheries.

When the relative failure of a cephalopod population does occur, reduced breeding success in predators may follow until the population recovers (Xavier *et al*. 2003). Cephalopod populations have been known to fail almost completely on decadal time scales following periods of considerable abundance. *Todarodes sagittatus* became an abundant species, supporting fisheries of up to 30 000 t in the Norwegian fjords for about 10 years before disappearing almost completely (Sundet 1985). Similarly, *Illex illecebrosus* has declined dramatically in northwest Atlantic, and especially Canadian, waters since the late 1970s, when it supported a substantial fishery (O'Dor & Coelho 1993). Although these events are well documented because of the impact they had on fisheries, the effects of the changes on the dependent predators has not been established

Cephalopod abundance can fluctuate widely between generations. Ecological opportunism and the short life cycle in cephalopods means that fluctuations in abundance are primarily environmentally driven, and there are numerous reports of plagues of cephalopods in populations which are unexploited, or only lightly exploited, and so not affected by fishing pressure (Gunther 1936; Rees & Lumby 1954; Nesis 1983; Ehrhardt 1991). There are also well-documented examples of large inter-annual fluctuations in abundance in stocks exploited by fisheries (O'Dor & Coelho 1993; Sakurai *et al*. 2000; Waluda *et al*. 1999, 2001). This behaviour of populations suggests the terrestrial analogy of the desert locust whose populations fluctuate dramatically, reaching plague proportions and creating famines.

15.2 Consumption of cephalopods by predators

15.2.1 Predator types

The main predators of cephalopods are seabirds, seals, whales and larger fishes. Generally, predators adapted for catching fish often take cephalopods as well. There do not seem to be any specific adaptations for predation on cephalopods other than

Table 15.1 Selected fish predators showing the relative proportions of different prey in their diets and the dominant cephalopods taken (modified after Smale 1996).

Predator species	Area	Depth	Sample number	Cephalopods (% mass)	Fish (% mass)	Other (% mass)	Dominant cephalopod prey
Continental shelf fishes							
Epinephelus marginatus	SW Indian O	4–40 m	90	48.1	24.3	27.6	*Octopus*, *Loligo*, *Sepia*
Petrus rupestris	SW Indian O	5–40 m	113	10	89.8	0.2	*Octopus*, *Loligo*, *Sepia*
Seriola lalandi	SW Indian O	2–30 m	206	64.7	35.3	0.01	*Loligo*, *Sepia*
Squalus megalops	SE Atlantic O	50–450 m	53	31.8	65.7	2.5	*Octopus*
Hemigaleus microstoma	N Australia	Offshore	14	94.7	<0.1	5.2	*Octopus*, *Sepiolid*
Slope and rise fishes							
Centroscyllium fabricii	SE Atlantic O	150–700 m	45	8.3	27.3	64.1	Unidentified
Centroscyllium fabricii	NW Atlantic O	Abyss, slope, rise	9	81.5	13.6	4.9	*Pholidoteuthis adami*
Centroscymnus coelolepis	SE Atlantic O	660–1016 m	71	71.2	13.5	15.4	Octopoteuthis, Lycoteuthis
Deania calcea	SE Atlantic O	620–640 m	61	74	25	1	Ommastrephidae
Deania calcea	SE Atlantic O	475–900 m	62	16.3	82.5	1.2	Unidentifed
Squalus acanthius	SE Atlantic O	120–500 m	121	11.9	86.5	2.1	*Todarodes angolensis*
Squalus cf. *mitsukurii*	SE Atlantic O	150–550 m	211	18.7	80.4	0.9	*Todarodes angolensis*
Pelagic fishes							
Thunnus albacares	SW Indian O, AB	Inshore	422	2	97	1	Loliginidae, Ommastrephidae, Octopoda
Thunnus albacares	SW Indian O, AB	Shelf edge	63	27	72	1	*Lycoteuthis*, *Loligo*, *Ommastrephes*
Thunnus albacares	SW Indian O, EL	Inshore and shelf edge	129	5	94	1	Ommastrephidae, Octopoda, Lycoteuthidae
Thunnus albacares	Eastern Pacific O	Pelagic	18	13	36	52	*Dosidicus*, *Argonauta*, *Thysanoteuthis*
Thunnus albacares	EC Atlantic O	Oceanic	132	27	72	1	Ommastrephidae, Enoploteuthidae, Octopoda
Thunnus albacares	EC Atlantic O	Oceanic	520	12	69	19	*Illex*, *Ommastrephes*, *Argonauta*
Thunnus albacares	NW Atlantic O	Oceanic	16	14	85	1	Ommastrephidae, Octopoda
Thunnus albacares	CW Atlantic O	Oceanic	39	5	94	1	Ommastraphidae
Thunnus obesus	EC Atlantic O	Oceanic	23	19	81	0.5	Ommastrephidae, Octopoda, Cranchiidae
Thunnus obesus	Eastern Pacific O	Pelagic	40	63	22	15	*Dosidicus gigas*
Xiphias gladius	Portugal	NR	37	22.3	62.8	15	*Illex*, *Taningia*
Xiphias gladius	NW Atlantic O	200+ m	151	67	33	<1	Ommastrephidae, Octopoteuthidae
Xiphias gladius	Florida Straits	<200 m (?)	65	90	<10	<3	*Illex*, *Ommastrephes*, *Onychoteuthis*
Alepisaurus ferox	Central Pacific O	150–200 m	24	23	76	2	*Japetella*, *Bolitaena*, *Moroteuthis*
Alepisaurus ferox	Hawaii	220–250 m	40	19	52	29	*Japetella*, *Onykia*, *Bolitaena*

SW, southwest; NW, northwest; SE, southeast; O, ocean; AB, Algoa Bay; EL, East London; NR, not recorded; EC, east central; CW, central west.

generalised adaptations for grasping in the beaks of birds and the dentition of marine mammals.

15.2.2 Consumption by fish

Consumption of cephalopods by predatory fish is very widespread, and has been summarised by Smale (1996). The fish that consume cephalopods usually have broad-spectrum diets that include other groups such as other fish and crustaceans. Very few fish, with the exception of some elasmobranches, feed exclusively on cephalopods. The exceptions include the tawny nurse shark *Nebrius ferrugineus* and the sickle-fin weasel shark *Hemigaleus microstoma*, and some deep-living spiny dogfish also seem to feed largely on cephalopods when they are available. Cephalopods rarely penetrate estuaries. They are more important as prey on the continental shelves, and some squids, such as *Loligo vulgaris reynaudi* off South Africa, may be more dominant as prey during their spawning aggregations. Cephalopods are generally more important in the diets of larger predatory fish, particularly the sharks, which inhabit the continental slope and rise (Sauer & Smale 1991, 1993). They may also be important to pelagic fishes, such as swordfish and tunas, in some parts of the oceans. With the exception of *Dissostichus eleginoides* (Xavier *et al*. 2002), cephalopods are rarely taken by benthic Antarctic fish, but they are important prey of some pelagic fishes in the Arctic. The abundance and size of prey is critical, and the behaviour of both predator and potential prey is decisive in the prey choice of fish. Factors such as prey switching with growth between areas and at different times have major influences on the diets of predators. There are very few studies that have obtained rigorous enough data to allow quantitative analysis of the significance of cephalopods (or other prey) in the diets of predatory fishes, and even the most comprehensive studies are not predictive because findings relate only to the time-period of each study. Nevertheless, cephalopods are important components of most marine food webs, and furthermore may play an indirect role in facilitating prey capture for secondary predators, and in providing rejecta to benthic scavengers (Smale 1996). A typical example of the complexity of the food web structure involving cephalopods and fish is shown in Fig. 15.2, and examples of some quantitative studies are given in Table 15.1.

15.2.3 Consumption by seabirds

There are many studies that have quantified cephalopod consumption by seabirds, and these have been reviewed by Croxall & Prince (1996) and Cherel & Klages (1998). Cephalopod predators include gannets, auks, terns, shags, cormorants, penguins, albatrosses and petrels. They occur in the diet of all these birds, but it is only in some species of albatross and petrel that they are consistently as important as fish or crustaceans. Nevertheless, several penguins, auks and terns take significant quantities of squid at some sites and in some seasons. Most studies of cephalopod diets have been on temperate and polar seabirds in the southern hemisphere. However, they may play a key role in the diet of many tropical seabirds. For reasons of practicality of sampling, most research has been carried out on dietary samples collected from breeding colonies

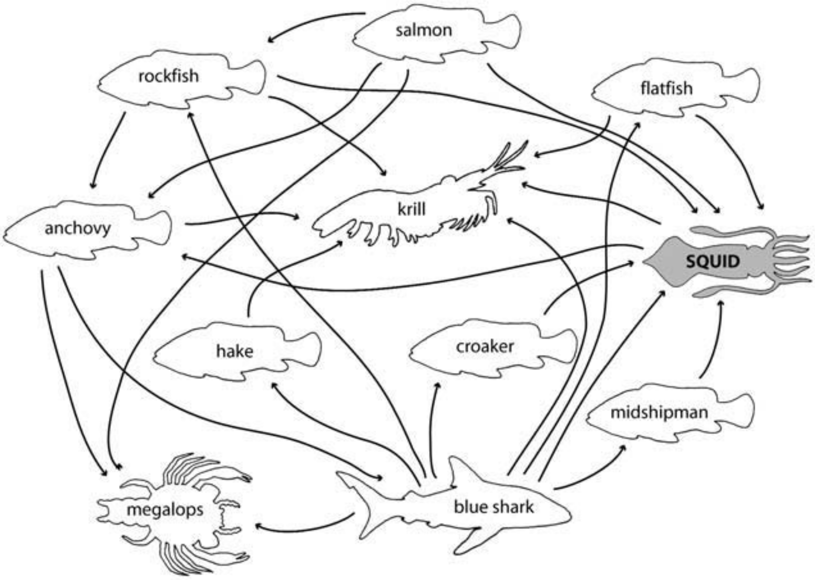


Fig. 15.2 Food web showing interactions between *Loligo opalescens* and commercially important or abundant fish on the California coast (after Morejohn *et al.* 1978).

during the breeding season, but cephalopods may be equally, or more, important to many marine birds outside the breeding season than has been documented. Several species and families of cephalopod are eaten by seabirds, but the squid families Ommastrephidae, Onychoteuthidae, Histioteuthidae and Gonatidae probably make the greatest contributions overall. There is little evidence for much size or species selectivity by seabirds when feeding on cephalopods, except within the general constraints imposed by the birds' size and habits.

The question of how flying seabirds catch cephalopods has stimulated much debate about whether they can catch live specimens unaided, or depend on the activities of other swimming predators such as fish and whales, or scavenge from their regurgitations, or indeed exploit the mass post-spawning mortalities of cephalopods. Many cephalopods make diurnal vertical migrations bringing them close to the surface at night, and there is substantial circumstantial evidence that some seabirds such as the grey-headed and black-browed albatrosses (Croxall & Prince 1994) and white-chinned petrels (Berrow & Croxall 1999) feed on live squid near the surface. They feed their chicks large quantities of intact, immature squid belonging to non-buoyant species, and there is no evidence that these were scavenged. Recent observations (Prince *et al.* 1994; Huin & Prince 1997) have also shown that some albatrosses are able to plunge and swim underwater to depths of about 10 m, which is much deeper than previously assumed, and deep enough to provide reasonable scope for feeding on live squid near the surface. It has been suggested that seabirds catch a disproportionate amount of squid species possessing light organs (Imber 1992), and that they rely on bioluminescence to locate their prey. However, this is not universally the case; grey-headed albatrosses, for instance, feed primarily on an ommestrephid, *Martialia hyadesi*, in sub-Antarctic waters, and this species has no photophores. It has also been suggested that seabirds may scavenge predominantly on squid species which are positively buoyant when dead (Lipinski & Jackson 1989), and this is more important as a factor determining prey species than bioluminescence.

There is no doubt that other species of seabird, such as the wandering and light-mantled sooty albatross, depend heavily on scavenged food. Remains of squid much larger than 20–30% of the bird's body weight have been found in gut contents, suggesting they have been feeding on scavenged remains. Many seabirds are known to form associations with whales (Enticott 1986; Pierroti 1988; Pitman & Ballance 1992), and as it is known that toothed whales frequently vomit at the surface (Clarke *et al.* 1981), which would provide a food source for scavengers. Indeed, Clarke & Goodall (1994) found in one study that the cephalopod composition of the diet of seabirds showed strong similarities to that of toothed whales in the same area. Squid fisheries also provide a source of food for scavenging seabirds, and in the Falkland Islands it has been shown that black-browed albatrosses may obtain a proportion of their diet by scavenging from the trawl fishery for *Loligo gahi* (Thompson 1989, 1992). Imber (1992) also found that in one year a substantial proportion of the diet of wandering albatrosses breeding on South Georgia was *Illex argentinus* which may have been scavenged from the fishery on the Patagonian Shelf.

Seabirds probably have a relatively low impact on cephalopod stocks compared with marine mammals, but nevertheless several species match the removals of some of the larger cephalopod fisheries (Table 15.2). Furthermore, they can provide valuable scientific data on cephalopod species and population biology. They catch larger specimens and a greater diversity of species than either scientific or commercial nets (Rodhouse 1990). Commercial squid catches correlate well with estimates of seabird consumption. Consumption of *Illex illecebrosus* by gannets and catches by the inshore

Table 15.2 Estimates of annual consumption (tonnes) of squid by seabirds in various sea areas (from Croxall & Prince 1996, who lists the original sources of information).

Locality	Area (km^2)	Consumption by seabirds		Squid as % of food intake
		Squid	All prey	
NE Atlantic	15 000 000	40 000	4 500 000	<1
Mediterranean	2 000 000	3 000	100 000	3
Iberian Atlantic	9 000 000	63 000	400 000	16
SE Bering Sea	132 700	60 000	400 000	15
Georges Bank, Newfoundland	52 500	21 000	105 000	20
Gulf of St. Lawrence	214 000	300	93 752	<1
California Coast	215 000	100 000	193 000	52
Hawaiian Islands	c. 500 000	223 000	410 000	54
Prince Edward Islands, S. Indian Ocean	125 000	100 000	586 000	17
Heard/McDonald Islands, S. Indian Ocean	c. 125 000	1 200	421 330	<1
South Georgia	1 000 000	466 000	7 820 000	6

fishing fleet in Newfoundland waters have been shown to be significantly associated over several years, and reductions in squid availability to gannets have preceded failures in the local fishery (Montevecchi & Meyers 1995). Seabirds have also provided the basis for identification of potential commercial fisheries and for the development of precautionary management procedures in sub-Antarctic waters of the South Atlantic (Rodhouse 1997).

If cephalopod consumption per unit area can be used as an index of prey abundance and its availability to seabirds, then there are significant differences in cephalopod abundance between oceanic regions (Croxall & Prince 1996). In the eastern Atlantic, Mediterranean and Heard Island areas, squid consumption by seabirds is 1000–10 000 g/km^2, while in the Bering Sea, Newfoundland, California, Hawaii and the two other sub-Antarctic areas, consumption is estimated to be 400 000–500 000 g/km^2. Exceptionally, in the Prince Edward Islands (Canada), the estimate reaches 833 000 g/km^2. Interestingly, analysis of human fisheries in all the main fishing areas of the world (Caddy & Rodhouse 1998) also suggests that the ratio of cephalopods to groundfish (trawl-caught) in the northeast Atlantic is very low in comparison with other productive areas.

15.2.4 Consumption by seals

For 31 of the 33 living species of seal, cephalopods are known, or suspected, to form a part of the diet (Klages 1996) (Table 15.3). The two exceptions are the Baikal seal and the Caspian seal, which both inhabit fresh water where cephalopods do not occur. The available evidence indicates that no species of seal specialises entirely on cephalopods, and only a few regularly eat appreciable quantities, although for several they do appear to be a seasonally important prey resource. For most seals, only rudimentary prey data have been published. However, these data reveal that the most common cephalopod taxa consumed by seals are members of the neritic family Loliginidae and the oceanic Ommastrephidae, Onychoteuthidae and Gonatidae, as well as benthic octopods. There are insufficient data to make any general estimate of the global consumption of cephalopods by seals, but some regional estimates have been made (Croxall *et al.* 1985; Rodhouse *et al.* 1992b).

The southern elephant seal (*Mirounga leonina*), which is capable of deep and sustained dives, utilises cephalopods as a major component of diet. From an analysis of 51 stomach-lavaged animals at South Georgia, Rodhouse *et al.* (1992b) identified the beaks of 16 species of cephalopods from 13 families. *Moroteuthis knipovitchi* (Onychoteuthidae) was estimated to contribute the greatest proportion of biomass in the diet (31.2%), and *Psychroteuthis glacialis* (Psychroteuthidae) was the most numerous squid (33.7%). The remaining biomass was mainly composed of the other large muscular squids, notably *Kondakovia longimana* (24.0%, Onychoteuthidae), *P. glacialis* (15.4%, Psychroteuthidae), *Martialia hyadesi* (11.2%, Ommastrephidae), *Alluroteuthis antarcticus* (10.8%, Neoteuthidae) and *Gonatus antarcticus* (3.6%, Gonatidae). Small numbers of octopuses of the genus *Pareledone* were also present. The total annual consumption of cephalopods by the elephant seal population of South Georgia has been estimated to be at least 2.3 million tonnes (Boyd *et al.* 1994).

Table 15.3 Biological characteristics of cephalopod prey consumed by seals (after Klages 1996, who lists the original sources of information).

	Cephalopod type consumed			Where consumed			
Seal species	Muscular	Oily	Ammoniacal	Inshore	Offshore	Benthic	Pelagic
Walrus	+					+	
Northern fur seal	+	+		+	+	+	+
Guadelupe fur seal	?	?	?	?	?	?	?
Juan Fernandez fur seal	+			+	+		+
Galapagos fur seal	+			+	+		+
South American fur seal	?	?	?	?	?	?	?
Cape and Australian fur seal	+			+	+	+	+
New Zealand fur seal	+				+	+	+
Antarctic fur seal	+		+		+		+
Subantarctic fur seal	+				+		+
Steller sea lion	+	+				+	+
Californian sea lion	+	+		+	+	+	+
South American sea lion	+					+	+
Australian sea lion	+			+		+	+
Hooker's sea lion	?	?	?	?	?	?	?
Harbour seal	+			+		+	+
Spotted seal	+			+		+	
Ringed seal	?	?	?	?	?	?	?
Harp seal	+	+		+	+	+	+
Ribbon seal	+	?	?	?	?	+	?
Bearded seal	+					+	
Hooded seal	+	?			+	+	+
Gray seal	+	?				+	?
Grabeater seal	?				+		+
Ross seal	+		+	+	+		+
Leopard seal	+				+		+
Weddell seal	+	+		+	+	+	+
Northern elephant seal	+	+	+	+	+	+	+
Southern elephant seal	+	+	+	+	+	+	+
Mediterranean monk seal	+					+	
Hawaiian monk seal	+					+	

+, present in diet; ?, not known; blank, absent.

15.2.5 Consumption by cetaceans

Research has revealed that over 80% of odontocetes and two baleen whale species regularly include cephalopods in their diet (Table 15.4). In 28 odontocetes, cephalopods comprise the main food. Predominantly cephalopod-eating species are found in the whale families Physeteridae, Ziphiidae, Phocaenidae and Delphinidae. By far the most important of the 28 families of cephalopods represented in the diet of cetaceans are the oceanic Ommastrephidae and Histioteuthidae, and the Cranchiidae, with the neritic Loliginidae assuming most importance on the continental shelves. Onychoteuthidae and Gonatidae assume greater importance in polar regions and the north Pacific. The other 22 families form a reservoir from which various cetaceans eat opportunistically and as their sizes permit. There are probably fewer than 60 cephalopod species regularly in the diet of cetaceans.

Table 15.4 Occurrence cephalopods in the diet of cetaceans. The percentage of cephalopods of various families in their diet is listed (wherever possible by the percentage mass in the stomach contents, but otherwise by the percentage of the total number or subjectively from the literature). After Clarke (1996c) who lists the original sources of information.

	Ziphiidae	Monodontidae	Physeteridae	Phocaenidae	Delphinidae	Stenidae	Globicephalidae	Total (%)
Ommastrephidae	23	50	100	20	45	0	17	18
Onychoteuthidae	46	50	100	20	20	0	0	15
Gonatidae	38	50	33	20	20	0	33	14
Enoploteuthidae	15	0	33	20	30	0	33	12
Octopoteuthidae	46	0	100	0	25	0	17	15
Histioteuthidae	23	0	66	20	30	0	66	16
Cranchiidae	23	0	66	0	15	33	100	12
Loliginidae	8	0	33	60	40	33	66	18
Sepiidae	8	50	0	0	20	0	17	7
Octopoda	15	100	0	0	40	0	50	15

The species composition of the food of whales varies regionally, seasonally and annually. The greatest differences in species composition are found between cetaceans that live and feed in oceanic water and those in continental shelf water. There is a positive correlation between the size of the prey and both the size of the whale species and the growth stage within a species. This leads to some partitioning of the food between and within species, and presumably reduces competition. Broad estimates show that the biomass of oceanic cephalopods consumed annually by the largest odontocete, the sperm whale *Physeter catodon*, may be over twice the biomass of the global fish catch taken by humans. Regional estimates show that consumption by cetaceans of even little-known cephalopod species may greatly exceed the local catches of commercial fish.

The consumption of cephalopods by sperm whales in particular has been the subject of considerable interest. Because 95% of their food consumption is estimated to consist of squid, and because their population numbers, sex ratio and size structure are well established by the International Whaling Commission (IWC), global estimates of the total annual consumption of squid eaten by *P. catodon* have been estimated to be up to 320 million tonnes (Clarke 1980, based on a total population of sperm whales of 1 950 000, of mean weight 15 tonnes, with a daily feeding rate of 2–3% body mass).

Taking a localised example, Clarke (1996c) demonstrated that the catch of sperm whales at whaling stations in the Azores, which was well documented in the years 1935–1949, could be estimated to have taken a total weight of 373 000 tonnes of cephalopods annually during their 2 months residence in Azorean waters. This would have been composed of 148 000 tonnes of octopoteuthids (mainly *Taningia danae*), 122 000 tonnes of histioteuthids (mainly *Histioteuthis bonellii*), 45 000 tonnes of *Architeuthis* spp. (Architeuthidae), 12 000 tonnes of ommastrephids (mainly *Todarodes sagittatus*) and 12 000 tonnes of onychoteuthids (mainly *Onychoteuthis boreal-japonicus*). To put these numbers into context, the total annual human catch of all fish species in the Azores is about 14 000 tonnes.

15.2.6 Discrepancy between estimates of cephalopod consumption by predators and fishery yield

Comparing the very large estimates of cephalopod consumption by whales, and other predators, with global fisheries data published by FAO, it is very obvious there are large discrepancies between global and regional estimates of predator consumption of cephalopods and fisheries yield. The data on cephalopod consumption by higher predators have been combined with estimated feeding rates and population size to produce estimates of global and regional consumption. As already discussed, Clarke (1980) has estimated that over 320 million tonnes of squid are consumed annually by sperm whales. Previously, Voss (1973) had extrapolated, on the basis of conservative estimates of predator consumption, that some 100–300 million tonnes per year of cephalopods could be available for capture by fisheries world-wide, and that the actual potential might be 500 M t/year. Another estimate of the global cephalopod biomass made by Rodhouse and Nigmatullin (1996) fell between 193 and 375 million tonnes. These estimates are very large compared with a total global fisheries catch of some 100 million tonnes per year and total cephalopod catch of about 3.0 million tonnes per year

(FAO 1999). So, are the estimates of predation and extra-polations of total biomass realistic, or are there biases that need to be considered?

The first thing to consider in relation to these discrepancies is the rapidly changing biomass of cephalopod populations. Because cephalopods are short-lived, mostly about 1 year, the biomass of a single cohort increases from that of the eggs spawned by one generation to a short-lived peak of biomass later in the year. There is then a rapid reduction at the end of one year when the population spawns and dies. Modelling the lifetime energetics of a single cohort of squid, Rodhouse & Nigmatullin (1996) showed that biomass peaked at about 9 months, and then declined towards the spawning season. This shows that for much of the annual cycle the population biomass may be relatively low although annual turnover is large. From this it is clear that the extent to which a predator population can exploit the production of a cephalopod population will depend on the timing of removal in the annual cycle. This will be reflected in estimates of population biomass based on predator consumption. If the predators consume cephalopods at the time of year when biomass is maximum, the average standing-stock biomass may be overestimated.

Another source of bias in estimating predator consumption arises if estimates of the retention times of the cephalopod beaks in predator stomachs are inaccurate. The lining of the seal stomach, for instance, is very convoluted and tends to retain indigestible cephalopod beaks, whereas fish bones are more easily digested and pass more rapidly through the alimentary tract. Retention of beaks would tend to lead to overestimates of cephalopod consumption.

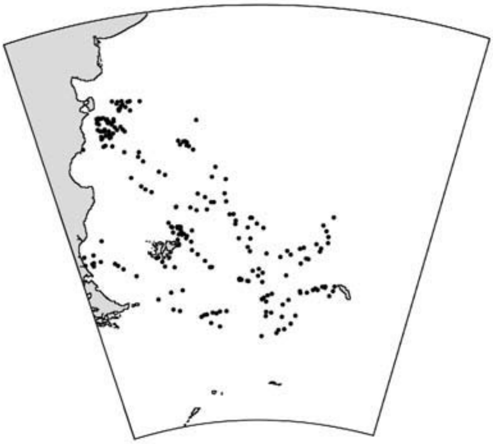
Even if biomass estimates are accurate, the fishery potential of cephalopods based on predation have probably been over-optimistic because many cephalopods are unsuitable for exploitation, either because of their unpalatable flavour or texture, or because their behaviour makes them unexploitable using commercial fishing gear. As an example, Rodhouse (1990) concluded that although a total cephalopod biomass of 3.7 million tonnes per year is consumed by predators in the Scotia Sea (Croxall *et al.* 1985), only one species out of the most common 12 had any potential for commercial fisheries in the short-to-medium term.

In conclusion, the total cephalopod biomass is undoubtedly large relative to the volume taken by commercial fisheries, but uncertainties about estimates based on predators necessitates more observational science to derive independent estimates. Conventional scientific sampling gear was inadequate for the task a quarter of a century ago (Clarke 1977) and there have been few developments since. New quantitative sampling technology is required.

15.2.7 Predator tracking and distribution of cephalopod prey

Technological developments for the study of higher predators at sea have also provided new opportunities to improve our understanding of the distribution of their cephalopod prey. Platform terminal transmitters (PTTs or satellite tags) are attached to free-living animals and relay the geographic location of the animal via satellite for as long as the life of the battery powering the unit (Jouventin & Weimerskirsch 1990). PTTs have now been deployed on several oceanic cephalopod predators, including wandering, black-browed and grey-headed albatrosses (Prince *et al.* 1998), black-footed and Laysan albatrosses (Hyrenbach *et al*. 2002), elephant seals (McConnel & Fedak 1996, 2000) and white-chinned petrels (Berrow *et al.* 2000).

The white-chinned petrel is a broad-spectrum predator which preys on myctophid fish, crustaceans including Antarctic krill and squid. PTT-tracked birds breeding on Bird Island, South Georgia, in the south Atlantic are clearly adept at finding and catching different species of squid during foraging trips away from the breeding site. They exploit three different habitats during the course of the breeding season (Fig. 15.3), feeding on the commercially exploited squid *Illex argentinus* whilst foraging on the Patagonian Shelf, on *Galiteuthis glacialis* in the Shag Rocks area immediately to the west of South Georgia and on a species of *Brachioteuthis* around the South Orkney Islands to the south (Berrow *et al.* 2000).


(a) foraging during egg incubation

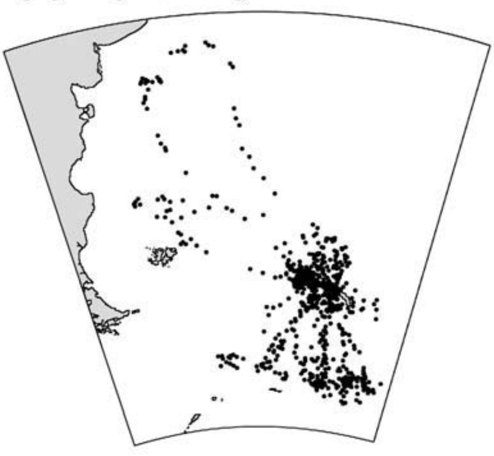

(b) foraging during chick rearing

Fig. 15.3 Foraging ranges of satellite-tagged white-chinned petrels, *Procellaria aequinoctialis*, revealed by plotting the locations of satellite-tracked individuals breeding on Bird Island in South Georgia. (a) During the egg incubation period. (b) During the chick-rearing period (Berrow *et al*. 2000).

Xavier *et al.* (2003) has undertaken a detailed analysis of the information that can be derived about the geographical distribution of cephalopods using data on gut contents of PPT-tagged albatrosses. This analysis revealed that knowledge of the distribution of well-known cephalopod species such as *Illex argentinus* could be extended, and also new data could be derived on the distribution of little-known cephalopods. A unique study of the relationship between sperm whale distribution and the abundance of the squid *Dosidicus gigas* in the Gulf of Mexico, however, failed to reveal clear relationships between the distribution of the predator and its potential cephalopod prey (Jaquet & Gendron 2002).

15.3 Interactions between predator populations and fisheries

15.3.1 The major fisheries

The squid stocks exploited by the major fisheries and their dependent predators, where they have been identified, are given in Table 15.5. Historically, *Todarodes pacificus* is the largest squid fishery in the world, but there are surprisingly few data on its predators. One study, on short-finned pilot whales (Table 15.5), has shown that it consumes *T. pacificus*, but given the substantial consumption of ommastrephids inhabiting shelf regions elsewhere in the world, it is likely that many other predators are at least partially dependent on this abundant squid.

Ommastrephes bartrami is an oceanic squid found in the diet of sperm whales and short-finned pilot whales in the Kuroshio Current system in the western Pacific, where it is commercially exploited (Table 15.5), and elsewhere where fisheries do not occur (Clarke & Roeleveld 1998). It is probably also consumed by other predators in the Kuroshio system and elsewhere in the Pacific it is the prey of sharks (Dunning *et al.* 1993; Seki 1993), Parkinson's petrel, *Procellaria parkinsoni* (Imber 1976), and some seabirds breeding in the Haiwaiian Islands (Harrison *et al.* 1983).

Despite the extensive fisheries for loliginids, there are few studies that reveal the presence of *Loligo* spp. in the diet of predators. Judging by the importance of loliginid species in areas where research has been done, e.g. *L. opalescens* in the California Current system where Morejohn *et al.* (1978) have demonstrated the role of this squid (Fig. 15.4), there are probably numerous predators of loliginids interacting with the many fisheries elsewhere in the world.

The beaks of *Nototodarus sloanii* and *N. gouldi* from predator gut contents are indistinguishable, and where they have been identified in gut contents it is on the basis of known distribution. Several hundred Hooker's sealions are caught annually as a by-catch of trawlers targeting *Nototodarus sloanii* around the Auckland Islands off New Zealand, and it is assumed they are preying on the squid in this area (Reijnders *et al.* 1993). However, there appears to be no interaction between the sealions and the jigger fishery operating around New Zealand. A *Nototodarus* sp., identified as *sloanii*, is also consumed by fiordland and yellow-eyed penguins in New Zealand waters (van Heezik 1989, 1990a, b). Elsewhere, in Australian waters, *Nototodarus gouldi* are preyed on by the Australian fur seal, *Arctocephalus pusillus* (Gales *et al.* 1993), the little

Table 15.5 Predators of the major squid species caught by the global light-fishing fleet (Rodhouse *et al.* 2001).

Province	Squid species	Catch (10^3 t/year)	Predator species	Predator consumption
Kuroshio Current	*Todarodes pacificus*	228–716	*Globicephala macrorhynchus*	No data
Kuroshio Current	*Ommastrephes bartrami*	248–378	*Physeter catodon* *Globicephala macrorhynchus*	No data No data
China Sea Shelf	*Loligo* spp. (*L. chinensis* + others)	17–24	No data	No data
Sunda-Arafura Shelves	*Loligo* spp.	137–195	No data	No data
New Zealand	*Nototodarus* sp. (probably *N. sloanii*)	29–83	*Phocarctos hookeri* *Arctocephalus forsteri*	No data 53% of cephalopod mass
New Zealand	*Nototodarus sloanii*	29–83	*Eudyptes pachyrhynchus* *Megadyptes antipodes*	61% of beak numbers 65% of cephalopod mass 95% of cephalopod mass
New Zealand	*N. gouldi*	1–39	No data	No data
California Current	*Loligo opalescens*	78	Fish:	
			Oncorhynchus tshawytscha	4th in terms of frequency
			Oncorhynchus kisutch	2nd in terms of frequency
			Porichthys notatus	2nd in terms of frequency
			Genyonemus lineatus	3rd in terms of frequency
			Sebastes goodei	3rd in terms of frequency
			Citharichthys stigmaeus	2nd in terms of frequency
			Pleuronechthys decurrens	1st in terms of frequency
			Opiodon elongatus	2nd/4th in terms of frequency
			Eopsetta jordani	2nd in terms of frequency
			Hippoglossus stenolepis	17th in terms of frequency
			Anaplopoma fimbria	9th in terms of frequency
			Prionace glauca	No data
			Seabirds:	
			Gavia arctica	2nd in terms of frequency
			Phalocrocorax pencillatus	4th in terms of frequency
			Puffinus griseus	2nd in terms of frequency >95% of mass in diet
			Puffinus tenuirostrus	1st in terms of frequency
			Puffinus creatopus	3rd in terms of frequency
			Fulmaris glacialis	7th in terms of frequency
			Larus heermanni	6th in terms of frequency
			Larus canus	4th in terms of frequency
			Larus glaucescens	1st in terms of frequency (with fish)
			Larus californicus	'major consumer'
			Rissa tridactyla	1st in terms of frequency
			Cerorhinca monocerata	1st in terms of frequency
			Uria aalge	2nd in terms of frequency

Table 15.5 *(cont'd)*

Province	Squid species	Catch (10^3 t/year)	Predator species	Predator consumption
			Seals and otters:	Present in diet
			Enhydra lutris	5th in terms of frequency
			Mirounga angustirostris	1st in terms of frequency
			Callorhinus ursinus	2nd in terms of frequency
			Zalophus californianus	
			Cetaceans:	
			Phocaena phocaena	1st in terms of frequency
			Lagenorhynchus obliquidens	1st in terms of frequency (with fish)
			Globicephala melaena	Primarily *L. opalescens*
			Physeter catodon	$6.66–13.14 \times 10^6$ t/year[1] $10.56–20.18 \times 10^6$ t/year[2]
Humboldt Current	*Dosidicus gigas*	0.3–195	Fish and cetaceans, swordfish, marlin, tuna, dolphin, blackfish	No data
			Thunnus obesus	No data
			Thunnus albacares	
Southwest Atlantic	*Illex argentinus*	157–401	Demersal/pelagic fish: *Merluccius hubbsi*, *Pomatomus saltatrix*, *Polyprion americanus*, *Pagrus pagrus*, *Sphyrna lewini*, *Trichiurus lepturus*	No data (estimated to comprise 38% of the food of fish on the Patagonian Shelf)
			Pelagic fish: Istiophoridae, *Isurus oxyrhincus*, *Thunnus albacares,* *T. alalunga*, *T. obesus*, *Xiphius gladius*	No data
			Seabirds: *Spheniscus magellanicus*	No data
			Marine mammals: *Kogia breviceps*, *Physeter macrocephalus*, *Arctocephalus tropicalis*	No data
	Martialia hyadesi	0.2–24	Seabirds:	
			Thalassarche chrysostoma	$14.2–18.7 \times 10^3$ t/year
			Thalassarche melanophrys	3.5×10^3 t/year
			Diomedea exulans	$0.04–0.06 \times 10^3$ t/year
			Phoebetria palpebrata	0.02×10^3 t/year
			Procellaria aequinoctialis	74.6×10^3 t/year
			Macronectes giganteus	0.3×10^3 t/year
			M. halli	0.006×10^3 t/year
			Eudyptes chrysolophus	4.0×10^3 t/year
			Seals:	
			Mirounga leonina	$77.0–308.0 \times 10^3$ t/year
			Arctocephalus gazella	$<15.7 \times 10^3$ t/year
			Cetaceans:	
			Physeter catodon	$<3.3 \times 10^3$ t/year
			Hyperoodon planifrons	73.7×10^3 t/year
			Globicephala melaena	$<48.0 \times 10^3$ t/year

Notes: [1]Based on a normal full meal; [2]based on a full meal at satiety.

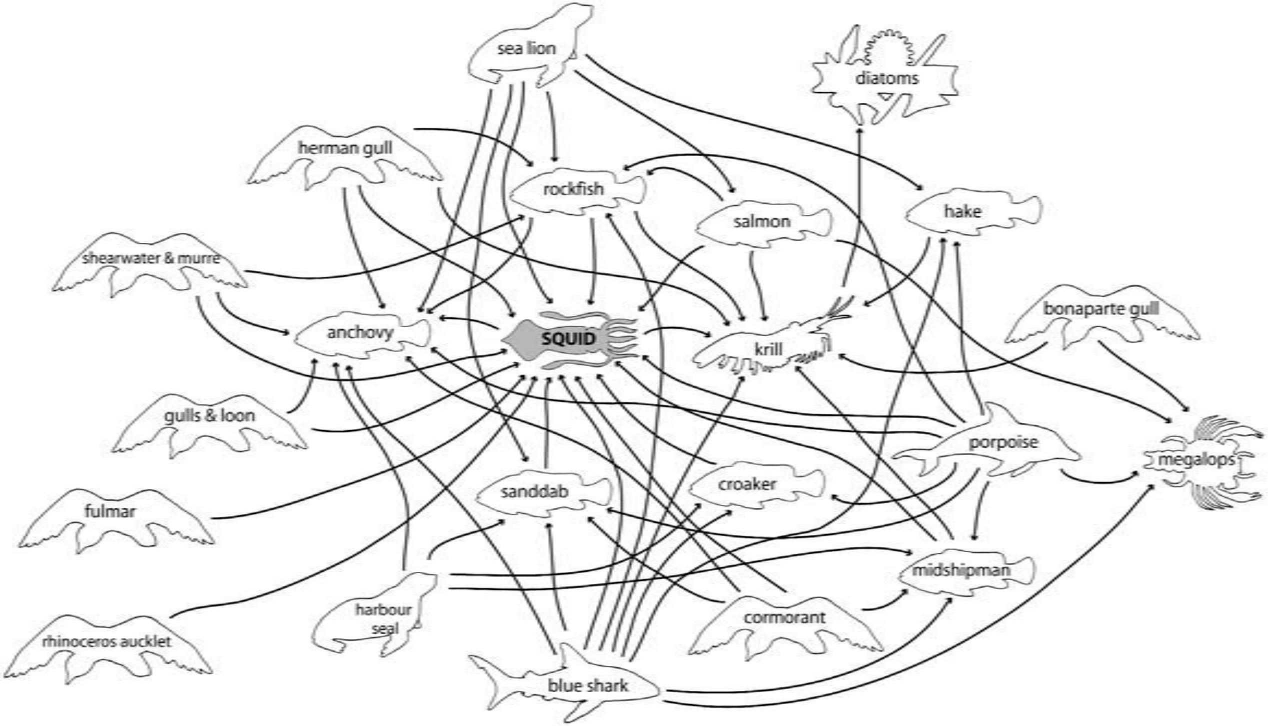


Fig. 15.4 Interactions of birds, mammals and fish in the *Loligo opalescens* centred food web off the coast of California (after Morejohn *et al.* 1978).

penguin *Eudyptula minor* (Gales & Pemberton 1990; Montague & Cullen 1988; Cullen *et al*. 1992) and the short-tailed shearwater (Skira 1986).

By far the greatest consumption of a commercially exploited cephalopod by a predator is *Dosidicus gigas* fed on by sperm whales in the Humboldt Current. R. Clarke *et al.* (1988) estimated that when sperm whales were at, or below, the level of maximum sustainable yield between 1959 and 1961, the minimum consumption of this squid was 6.7 million tonnes per year and could have been as high as 20.1 million tonnes per year, or at least 34 times the highest annual catch recorded in the Peruvian fishery since the start of industrial fishing in 1991 (Yamashiro *et al.* 1998). R. Clarke *et al.* 1988 argued that *D. gigas* is almost the only prey of sperm whales in the Humboldt Current. Given the huge consumption of *D. gigas* by sperm whales, it is notable that although the diet of sperm whales has been analysed in the south Atlantic (Clarke 1980), New Zealand (Clarke & Roper 1998) and the Kuroshio Current (Okutani *et al.* 1976; Okutani & Satake 1978), there are no records of consumption by the whales of the target species of the fisheries in these areas. *Todarodes pacificus*, *Nototodarus sloanii*, *N. gouldi* and *Illex argentinus* are smaller than *D. gigas* and, probably more importantly, they live in shallower water over the continental shelves where sperm whales do not regularly feed.

Illex argentinus supports the most important fishery in the south Atlantic. Extensive studies of the diet of penguins in the Falkland Islands have shown that although they feed on squid, their diet is dominated by *Gonatus antarcticus*, and only small quantities of *I. argentinus* are taken. However, the prevalence of *I. argentinus* in the diet of white-chinned petrels over the central part of the Patagonian Shelf, north of the Falkland Islands (Malvinas) suggests that such wide-ranging species, together with marine mammals and possibly other seabirds from Argentina, and especially the Peninsula Valdez and winter migrants from the Falkland Islands, may take *I. argentius* in substantial quantities. A limited analysis of the diet of fish predators has shown that *I. argentinus* is important in the diet of the fish *Thunnus obesus*, *Xiphius gladius* and *Polyprion americanus*. It has also been estimated that it comprises about 38% of food of fish on the southern Patagonian Shelf (Haimovici *et al.* 1998). There is a complex trophic system in this region (Angelescu & Prenski 1987), in which *I. argentinus* and hake, *Merluccius hubbsi*, feed on anchovy, the squid prey on young pelagic hake, and older hake feed on all sizes of the squid. Hake are therefore competitor, predator and prey of *I. argentinus*. In view of the size and importance of this fishery and the importance of the region for top predators (Croxall & Wood 2002), it would be very useful, for management purposes, to have more information on the importance of the species in the diet of seabirds, seals and marine mammals.

Although *Martialia hyadesi* is only occasionally caught on the Patagonian Shelf, its importance in the diet of Antarctic seabirds and marine mammals, and as a potential fishery in Antarctic waters (Rodhouse 1990), means that its role in the diet of Antarctic predators has been analysed. This has led to the Commission for the Conservation of Antarctic Marine Living Organisms (CCAMLR) establishing precautionary measures in the event of a fishery commencing in the Antarctic (see Chapter 19). It has long been known that squid are important in the Southern Ocean ecosystem (Harrison-Matthews 1929a, b), and research on predator diets in the Scotia Sea (Clarke 1980;

Clarke *et al.* 1981; Clarke and Prince 1981; Clarke and McLeod 1982a, b) has added considerably to knowledge of the squid fauna of the region. A comparison of remains in stomach contents with whole material from the Falkland Islands fishery (Rodhouse & Yeatman 1990) has revealed *M. hyadesi* is a key species in the diet of albatrosses, white-chinned petrels, king penguins and southern elephant seals on South Georgia (Rodhouse *et al.* 1987, 1990, 1992a; Rodhouse & Prince 1993; Croxall & Prince 1994; Croxall *et al.* 1995; Rodhouse *et al.* 1998a). This is a circumpolar species associated with the Antarctic polar frontal zone (APFZ) (Piatkowski *et al.* 1991; Xavier *et al.* 1999), which in the south Atlantic forms a broad loop linking the ecosystems of South Georgia and the north Scotia Arc with the Patagonian Shelf edge (see Fig. 17.9). It occupies the niche of epipelagic fish (Rodhouse & White 1995) feeding on mesopelagic fish and crustaceans (Rodhouse *et al.* 1992b) in a community dominated by tunicates, crustaceans, fish and coelenterates, as well as other squid species (Piatkowski *et al.* 1994; Rodhouse *et al.* 1994a; Pagès *et al.* 1996; Rodhouse *et al.* 1996). They are associated with mesoscale oceanographic features in the APFZ (Rodhouse 1997) where seabirds forage for them (Rodhouse *et al.* 1996, 1998a). They occasionally spread over the Patagonian Shelf edge and are caught by the fleet primarily targeting *Illex argentinus* (Rodhouse 1991; Gonzalez *et al.* 1997; Ivanovic *et al.* 1998). Small juveniles caught near the shelf edge around the Falkland Islands indicate that it spawns in this area, probably outside the shelf break (Rodhouse *et al.* 1992c), but the life cycle is poorly understood.

15.3.2 Managing cephalopod fisheries in an ecosystem context

For much of the history of fisheries science, the exploited stocks of marine organisms have been managed on a species-specific basis, with careful analysis of the rates of growth, mortality and reproduction so that removals from individual stocks can be matched to the theoretical concept of a ‘maximum sustainable yield’ (MSY). Management paid scant, if any, attention to the health of the ecosystem from which removals were being made, despite the fact that by the last decades of the twentieth century the maximum capacity of the world’s oceans to sustain fisheries was clearly being approached rapidly. Furthermore, the MSY approach is invalid in systems where harvesting takes place at more than one trophic level (Beddington & May 1980). There is now an increasing realisation that the world’s fisheries are damaging the environment in which they take place (Jennings & Kaiser 1998), that large-scale ecological changes in marine ecosystems have been caused by fisheries (Pauly *et al.* 1998, 2002; Caddy 1995; Caddy & Rodhouse 1998), and that as fisheries have extended to the remotest parts of the world’s oceans, removals have the potential to do extensive damage to dependent populations, especially higher predators (Everson 1992).

The first effective measures to manage fisheries in an ecosystem context were introduced by the Commission for the Conservation of Antarctic Marine Living Organisms (CCAMLR) in the mid-1980s. This was in response to the developing Antarctic krill fishery, which threatened to have damaging effects on dependent seabirds, seals and whales in the southern Ocean. Other international fishery organisations have since adopted this approach (Gislason *et al.* 2000), and cutting-edge fisheries research is increasingly tackling problems of managing fisheries in a whole ecosystem context.

Given the level of interactions between cephalopod predators and the major fisheries for cephalopods, the ecosystem approach will have particular relevance to these stocks. The fisheries can have effects at different temporal and spatial scales. In the short-term, removals in localised areas can substantially deplete the biomass to the immediate detriment of dependent species. In the longer-term, fishing at intensities which reduce the level of escapement from the fishery could reduce the spawning stock below viable numbers, and hence damage recruitment in succeeding years with long-term consequences for higher predators. Although no cephalopod fishery is currently managed systematically in an ecosystem context, a precautionary approach using ecosystem principles has been set out for managing a potential new squid fishery in the Antarctic (Rodhouse 1997).

Chapter 16

Fishing methods and scientific sampling

Summary: Fishing methods specific to cephalopods arise from traditional hand-fishing techniques. The targeted commercial methods exploit the behavioural characteristics of the target species and provide uniquely high-quality catches with little collateral ecological impact or by-catch of other organisms. Examples are the use of jig-fishing with lights for squid, which relies on the tendency of squid to be attracted to lighted fishing vessels, attacking the prey and the moving fishing jigs which mimic the prey. This accounts for about half of the global catch of cephalopods, and is undertaken by fleets of dedicated vessels, specially equipped to operate multiple lines of jigs using programmable automated machines. Pot-fishing for octopus and cuttlefish is a highly selective and low-impact form of fishing common throughout the world in coastal areas for artisanal and small-scale commercial use. Trawling, in various forms, is the second most important fishing method for squid, octopus and cuttlefish, but provides a mixed catch of a lower quality and value. Gill-net fishing for oceanic squid in the Pacific, now effectively ceased, used to be highly productive, but resulted in substantial mortalities of small cetaceans. Scientific sampling of cephalopods by traditional research nets is likely to be highly inefficient, as suggested by the mismatch of both size frequency and species composition of the net-caught fauna with the analysis of diet composition of squid predators. Acoustic methods of detection are of value for selected assessment purposes, and the increased use of submersibles and remotely operated vehicles is providing new biological information on deep-water species.

In common with many marine species of fishery importance, the bulk of scientific knowledge on populations and species ecology arises from the commercial catch. Results from standard scientific sampling methods, often directed at the less abundant species and less productive habitats, may be available for comparison. Neither approach produces unbiased data, but both can produce useful information and specimens.

Fisheries world-wide are broadly classified as industrial or artisanal. The distinctions are based on the scale of the operation, and whether the catch is commercially traded. Thus, industrial fisheries typically involve substantial capital investment in vessels and gear, the employment of labour to operate mechanised methods, and selling the catch for processing and distribution. Artisanal fisheries primarily supply local consumption at family or village level, capital investment is minimal, and several fishermen may work together but usually on a cooperative or share basis.

Methods and gear for commercial fishing are relatively standardised and activity is focused on the main productive fishing grounds. The catch becomes a traded commodity, priced and sold through major trading markets and allowing the results of fishing to be readily quantified and described in some detail. Numerical indices arising from these data allow statistical comparisons to be made between commercial fisheries for different species and in different geographical regions and caught by different methods. Measures of fishing effort can be derived related to catching success and possibly to the actual relative abundance of the target species.

Another descriptor often applied to commercial fishing is whether it is targeted or ‘by-catch’. This distinction may be used in various ways, for example, the specialised fishing for squid with moving jigs and lights does not catch other species, and is clearly targeted fishing. Bottom trawls, by contrast, are generalised and indiscriminate methods, catching most animals within range of the net opening which are of sufficient size to be retained by the net mesh. A bottom trawl is the main method used for some large-scale benthic (octopus) and demersal (loliginid squid) species, but when squid or octopus are caught as a minority component of a mixed trawl catch of fish they are usually classed as a by-catch. However, the same net can be set up for different grounds or at a different time of day to target the cephalopod catch.

Artisanal fisheries are very diverse and located in most coastal regions worldwide. They rely on local materials and fishing traditions, and are usually highly adapted to local environmental conditions and seasons. A detailed description of methods is seldom available, the necessary information being passed on from person to person, and the catch is normally unrecorded. In these circumstances, we can only guess at the real value of artisanal fishing to the local community, its efficiency compared with other activities, and its possible impacts on the ecology of the local resource.

The statistical returns for catch and effort in cephalopod fisheries are made more difficult to interpret due to a lack of discrimination between the types of fishing activity. Commercial fishing gear has often evolved from hand methods, scaled-up or replicated into commercial methods, and blurring the distinctions between fishing gear categories. Statistics arising from the commercial catch for cephalopods, in common with other locally available marine resources, are particularly affected by the method of sale. Catches that are sold through commercial markets will usually be recorded with some degree of accuracy. Coastal dwellers, however, fishing largely by hand-methods on artisanal scales, normally consume or distribute their catch locally leaving no recorded data. The true impact of these local-scale fisheries is therefore usually undocumented, but is probably significant and likely to have a biological impact on the local ecosystem.

Fishing for cephalopods, whether commercial or artisanal in scale, is based on traditional fishing techniques commonly used for other resource species, invertebrate or fish. When adapted to cephalopods, specialised modifications exploiting their particular behaviour patterns are introduced to target the gear. There is relatively little scientific information on the relative effectiveness of different gears, but there are a number of descriptions of equipment and techniques written primarily for the fishing and processing trade.

16.1 Fishing in antiquity

Beautifully executed illustrations of octopuses, squid and cuttlefish are found among the artifacts of the classical world of the Mediterranean. Cousteau & Diolé (1973) reproduce some of these illustrations from painted vases, mosaics and carvings now held in the world's museums. Octopuses were appearing not only on vessels from the sixth and fifth centuries BC, but also on metal coins of several ancient civilisations.

Earthenware pots and jars of various sizes, made to contain wine, oil and other commodities throughout the Mediterranean, were probably the most widely used method of catching octopuses. Laid on a rocky bottom and lifted at regular intervals, they are an effective fishing method in just the same way as pots are used today almost everywhere in coastal regions. We can also presume that hand-fished jigs and lures of various designs will have been commonly available and widely used. Traps set to attract spawning squid and cuttlefish probably also had a very ancient origin.

The wonderful mosaic from the buried city of Pompeii (book cover), now held in the Museum of Antiquities in Naples, Italy, clearly shows us the significance of cephalopods among the range of species of interest and significance to the ancient world. As well as their obvious interest for food, octopuses seemed to have had a symbolic interest as a protector (illustrated on the shields of warriors), and were celebrated for their ability to cling on to rocks, for example, by a relief carving on to an anchor stone discovered in the Palace of Knossos in Crete, where the octopus was an important cultural image during the late Minoan period.

16.2 Biological attributes exploited by fishing

It will become clear that many of the fishing methods for cephalopods directly exploit the biological attributes of the target species. Pot-fishing for *Octopus* depends primarily on the tendency of the animal to seek places of shelter from superior predators, and for mature females finding a secure site for spawning. Traps baited with live prey (crabs) rely on the predatory drive of *Octopus* to enter the trap. Similarly, the moving jig lures for squid exploit the universal habit of attack by cephalopods leading to entanglement with the hooks. The nocturnal feeding habits of most cephalopods are also exploited by fishing, using lights at night to aggregate them for net fishing or to illuminate the lures in the visual field. Conversely, squid tend to be close to the bottom during daylight, where they are targeted by bottom trawls, only dispersing naturally upwards into the water column at night (Rathjen 1984). The consequence of exploiting these specific behaviours is the highly targeted nature of most cephalopod fisheries.

Coastal squid and cuttlefish frequently gather in annual spawning aggregations. As dioecious species (sexes are separate) needing one-to-one mating to achieve fertilisation, frenzied breeding activity, with males grabbing at almost any moving object in an effort to achieve mating, leads to easy capture by jigs and scoop nets. These same species (the loliginids and sepioids) are also dependent on suitable bottom substrate conditions for spawning their egg masses. Fishing at these times and places clearly targets the pre-breeding population. If, in addition, trawls are used which damage the beds of spawned egg masses, then the continuity of the population is clearly vulnerable to over-fishing.

The major fished populations of the ommastrephid squid breed offshore in midwaters and their breeding aggregations are not vulnerable to targeted fishing. However, many of the main genera such as *Illex*, *Todarodes*, *Nototodarus* and *Todaropsis* undertake large-scale migrations over the shelf to feed and grow. It is during this migratory phase, when the squid are feeding and shoaling, that many of the industrial fisheries take place.

16.3 Industrialised fishing by mechanised methods

16.3.1 Jigs and jig-fishing

Unbaited lures called jigs, fished through the water column from automatically programmed reels, are the most distinctive and productive commercial fishing technique for squid. Particularly effective for the predatory pelagic squid of shelf and oceanic waters (family Ommastrephidae), variations of the jigging method are used in all the major oceans. The specificity and success of jigging as a fishing technique applied to squid has generated a whole range of specialised jig designs, fishing equipment and targeted vessel plans (Ogura 1983). A range of current jig designs and sizes is shown in Fig. 16.1. The basic commercial squid jig is composed of an elongate, barrel-shaped plastic stem in various colours, with a metal ring at either end. One to three rings of reflected unbarbed hooks surround and extend the stem at one end. The stem length typically ranges from 42 to 75 mm, and is extended by the hooks to overall lengths up to about 115 mm (Hamabe *et al.* 1982).

Variations in the colour, size and number of hooks associated with particular fishing operations are often a characteristic of the species and area to be fished and the preferences of the fishing skipper. There is little objective information to suggest that squid discriminate much between these minor variations in pattern. On the contrary, experiments on visual discrimination in *Todarodes pacificus* (Flores 1983) suggested that the animal is colour blind. Catch rates are rather higher using finer monofilament lines, implying that the thicker, more visible, line deters the squid. There are numerous

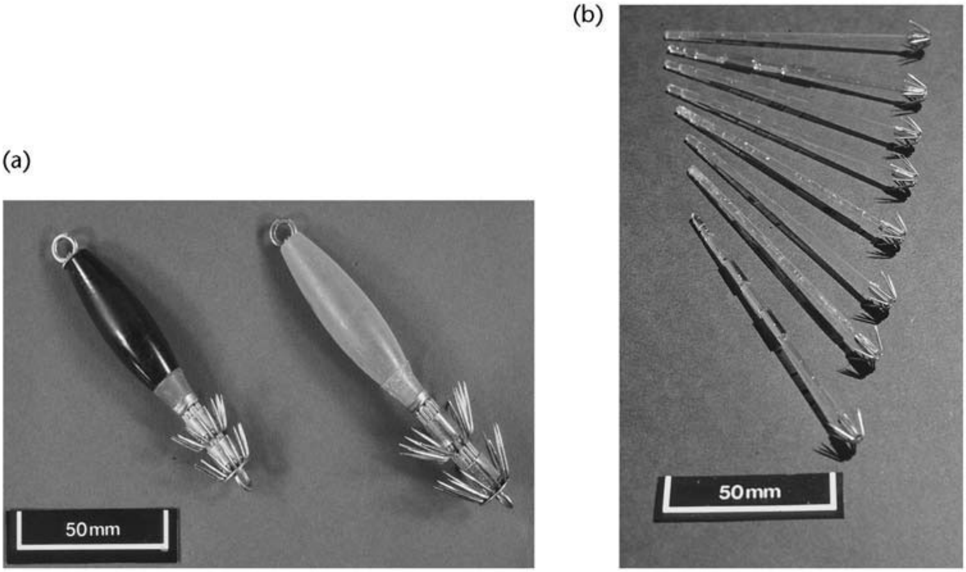


Fig. 16.1 Typical jig designs for squid. (a) Barrel-shaped, with a double row of reflected hooks and a ring at either end for commercial jigging machines fishing for ommastrephids. (b) A plastic spindle with a single row of reflected hooks and a single ring, commonly used for hand-fishing for loliginids.

designs of jigs for squid, individually adapted to species, location and the preferences of the fishermen. Some fishermen even incorporate small lights interspersed between the jigs on a line.

The principle of commercial-scale fishing using squid jigs is to operate them in series on heavy monofilament line at about 1-m intervals. Weighted at one end, each line, up to 150 m long, is wound onto an elliptical steel reel. Two reels are mounted together, about 2 m apart, on a single shaft driven by an electric or hydraulically powered motor (Fig. 16.2). The reel motors, under programmable, automated control, allow the lines to drop rapidly through the water column to the predetermined depth before rewinding at rates of 45–90 m/min. As the lines are drawn up through the water column, the velocity of the jigs is variable owing to the elliptical reel and the motion of the vessel. Squid attacking the lures are hooked through the tentacles and drawn upwards to the surface.

The fishing line carrying the jigs runs over a deep V-shaped plastic lead roller, held outboard laterally from the side of the fishing vessel on a moveable frame or scaffold. When fishing, these frames hold the lines some 1–3 m clear of the sides of the vessel and are raised vertically for stowage when the vessel is underway or in port (Fig. 16.2). As the hooked squid are passed rapidly over the lead roller, the sudden change in the angle of the line flings them forward, free of the unbarbed hooks, to fall onto the plastic mesh screen beneath the line between the roller and the reel. From there, the attendant fisherman rakes the catch inboard. In good fishing conditions, catch rates of 25–50 tonnes of squid per vessel per night can be achieved, i.e. as much as 10 kg, or exceptionally 20 kg, per jig per night's fishing.

Mechanised squid-jigging is one of the most highly targeted forms of fishing. Normally, the catch comprises 100% of the target species. Even if two or more squid species are caught in the same fishing session (e.g. catches of *Martialia hyadesi* may be mixed with *Illex argentinus* in some years in the North Falklands fishing zone), the individuals caught are of the highest quality, and are undamaged by contact with fish or other invertebrates, or rough treatment by net meshes. In these circumstances, investment is justified in highly specialised vessels with a deck-space layout to maximise the number of jig machines worked (Fig. 16.3) and processing facilities specifically tailored for handling the squid catch. To increase the number of jigging machines operated at a time, larger vessels carry the lead roller and lines away from the side of the vessel using alternate long and short frame arms (Fig. 16.2). In this way, large vessels can operate as many as 100 or more lines of jigs simultaneously.

During fishing operations, the vessel is held stationary in the water, usually by the aid of a large drogue or sea-anchor (Fig. 16.4). It is critically important that the numerous jig lines move though the water column as vertically as possible to avoid tangling of adjacent lines and to operate correctly within the main lighted zone.

16.3.2 Use of lights in jig-fishing

Jig-fishing for ommastrephid squid is normally carried out at night aided by powerful lights. The coastal Japanese fleet used kerosene or acetylene lamps for decades before the introduction of incandescent electric lights for fishing. On small vessels, the lamps

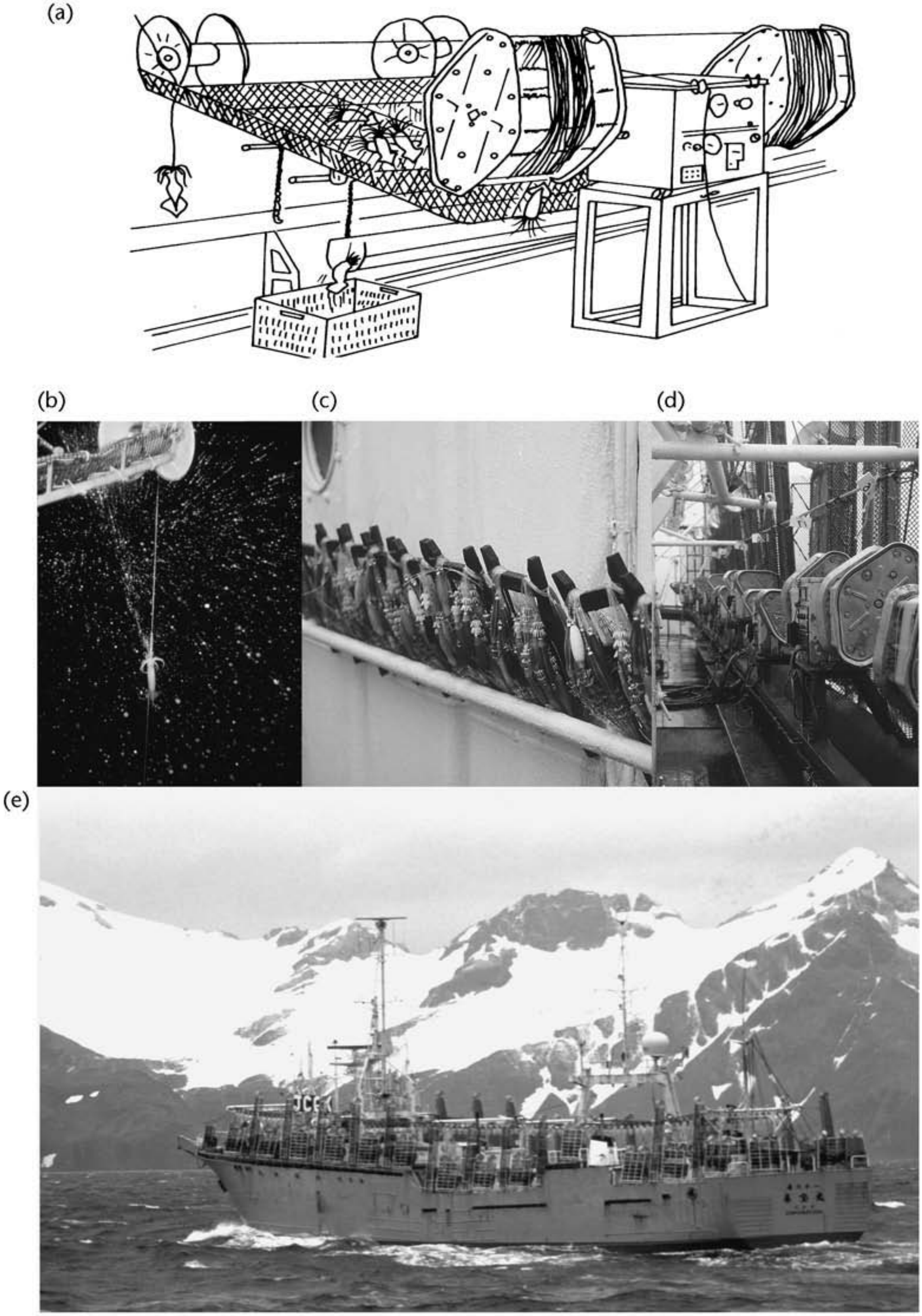


Fig. 16.2 (a) The main components of mechanised jig-fishing gear for squid (Suzuki 1990). (b) *Illex argentinus* jigged at night. (c) Prepared jig-lines ready for rigging. (d) Elliptical reel for jig-lines. (e) A Japanese jigging vessel travelling at sea off South Georgia with jigging gear stowed.

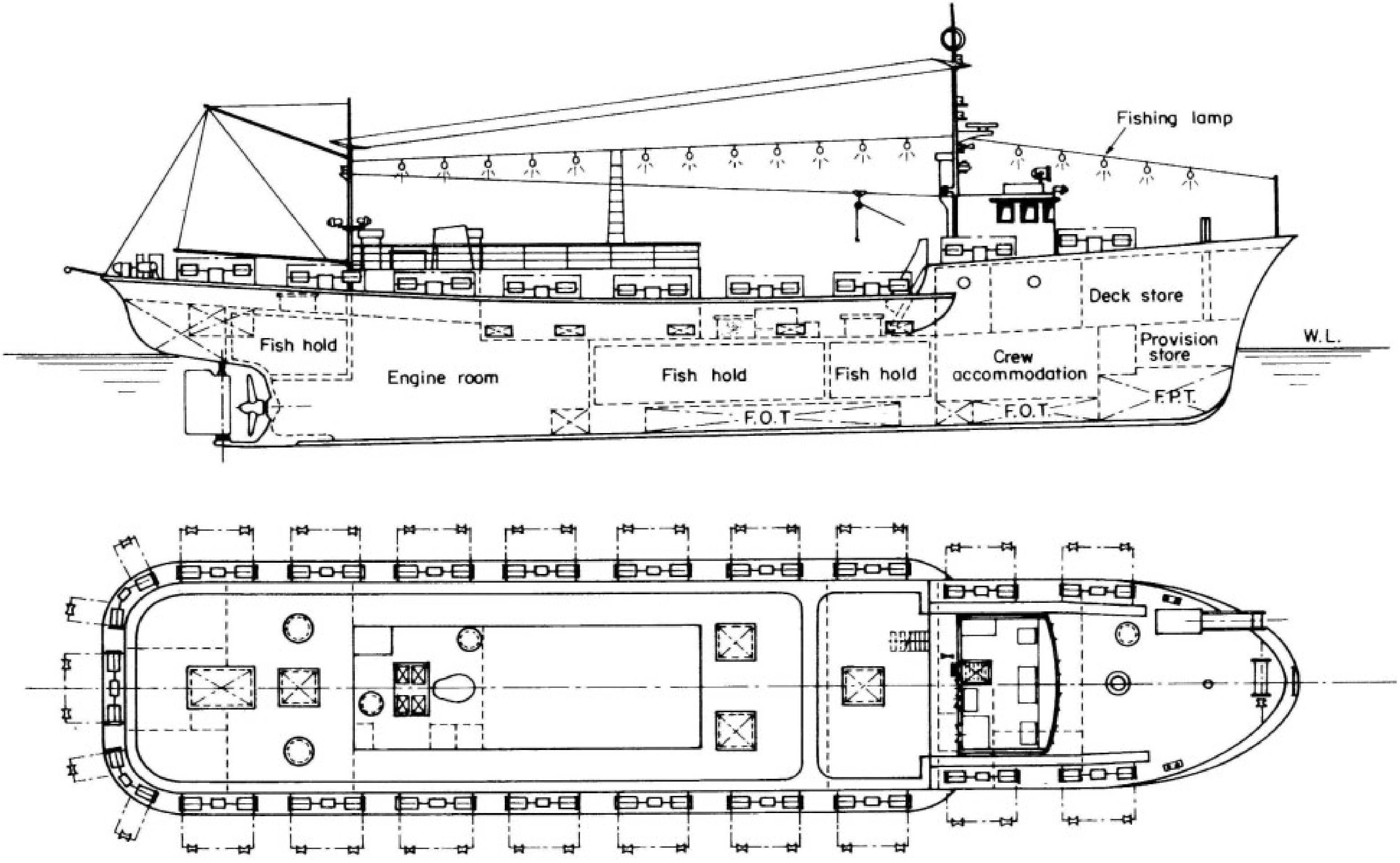


Fig. 16.3 Deck layout of a coastal mechanised squid-jigging vessel (after Hamabe *et al*. 1982).

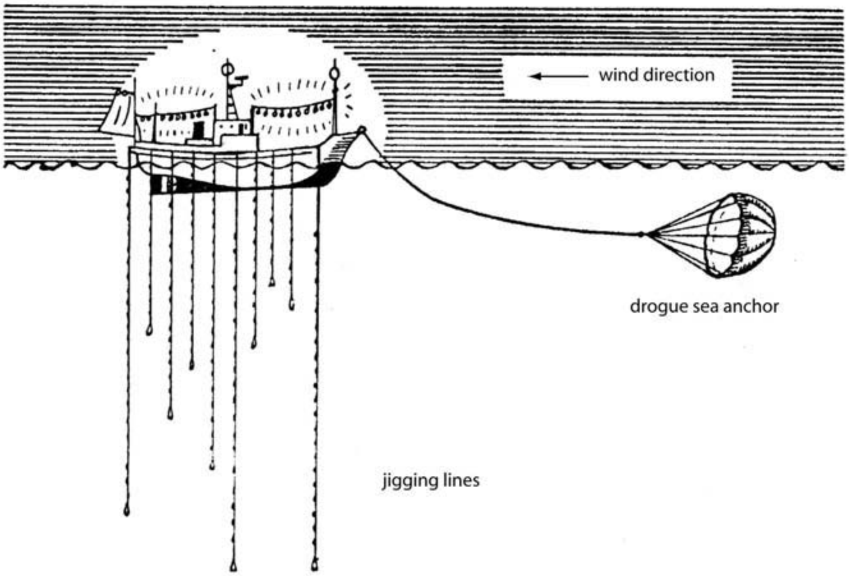


Fig. 16.4 The drogue or sea-anchor used to retain the jig-fishing vessel stationary within the fished water mass (after Yajima & Mitsugi 1976).

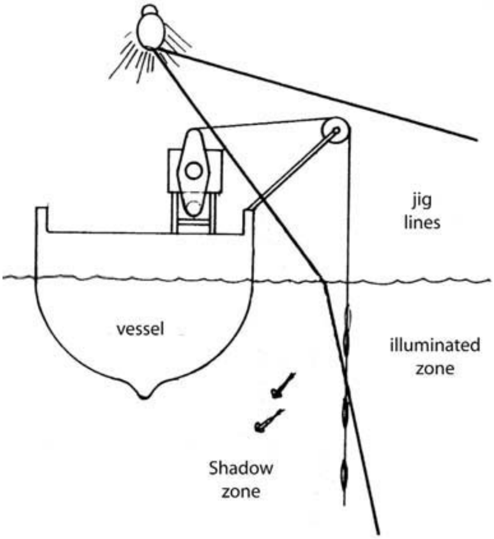


Fig. 16.5 Zone of illumination alongside a squid-jigging vessel in which the jigging lines are fished. Squid congregate in the shadow zone beneath the vessel from where they attack the lures (after Rathjen 1984).

are strung centrally above the midline of the deck, while on larger vessels, two lines of lights are strung along the length of the vessel, inboard of the sides. The rigging of the lights is intended to throw light downwards onto the sea surface, casting a shadow immediately alongside the vessel (Fig. 16.5a). The squid congregate in the non-illuminated zone outside the lights and in the shaded area beneath the fishing vessel.

From there, the moving jigs appear clearly illuminated and the squid are provoked to attack.

Despite the almost universal use of incandescent lights for jig-fishing, there is not complete agreement as to the degree of illumination required for them to be effective. This is because squid fishing of this type is almost always undertaken where squid shoals are dense and vessels work close to each other as a fleet. In these circumstances, the relative intensity of the lighting may be more relevant to competition for catch between adjacent vessels rather than the requirement to attract squid. Experimental rates of retinal adaptation in *Todarodes pacificus* suggest that the squid are better equipped to find and seize jigs in relatively low illuminance areas of the illuminated zone (Inada 1997). Commercial fishing with jigs is undertaken during the day as well as at night, but catch rates for *Nototodarus gouldi* are lower during the day and differ between jigging methods. These effects are probably due to diel migration patterns bringing squid closer to the surface at night (Nowara & Walker 1998). Similar observations are commonplace in the other ommastrephid squid fisheries.

Suzuki (1990) describes the rapid growth in numbers and the power of the lights in the Japanese fleet fishing for *Todarodes pacificus*, and the consequent increase in the cost of fishing through fuel consumption to power the lights. Data compiled on the light power and catching efficiency using lights suggested that a power consumption of around 3 kW/m length of vessel (small coastal jiggers of less than 20 tonnes) is optimal. It has been shown that power consumption of over 2 kW/m length of vessel (Karibe *et al.* 1974) or greater than 6 kW per jigging machine (Hirayama 1982) does not increase fishing efficiency but increases costs. Submarine lights, lowered on cables from the vessel (one or two per jigger) are also frequently used. By slowly moving the lights towards the surface, concentrations of squid are gradually drawn upwards.

The concentration of lights used for fishing by the major squid fishing fleets is clearly visible from space. Visible-band satellite imagery of the earth from space is capable of showing the spatial and temporal positioning of squid fishing (Rodhouse *et al.* 2001, Chapter 18). Recent developments in processing these images, which were collected for the primary purpose of global-scale meteorological work, have allowed the disposition of whole fleets to be visualised and related to the large-scale water movements influencing squid distribution.

16.3.3 Trawl fishing

Trawl fishing, in which a large net mesh bag is drawn through the water or over the bottom, with the opening spread wide by a pair of otter boards or trawl doors (hydrofoils), is a generic and universal method of fishing. Dependent on powerful vessels to fish and to lift the nets, it is a commercial technique known for the indiscriminate capture of just about anything in its path. Trawl fishing for squid is widely used world-wide, and probably accounts for the majority of the squid catch in shallower water.

In many areas the squid are caught as a by-catch of fisheries targeting fish species. Whether the squid caught are kept and landed depends very much on the quantities available and market conditions at the time. Most of this commercial catch arises from unmodified trawling gear, but there are some examples of trawl nets modified or tuned for catching squid (Koyama 1976; Engel 1976; Cahill & Mansfield 1984), mostly by increasing the height of the head rope of the net. The mesh size of a trawl net naturally operates size selectivity of the squid catch, just at it would for a demersal fish (Hastie 1996).

Bottom trawling, the most common of the trawling methods applied to squid, takes place mostly in the Atlantic and to a lesser extent the Pacific. It is the main harvest gear in important *Octopus*-producing areas such as the northwest coast of Africa (the Saharan Bank), and for squid (*Loligo*) in the northwest Atlantic (off North America) from Nova Scotia to Cape Hatteras and the southwest Atlantic to the Patagonian Shelf (Rathjen 1984). Directed trawling for these squid requires adaptation of the fishing method to their behaviour patterns.

Pelagic or mid-water trawling describes the operation of the net in the water column between the surface and the bottom. It is particularly adapted to a wide range of fisheries for members of the gadoid and mackerel families. It has not been widely applied for squid fishing, but pelagic trawls are sometimes deployed just off the bottom above rough ground where there are entanglement hazards. The relative lack of use of these very large-scale methods probably indicates that squid are simply not sufficiently aggregated in mid-water shoals for the methods to be effective.

16.3.4 Other commercial fishing nets

The attraction of squid to light sources at night is also used directly for a variety of types of net fishing with small nets. Rathjen (1984, 1991) describes several of these. Off Monterey, on the California coast, strong lights were deployed from small boats at night to attract squid (*Loligo opalescens*), already congregated in breeding aggregations, around the boat. From there they were simply harvested, scooped up by hand-nets or by lifting a large ring-net up through the accumulated shoal. Traditionally the lampara seine net, originally introduced for the sardine fishery, was also used for these squid (Fig. 16.6). A small skiff lampara set the suspended net around the shoal and then returned to the fishing boat. Both ends were then hauled, enclosing and concentrating the shoal which was then removed by dip-netting. There is small-scale use of other types of seine net where squid can be concentrated close to shore (Rathjen 1984). The facility of concentrating *Loligo opalescens* at night by strong light sources has sometimes been exploited by the use of powered underwater fish pumps (Kato & Hardwick 1976; Fig. 16.6).

Set nets, suspended in the water column, are used to intercept the Japanese firefly squid *Watasenia scintillans* during its annual breeding migration into Toyama Bay (Tomiyama & Hibiya 1978). The inshore movement and migration of some squid allows significant captures to be made in coastal trap nets. Sometimes fixed to the bottom, sometimes held to pilings or anchors and with a leader running into the beach, the trap nets or pound nets of coastal areas of northeast America and Canada are typical examples. Here, migrating *Loligo pealei* and *Illex illecebrosus* can be caught along with other coastal demersal fish. Trap fisheries for loliginids (*Sepioteuthis lessoniana*) and sepeoids (*Sepia pharaonis*, *S. aculeata*) are common in the Gulf of Thailand and catch

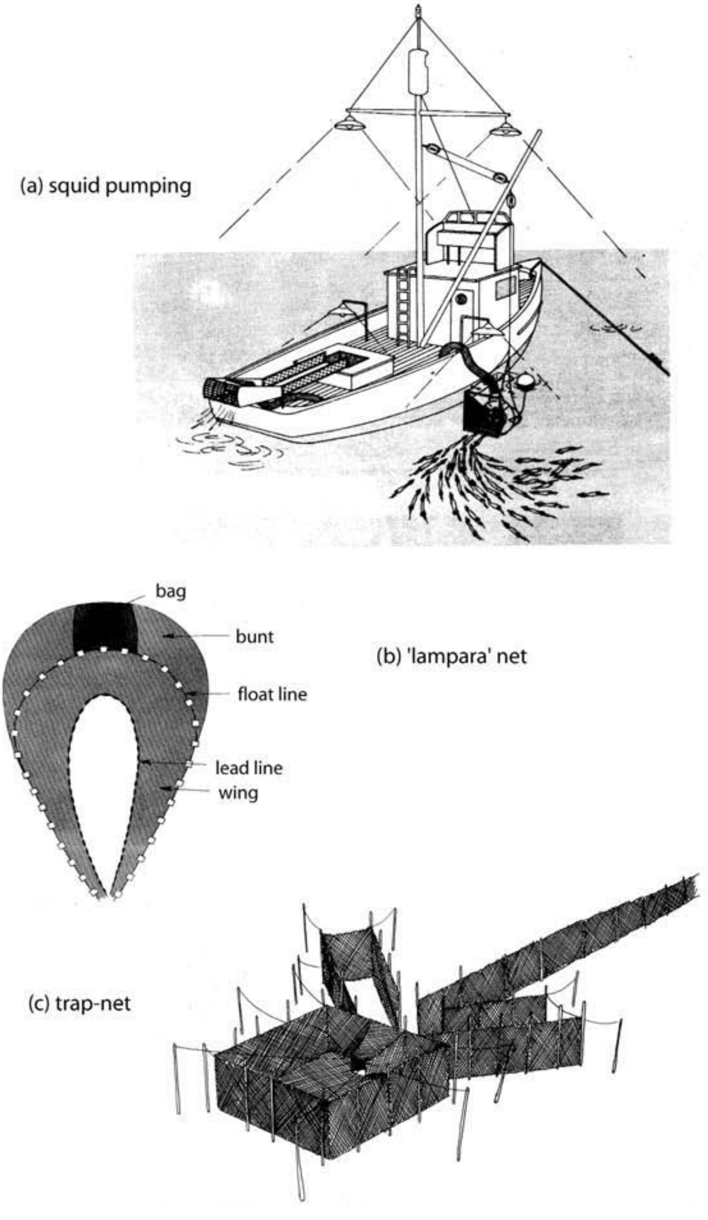


Fig. 16.6 Adaptations of fishing gear to squid fishing. (a) Pumping system. (b) A seine or lampara net, traditionally used for *Loligo opalescens* on the California coast (after Kato & Hardwick 1976). (c) Fixed trap-net for fish and *Illex illecebrosus* in Newfoundland (after Rathjen 1984).

several thousand tonnes annually (Chotiyaputta & Yamrungreung 1998). These traps, set in 4–40 m of water, are baited with egg clusters of squid and cuttlefish to attract more breeding animals into the trap.

During the 1970s, gill nets began to be deployed in the high seas of the north Pacific, targeting the large ommastrephid *Ommastrephes bartrami* (Araya 1983). This highly

Table 16.1 Estimated by-catch of cetaceans (numbers of individuals) by the north Pacific drift-net fishery for *Ommastrephes bartrami* for the years 1989–1991 (after Yatsu *et al.* 1994).

	1989	1990	1991
Dall's porpoise	3065	3093	3204
Northern right-whale dolphin	12449	7909	9320
Pacific white-sided dolphin	6154	4447	3784
Common dolphin	286	562	1035
Other unidentified cetaceans	1079	624	664

productive fishery grew rapidly in area, spreading eastwards across the Pacific and increasing in intensity. The very large monofilament nets, although generally fished below the surface to avoid the incidental capture of large fish and other organisms, inevitably resulted in substantial by-catch mortality of marine mammals until it was effectively closed in 1992. For the period 1978–1992 the Japanese catch of *O. bartrami* fluctuated between 123 719 and 215 778 tonnes (Yatsu *et al.* 1994), and the estimated by-catch of cetaceans for the latter years of the fishery is shown in Table 16.1.

The north Pacific drift-net fishery for *Ommastrephes bartrami* peaked at about 400 000 tonnes during the 1980s (Murata & Nakamura 1998), but was banned by UN moratorium in 1991 owing to the unacceptable by-catch of marine mammals, seabirds and other non-target species. Since then, the fishery has been re-established as a jig-fishery with lights, with Japanese vessels catching around 70 000 tonnes in the mid-1990s (Nagasawa *et al.* 1998), and Chinese and Taiwanese vessels taking another 80 000 tonnes. Drift-net fisheries for other species such as tuna are also responsible for large marine mammal by-catch mortalities, but the scale of the mortality due to squid drift-net fishing compared with other methods provides an acute comparison with the specificity of jigging.

16.4 Fishery surveys

In parallel with conventional fishing activity, fishery agencies usually undertake scientifically structured surveys in the expectation that the results will help to reveal the processes determining the availability of stock to fishing, or provide a means of estimation or prediction which will be useful for management purposes. For cephalopods, fishery surveys may be undertaken with smaller-meshed nets (Pierce *et al.* 1998) in order to gain a truer picture of population structure, and more commonly by dedicated plankton surveys (Okutani & Watanabe 1983) or even egg-bed surveys (Augustyn & Roel 1998) aimed at predicting the annual recruitment strength. In Japanese waters, surveys for stock size and density for several species are routinely undertaken by jigging surveys, and an approximate correlation with annual yield is demonstrated (Murata 1983). Scientifically structured surveys for exploited stocks are routinely used off Japan and in the north-west and southwest Atlantic.

16.4.1 Acoustic methods of detection

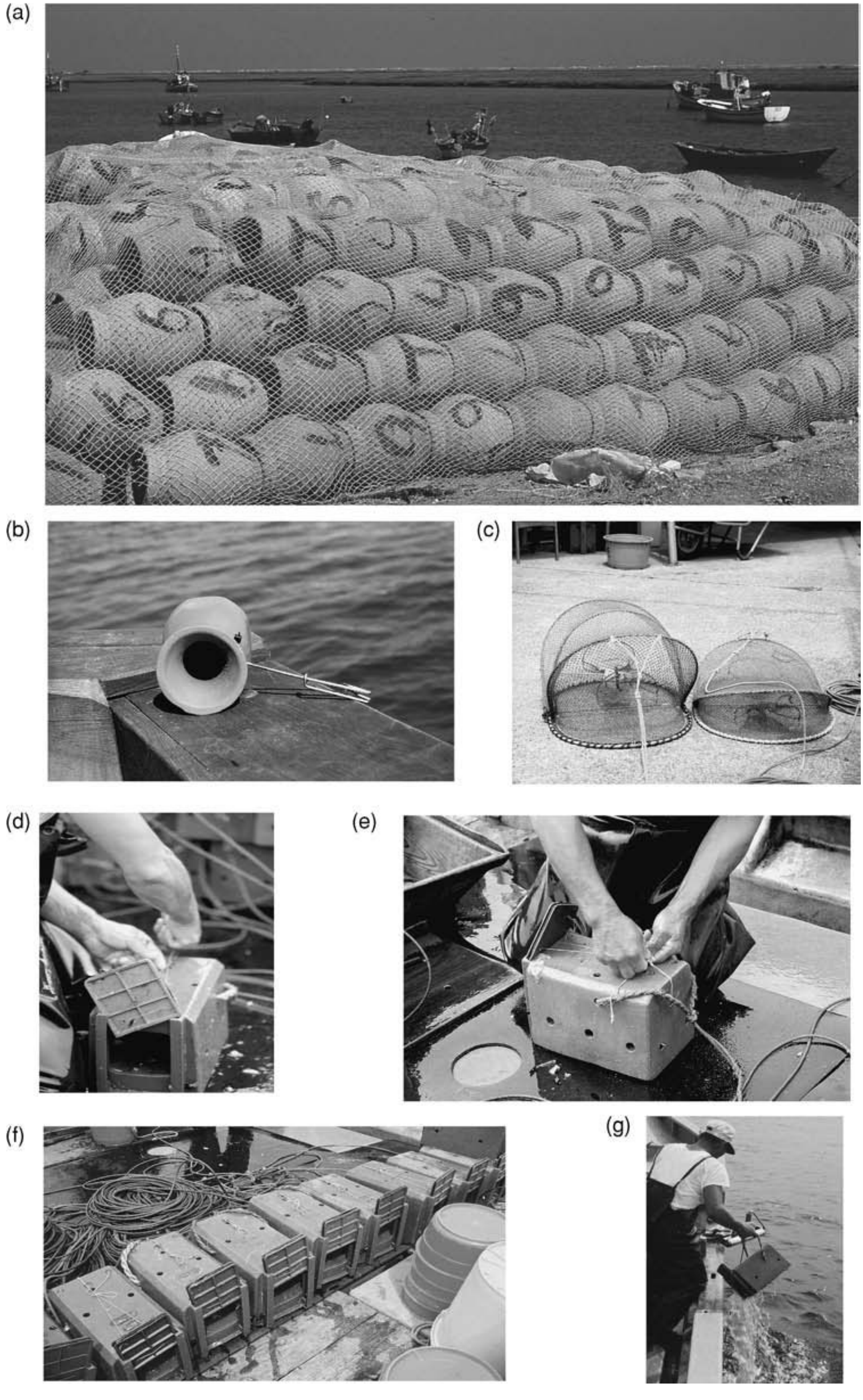
The use of acoustic methods for the detection of living marine resources, including squid, has been available for several decades. Pioneered in Japan (FAO 1972; Suzuki 1976), it has been shown that the returning echoes from squid appear on echograms as groups of 'spindles' on the trace. Compared with fish with swim bladders which give a strong acoustic echo, squid give only relatively weak reflections. This means that unless the squid shoal is very dense and not mixed with other species, echo-soundings are generally less effective for the detection of squid. Although they are used in areas of the world where the fishery is targeted and non-squid targets are not normally present, such as the Falkland Islands (Malvinas), echo-sounding is only occasionally used for biomass surveys of the kind conducted for fish species (e.g. *Loligo opalescens* off the Oregon coast, Jefferts *et al.* 1987). Target strengths for several squid species have been estimated, and trials have been made where presumed acoustic reflections from squid have been validated by trawl surveys (Goss *et al.* 1998). Deep-water acoustic targets seen during routine pelagic biomass surveys off South Africa have been associated with spawning aggregations of *Loligo vulgaris reynaudi* (Roberts *et al.* 2002) and may provide a new method of identifiying spawning shoals. As well as echo-sounders, sonar imaging has also been used to plot the distribution of squid accumulations in relation to the illumination from the fishing lights of a squid-jigging boat (Arakawa *et al.* 1998). The applications and limitations of the use of acoustic methods to survey cephalopod populations are given by Starr & Thorne (1998).

16.5 Traditional fishing by hand methods

Throughout the world, in tropical and sub-tropical regions, wherever there are accessible beach flats and lagoons, the hand-collection of octopus and occasional cuttlefish and squid takes place. For octopus in particular, the spear or gaffe is a very effective way of drawing them from crevices and shelters in the rock surface. There are very few examples of quantification of these fisheries, but it can be presumed that in areas of Africa, Asia and many island states, hand and spear collection of octopus makes a significant contribution to local food supplies and the local economy. As well as contributing essential information about the fishery, studies on these small-scale hand fisheries, such as that for *Octopus cyanea* in Tanzania, can provide valuable new information on the biology of the species concerned (Guard & Mgaya 2002).

16.5.1 Hand-jigging for squid

Hand-jigging for squid is globally widespread, but the catch is rarely quantified. Even in advanced fishing nations, hand methods persist and can account for a significant local economy. For example, Simón *et al.* (1995) estimated that the small-scale hand-jig fishery of the Galician region of Spain was taking about 75% of the trawl catch from the same region. In the Peru Current system, small-scale hand-jigging fishermen


(a)
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exploit the locations of the large-scale commercial jig-vessels by fishing amongst the larger vessels where the squid are already attracted by the lights of the fleet.

16.5.2 Pot-fishing for octopus and cuttlefish

The most obviously specialised and dedicated method for catching octopus on a small commercial scale is the deployment of pots or individual traps. Numerous designs from around the world are available (e.g. Paust 1988); they differ in materials and detail, and some of the variants are shown in Fig. 16.7. Most of these are unbaited pots, and rely on the behaviour of the animal to seek shelter. A specialised variant used by Japanese fishermen are trap-door pots in which a live crab is used as bait. When the octopus attacks and eats the crab it releases an elastic-powered door and is trapped inside (Fig. 16.7d–g). The impact and commercial significance of these pot and trap methods for octopus is not usually properly quantified. They can make little significant contribution to the global statistics of catch, but they operate most successfully and apparently sustainably in many areas of the world.

Most of the major commercial pot fisheries for octopus continue to use relatively traditional designs such as the clay pots (mummarelas or nasas) of the Mediterranean and even clam shells in Japan. Fishermen also adapt modern materials such as concrete, plastic tubes and rubber tyres to provide cheaper methods of production and greater ease of deployment (Paust 1988; Roper 1997). Octopus may also be a nuisance predator in pots set for other species, and become a by-catch from those fisheries. Joll (1977b) details the extent of predation by *Octopus tetricus* on the Australian pot fishery for crayfish (*Palinurus longipes*), and Boyle *et al.* (1986) found a substantial incidence of predation by *Eledone cirrhosa* on pot-caught lobsters *Homarus* and *Nephrops* in Scotland.

An interesting variant of fishing *for Octopus* is fishing *with Octopus*. Both Lane (1957) and Cousteau & Diolé (1973) record stories of the use of tethered octopuses to retrieve objects from the seabed. These range from the use of octopuses in Japan to salvage porcelain from sunken ships, through to the retrieval of coal from a collier by Cretan fishermen during World War I. Attached to a line and lowered to the bottom, the octopus grasps loose objects within range and holds on while it is pulled back to the surface by the salvage team.

Cuttlefish are also caught in pots. In Senegal, for example, pots are a traditional means of capture (Bakhayokho & Ito 1991). They are baited with dead fish, usually shark or skate, or with live female cuttlefish to attract males or with coconut palm spikes to attract females for egg laying. Research has shown that none of these baits increases the attractiveness of these pots over an empty one.

Fig. 16.7 (*opposite*) Various forms of octopus pots and traps. (a) Traditional earthenware pots stacked on shore in the Algarve region of Portugal. (b) Small octopus pot from Mexico intended to be clipped to long set lines. (c) Japanese nets for octopus. (d) Japanese trap for octopus with an elastic-powered trap door which is triggered when live crab bait is taken by the octopus, thus releasing the string holding the door open (e). These traps are set in lines of about 25 (f) from coastal vessels operated by a single fisherman (g).

A distinctive feature of all of these hand methods for cephalopod capture, as well as the commercial catch from jigging and potting, is the exceptionally high quality of the product. Not only is this far superior to trawled material, but there is no incidental ecological damage either to the habitat or to by-caught non-target species (a notable contrast to the bottom trawling and oceanic drift-netting described above).

16.6 Scientific sampling of cephalopod populations

16.6.1 Mid-water trawls

It has long been known that the methods of scientific sampling for the quantitative assessment of oceanic cephalopod populations are likely to provide serious underestimates of population density as well as biased size-frequency and species composition. In their analysis of the problems of sampling oceanic species, Wormuth & Roper (1983) summarise the factors involved in net avoidance and catch bias to include:

(1) visual detection of the net owing to daytime surface lighting;
(2) visual detection of the net owing to bioluminescence triggered from other organisms in the water;
(3) noise or vibration due to the towing warps or components of the net itself;
(4) effect of the size and shape of the net opening and mesh size;
(5) speed and mode of fishing (descending/ascending);
(6) behaviour patterns such as diel migrations or schooling.

Most nets fished in mid-water from research ships for conventional biological sampling down to 1000 m are limited in opening size (usually 20 m^2 for rectangular mid-water trawls), mesh size (say 6–10 mm square) and towing speeds (2–3 knots). Since they operate in clear mid-water for cephalopod species that may be large active swimmers with excellent sensory capabilities, it is hardly surprising that they are not effective samplers. To prove that they are inadequate, and to estimate the degree of bias or misrepresentation is an altogether more difficult task, since there is no baseline with which to compare the results and validate the data.

The significance of these deficiencies has been accentuated through a detailed comparison of the results of mid-water net hauls for squid with the estimation of the diets of squid predators feeding in the same general area. These approaches have shown (Clarke 1977, 1983) that squid size in mid-water net catches is not representative of the squid fauna eaten by sperm whales (Fig. 16.8). In all cases, the average size of squid caught by nets was below the minimum individual size estimated to have been caught by the whales, and in 11 out of 13 squid families represented, the maximum size caught in nets was less than the minimum size represented in whale diet. The proportion of different squid families represented in the net catch and the predator diet was also distinctly different.

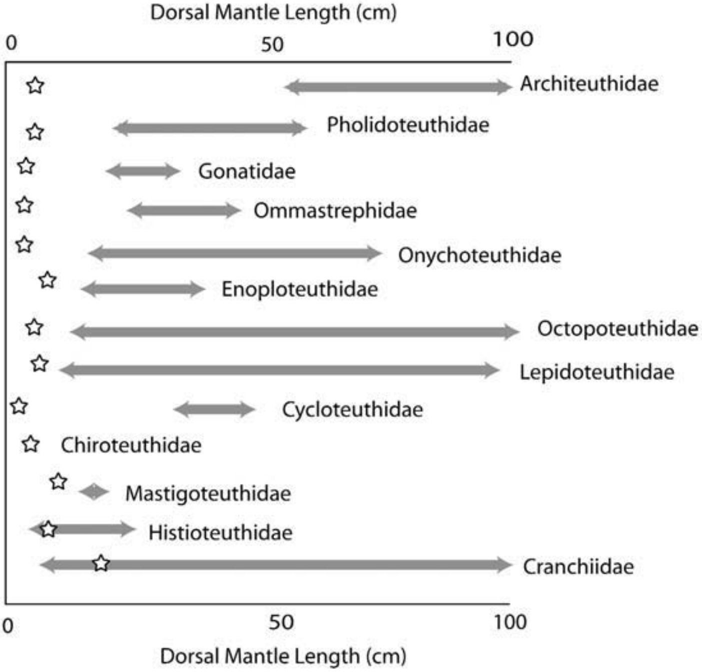


Fig. 16.8 Mantle lengths of squids from a range of families caught in oceanic nets, compared with the size of those estimated to be consumed by whales. After Clarke 1977. Arrows indicate the range of mantle lengths of squid of each family estimated from beaks retrieved from whale stomachs. ☆ indicates the largest mantle length of squids captured by scientific sampling nets used in the same region.

The interpretation of these differences depends on the degree of confidence placed on whales or nets (or neither) as reliable samplers of the mid-water squid fauna. Nets can be viewed as hopelessly inadequate, or whales as highly selective in their feeding on mid-water cephalopods.

The experimental use of underwater electric lights mounted on small commercial-scale bottom trawls indicates that although a number of fish species responded to light, there was little evidence that the catch was significantly altered (Clarke *et al.* 1986). On scientific mid-water trawls, the use of electric light on the trawl had significant effects. Clarke & Pascoe (1985), in a series of comparative hauls from the Bay of Biscay down to 800 m depth, found a significant effect from added lights in increasing the catch of the largest fish species. There were lower numbers of decapod crustaceans in the trawls carrying lights, but for cephalopods the results were inconclusive, with only a suggestion that at selected depths (300 m and 800 m) the number caught may have increased. A more comprehensive survey directed specifically at the mid-water cephalopods (Clarke & Pascoe 1998) showed that species of *Taonius*, *Heliocranchia*, *Pyroteuthis* and *Pterygioteuthis* increased significantly with lighted rectangular mid-water trawls. Catches of *Taonius pavo* increased progressively with increasing light; *Abraliopsis pfefferi* and *Liocranchia reinhardti* were caught at increasing sizes over the same range of light power.

16.6.2 Underwater video

The use of automated cameras for photographing squid underwater was first described by Baker (1957), who captured images of *Ommastrephes pteropus* at 1000 m in the Atlantic. The increased availability of manned submersibles for deep ocean research, and the potential for video-recording them, can be expected to begin producing considerable new information on the biology of deep-water fauna. Roeleveld *et al.* (1989) provided the first pictures of an animal identified as the rare deep-water squid *Octopoteuthis* live at 1000 m, and Vecchione & Roper (1991) catalogue 158 observations of cephalopods from submersibles. As well as video and collected specimens, real-time observations of behaviour can be made.

The mating behaviour of deep-water octopods has been seen and filmed from the deep-diving submersible *Alvin* (Lutz & Voight 1994). The same submersible has been used to make the first observations of egg brooding by *Graneledone* and *Benthoctopus* at 2600 m deep, as well as to discover that these deep-water species apparently make boreholes in their bivalve prey in common with their shelf relatives (Voight & Grehan 2000). Valuable scientific data on mesopelagic species such as *Gonatus onyx* are emerging from remotely operated underwater vehicles (ROVs) that could not have been obtained by other methods (Hunt & Seibel 2000). Even in coastal waters, the increased availability of ROVs provides a platform from which to collect behavioural data from squid *Loligo opalescens* behaving naturally (Hunt *et al.* 2000). Most remarkable has been the inference from submersible observations that rather large squids, previously unknown to science and of which no known adult specimens have been captured, may be present in the bathypelagic of the world oceans (Vecchione *et al.* 2001a; Guerra *et al.* 2002a).

16.6.3 Plankton sampling – nets and light traps

In oceanic waters, squid paralarvae may be collected in great abundance by standard plankton tows (Piatkowski *et al.* 1993; Piatkowski 1998; Vecchione 1998). Generally speaking, the bongo net design (two circular net openings mounted in parallel and towed from the central point) is the preferred method (Vecchione 1991b; Bower *et al.* 1999b). The paralarvae of loliginid squid in coastal waters are frequently very difficult to capture, even where, from the incidence of adult breeding aggregations and spawning, they would be expected to be abundant (Hatfield & Rodhouse 1994b; Collins *et al.* 2002), with the implication that the net sampling is very inefficient.

In the coastal tropical waters of the Great Barrier Reef, specialised designs for drifting light traps have proved successful for catching fish larvae (Doherty 1987). The same automated light traps have also worked well for studying the distribution patterns of paralarval squid (Moltschaniwskyj & Doherty 1995), and this may well prove to be a good quantitative method in certain circumstances.

Chapter 17

Fishery resources

Summary: The potential of cephalopod fisheries to increase world food production from the sea attracted attention in the last two decades of the twentieth century, and at the same time catches increased much faster than the total catch of exploited marine species. An overview of the global fishery resources of cephalopods, based to a large extent on fishery statistics published by the FAO on capture production, shows that between 1990 and 1999 the world annual catch of cephalopods increased from 2.4 to 3.4 million tonnes, and this continued a trend that had been apparent for several decades. It probably reflected a shift in fishing effort from traditional to less traditional species (fishing down the food web), but it has also been proposed that cephalopod stocks have increased as groundfish stocks have diminished. The FAO data provide information on the global distribution of the exploited stocks, but there is a large proportion of the total cephalopod catch which remains unidentified. There are problems with the identification of cephalopods, especially in local artisanal fisheries, and there are undoubtedly undescribed species in the seas, some of which probably contribute to catches, particularly in areas of high marine biodiversity. Nevertheless, scientific knowledge of the taxonomy and distribution of the cephalopods allows some interpretation of the FAO statistics where species have not been reported. Trends in the global statistics and knowledge of the ecology of the cephalopod fauna, where exploitation is currently slight or non-existent, provide some insight into the current state of exploitation and future production potential of the cephalopods. Cuttlefish catches indicate an increasing trend, suggesting that there is still some opportunity for increased catches in the future. Most of the squid stocks currently fished appear to be fully exploited, and variations in catch rate are probably due to environmental variability. There are, however, some unexploited stocks, mostly off the continental shelves, which appear to have the potential to support new fisheries. The catch rate in the octopus stocks is relatively stable, indicating that the fished species are fully exploited. In heavily overfished cephalopod stocks, reducing fishing effort would probably have the effect of increasing the total catch.

The fisheries for cephalopods, especially squid, attracted a great deal of interest world-wide over the last two decades of the twentieth century. Declining catches in many traditional fisheries led to new interest in the potential of non-traditional marine resources, especially invertebrates such as the cephalopods, to meet the ever-increasing demand for high-quality protein (Caddy 1983a; Roper *et al.* 1984). The interest in cephalopods was fuelled by estimates of global cephalopod consumption by higher predators, especially sperm whales, but also seabirds and seals, which suggested that they consume a greater mass of cephalopods than the total catch by the fishing fleets of all marine species combined (Voss 1973; Clarke 1983).

Cephalopod catches increased substantially world-wide over the same period, and this highlighted the fact that their populations are highly variable (see Chapter 18). The *Illex illecebrosus* fishery in the north-west Atlantic, which was developed very rapidly by the east-Asian squid-jigging fleet in the late 1970s and early 1980s following a declining catch rate of *Todarodes pacificus* in the north-west Pacific, collapsed suddenly and led to a rapid switching of effort to the south-west Atlantic in the early 1980s to target *Illex argentinus.* Subsequently, catches of *Todarodes pacificus* have continued to fluctuate, but the fishery for *Illex illecebrosus* has never returned to Canadian waters although consistent, but lower, catches are taken off the eastern USA further south.

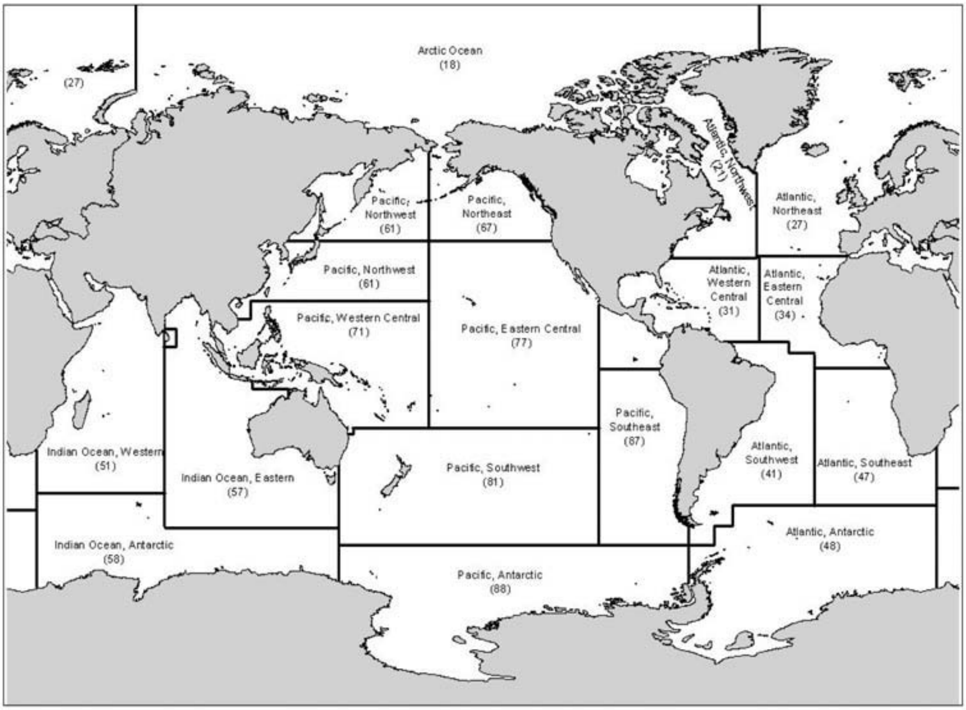


Fig. 17.1 World map of the regional sea areas used by the FAO (Food and Agriculture Organization of the United Nations) for the collection of international fishery statistics.

This large-scale variability has attracted attention to the likely role of oceanographic variability in driving recruitment processes in squid stocks (O'Dor & Coelho 1993; Bakun & Csirke 1998) (see Chapter 18).

The primary source of data on world catches and trends over recent decades is the UNESCO Food and Agriculture Organization (FAO), based in Rome. The FAO publishes an annual yearbook of fishery statistics for all exploited marine species, including the cephalopods, grouped by statistical area (Fig. 17.1). The nature of the collection of statistics by FAO, relying as it does on the coordination of statistics from numerous sources and the time needed to process the data, means that the statistics published each year refer to the catch 2 years prior to publication. In order to illustrate the global situation in the cephalopod fisheries at the start of the third millennium, we have drawn on the FAO Yearbook (2001) and focus on the trends. The latest statistics can readily be obtained from the published yearbook, but we caution against using these very coarse-scale data to analyse patterns at the stock or population level (see: www.fao.org.).

17.1 Global statistics

Between 1990 and 1999, the total world annual catch of cephalopods increased from 2.4 to 3.4 million tonnes per year. This continued a trend of increasing cephalopod

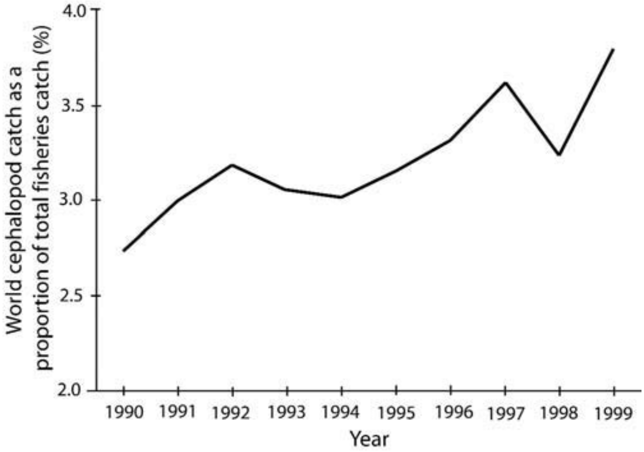


Fig. 17.2 Total world cephalopod catch as a proportion of the total world catch (expressed as a percentage) between 1990 and 1999. Data from the Food and Agriculture Organization of the United Nations (after FAO Fisheries Department, 2001).

catch that had been apparent for several decades (Caddy & Rodhouse 1998), and which had been maintained in spite of a substantial decline in the rate of increase of the total world capture production of all fishery species. The relative increase in cephalopods since 1990, as summarised in the 2001 FAO annual yearbook, is shown in Fig. 17.2 compared with the increase in total capture production of all fishery species. By the end of the decade, cephalopod production had increased by about 42% compared with less than 9% in the case of the total fishery catch. This probably reflected a shift in fishing effort from traditional to less traditional species by a process coined 'fishing down the food web' (Pauly *et al.* 1998). Another hypothesis that has also been proposed is that cephalopod stocks have increased as groundfish stocks have diminished (Caddy 1995; Caddy & Rodhouse 1998). This hypothesis remains to be tested, but there are theoretical grounds for supposing that the cephalopods experienced reduced predation from groundfish as these stocks were overexploited. Alternatively, the ecologically opportunistic cephalopods, with their high growth and reproductive rates and short lifespan, would be capable of expanding their populations to fill vacant ecological niches created by the overexploitation of fish stocks.

The FAO statistics reveal that there are real problems in the identification of the cephalopod species caught by the fisheries, and this is highlighted by the fact that in 1999 less than 60% of the world cephalopod catch was identified to species. There are a number of reasons for this. There are certainly numerous undescribed and unnamed species in the world's oceans, some of which may well be caught by the commercial fisheries, especially in regions of high marine biodiversity. Even where the species caught are known to science, identification is invariably a specialist task, and the specialists needed to make the identifications are not always available, especially in developing regions of the world. This is especially the case in artisanal and subsistence fisheries and where the resources needed to monitor the catch are not available or justifiable by national governments with other priorities. Nevertheless, improvements

Table 17.1 Cephalopod catch data for the period 1990–1999 extracted from the *FAO Yearbook of Fishery Statistics*: *Capture Production* (2001).

		1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Cuttlefish	*Sepia officinalis*	16 026	11 702	13 121	12 441	12 312	9930	11 043	13 621	12 222	14 638
Squid	*Loligo gahi*	57 053	45 776	71 836	44 319	55 460	85 186	68 486	21 720	51 605	42 505
	Loligo pealei	16 251	19 571	19 711	22 200	22 502	18 926	12 490	16 161	18 879	18 749
	Loligo reynaudi	4986	7036	2805	6271	5814	7047	7549	3696	6670	7169
	Ommastrephes bartrami	–	–	–	–	–	–	–	49 870	54 951	36 077
	Illex illecebrosus	25 584	19 682	23 868	25 582	30 670	18 550	27 678	32 657	25 836	7950
	Illex argentinus	410 117	559 505	609 823	638 453	505 698	520 938	656 481	980 300	664 719	1 091 299
	Dosidicus gigas	14 893	45 760	109 360	124 390	195 229	136 288	142 186	162 504	27 466	134 773
	Todarodes sagittatus	8289	7493	7849	6462	5758	5171	5875	5553	6346	4686
	Todarodes pacificus	321 459	402 976	545 209	548 365	504 425	513 413	715 908	603 367	378 605	497 877
	Nototodarus sloani	29 808	35 069	64 434	45 148	79 449	94 098	53 699	64 602	55 570	31 358
	Martialia hyadesi	11 557	1373	1043	1252	392	23 986	3845	8376	55	27
Octopus	*Octopus vulgaris*	36 452	38 085	41 320	36 422	34 314	35 764	46 062	37 768	34 230	34 262
	Total of identified species	952 475	1 194 028	1 510 379	1 511 305	1 452 023	1 469 297	1 751 302	2 000 195	1 337 154	1 921 370
	Total of cuttlefish	295 697	303 407	267 189	309 794	382 665	419 984	379 840	467 272	475 405	466 826
	Total of squid	1 496 112	1 630 347	1 873 585	1 721 712	1 716 545	1 774 973	2 051 102	2 256 566	1 517 607	2 185 729
	Total octopus	294 206	317 487	296 996	293 819	240 689	300 505	300 654	306 368	302 330	353 841
	Identified cephalopods as % of all cephalopods	40.1	46.3	54.5	56.1	52.7	51.0	56.5	58.5	51.0	57.0
	Identified cuttlefish as % of all cuttlefish and bobtail squids	5.4	3.9	4.9	4.0	3.2	2.4	2.6	3.6	2.6	3.1
	Identified squid as % of all squid	60.2	70.2	77.7	84.9	81.9	80.2	82.6	86.4	85.7	85.7
	Identified octopus as % of all octopus	12.4	12.0	13.9	12.4	14.3	11.9	15.3	12.3	11.3	9.7

in our knowledge of the cephalopods, driven by the considerable scientific interest in the group in the last decades of the twentieth century, has probably also contributed to a trend towards improved species identification of catches.

Historically, there are many reasons why the geographical origin of catches may not be properly attributed at the place of landing. These problems of identification and accurate geographical placement of the origin of catches mean that the FAO data need to be viewed with some caution. Nevertheless, they do provide the only world overview of catch statistics and a valuable resource for the analysis of large-scale trends in the world fishery.

Of the species of cephalopod identified by the FAO there is only one cuttlefish and one octopus species, the rest being loliginid and ommastrephid squid (Table 17.1). Although there is a trend from only about 40% of the catch being identified in 1990 to 57% being identified in 1999 (Table 17.1), no new species were added to the list during that decade. It is notable that only four identified species contribute more than 50 000 tonnes per year to the world catch, these are *Todarodes pacificus* from the western Pacific, *Dosidicus gigas* from the eastern Pacific, and *Illex argentinus* and *Loligo gahi*, from the south Atlantic.

17.2 Global distribution of stocks

17.2.1 Cuttlefish

The only cuttlefish (Sepiidae) identified to species level in the FAO yearbook is *Sepia officinalis*. This eastern Atlantic species extends from the Baltic and the North Sea to South Africa and throughout the Mediterranean in coastal waters and over the shelf to about 200 m (Fig. 17.3). In 1999, about 80% of the total world catch of 14 638 tonnes was from the Mediterranean. Much of the catch of cuttlefish NEI (not elsewhere included) from area 34, which amounted to 51 022 tonnes in 1999, is probably also *S. officinalis* caught off west Africa, although it is not identified as such. It is probable that *Sepia officinalis* is replaced by other similar species on the north-western coast of Africa southward of about 15°N, since the previously recognised subspecies (*Sepia officinalis hierredda* of tropical West Africa and *S. o. vermiculata* of South Africa and the western Indian Ocean) are now to be recognised as distinct species (Khromov *et al.* 1998).

Roper *et al.* (1984) identify 31 species of cuttlefish (*Sepia* and *Sepiella* spp.) and 18 species of bobtail squids (several genera from the families Sepiadaridae and Sepiolidae) of interest, or potential interest, to fisheries. The cuttlefish occur throughout the seas of the old world in temperate and tropical waters, but are absent from both the east and west coasts of the Americas. The bobtail squids are widely distributed throughout the world's oceans apart from the polar regions. No catch data for bobtail squid are reported to the FAO, but several species are exploited by small fisheries for local consumption in China, Japan and some South American and Mediterranean countries, although it is unlikely that these small species could develop into commercial-scale fisheries.

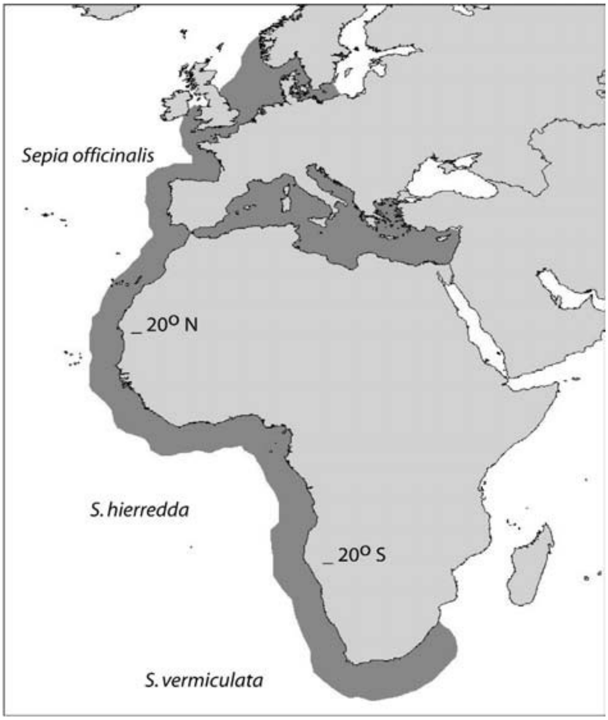


Fig. 17.3 Estimated distribution of the cuttlefish *Sepia officinalis* Linnaeus 1758 on Atlantic and Mediterranean coasts (modified after Roper *et al.* 1984) but, south of about 15°N, including that of *S. hierredda* Rang 1835 and *S. vermiculata* Quoy and Gaimard 1832, both previously recognised as sub-species (Khromov *et al.* 1998; Guerra *et al.* 2001a).

17.2.2 Squid

Distribution maps of the major stocks of squid which are identified to species level in the FAO statistics are shown in Figs. 17.4 and 17.15. The flying or arrow squids (family Ommastrephidae) are caught offshore over continental shelves and off-shelf over the deep ocean. They all come close to the sea surface at night, but some may migrate to depths of up to 1000 m during the day (Yatsu *et al.* 1999). The fisheries for members of this family, mostly using jigs and powerful incandescent lights, can be detected in images collected by orbiting satellites of the US Defense Meteorological Satellite Programme (Rodhouse *et al.* 2001) (see Chapter 18).

Todarodes pacificus, the most important squid fishery in the Pacific Ocean, is distributed in the margins of the north-west Pacific from 20°N to 60°N, and the major fisheries are around Japan, especially in the southern part of the Sea of Japan and in the Tsushima Strait between Korea and Japan.

Illex argentinus (Fig. 17.5) is a southwest Atlantic species extending from about 30°S, off Brazil, to 52°S off Argentina and around the Falkland Islands (Malvinas). The fishery is mostly concentrated along the edge of the Patagonian Shelf, but it extends over the shelf to the north of the Falkland Islands (Malvinas). *Illex illecebrosus*

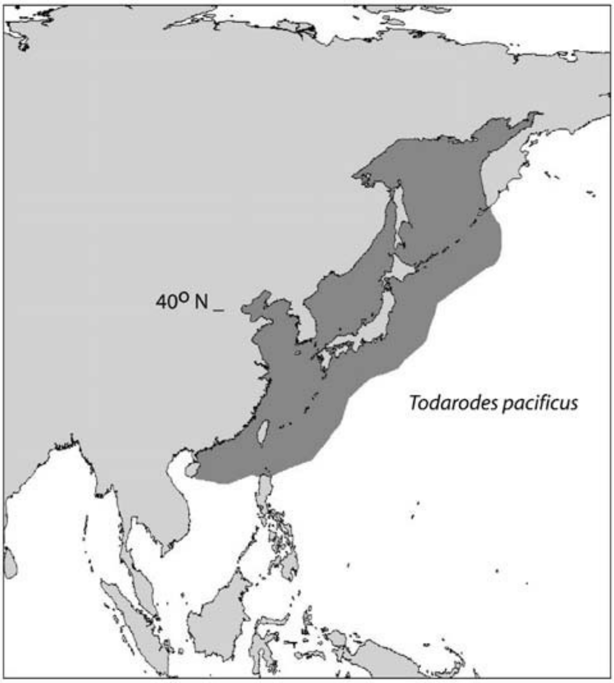


Fig. 17.4 Principal distribution area of the fished populations of *Todarodes pacificus* in the seas around Japan and China in the northwest Pacific Ocean (after Roper *et al*. 1984).

Fig. 17.5 The distribution of the migratory fished stocks of *Illex argentinus* off South America in the southwest Atlantic Ocean (after Roper *et al*. 1984).

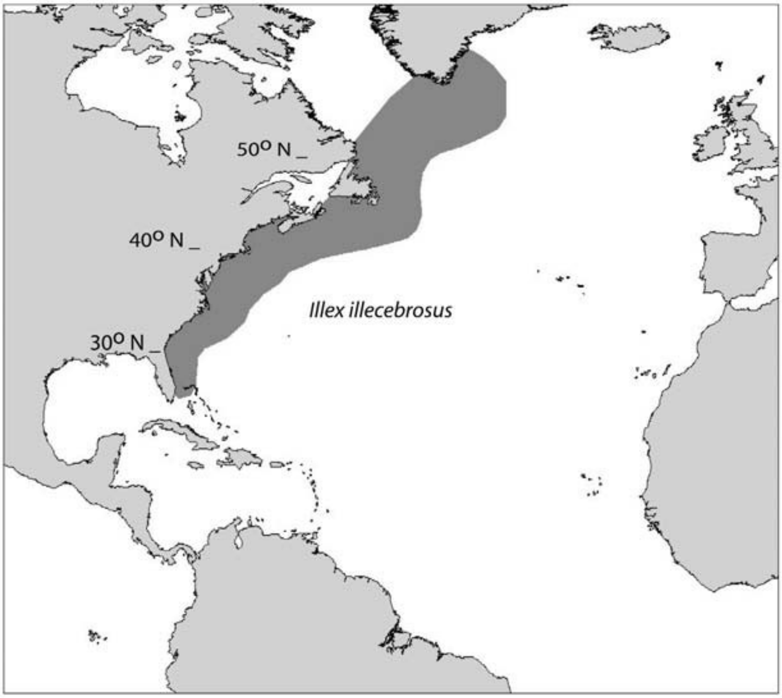


Fig. 17.6 The distribution of *Illex illecebrosus* off Canada and the United States in the northwest and central western Atlantic Ocean (after Roper *et al*. 1984).

(Fig. 17.6) occurs in the north Atlantic from 25°N off Florida to about 60°N off the Canadian coast. Its habitat is similar to that of *I. argentinus*, being concentrated near the shelf edge but extending in over the shelf and into deeper water to a depth of about 1000 m. Since the early 1980s, when the east Asian jig-fishery for the species off Canada collapsed, it has largely been exploited by trawlers off the US coast so the fishery cannot be visualised through their light emissions by satellite.

Nototodarus sloani, *N. gouldi* and *Martialia hyadesi* (Figs. 17.7–17.9) are southern hemisphere species. *Nototodarus sloanii* is exploited in sub-Antarctic waters over the shelf of the South Island of New Zealand, and gives way to the smaller stock of *N. gouldi* in the subtropical waters around the North Island. *N. gouldi* is also caught off southern Australia and Tasmania. *M. hyadesi* has a circumpolar distribution in the Southern Ocean, but is only exploited sporadically in the southwest Atlantic sector by the fleet primarily targeting *Illex argentinus*.

Ommastrephes bartrami (Fig. 17.10) is an epipelagic species which occurs over the deep ocean in the Atlantic, Pacific and Indian Oceans. In all three oceans it is absent from equatorial waters, and extends from the subtropics to temperate waters in the northern and southern hemispheres. Despite its wide distribution it is only exploited commercially in the northwest Pacific off northeast Japan by Japanese and Taiwanese vessels.

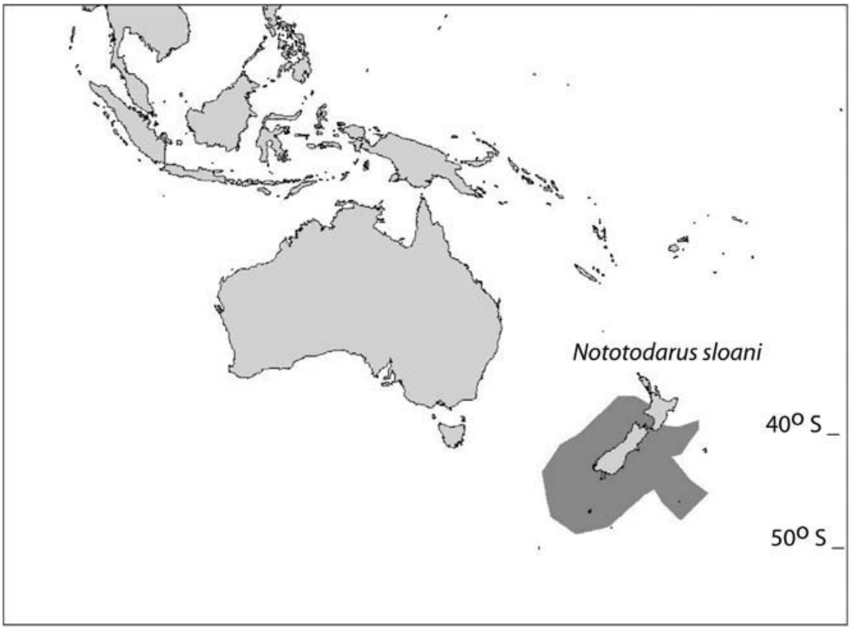


Fig. 17.7 The distribution of *Nototodarus sloanii* around New Zealand and Chatham Islands in the southwest Pacific Ocean (after Roper *et al*. 1984).

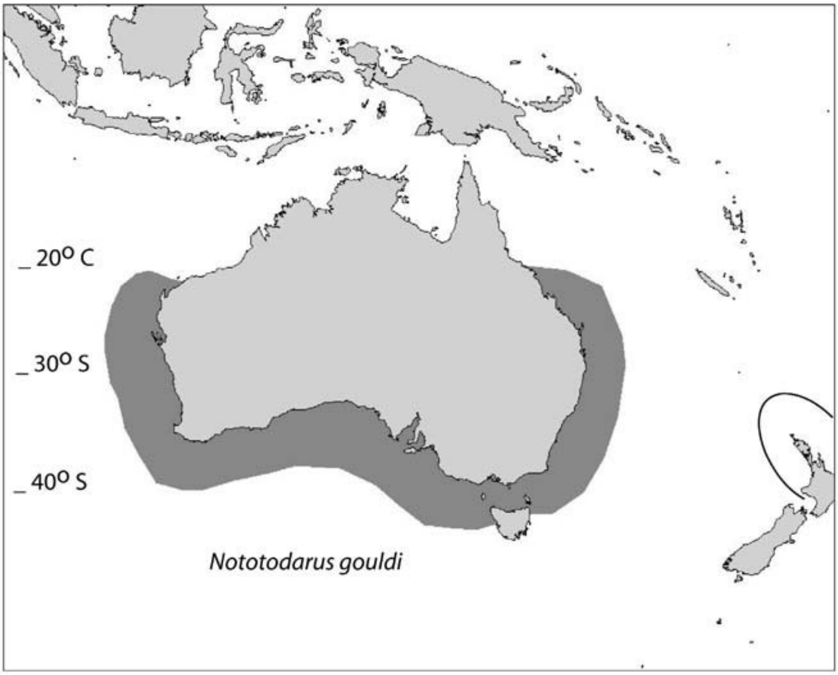


Fig. 17.8 The distribution of *Nototodarus gouldi* around South Australia in the southwest Pacific and Indian Oceans (after Roper *et al*. 1984).

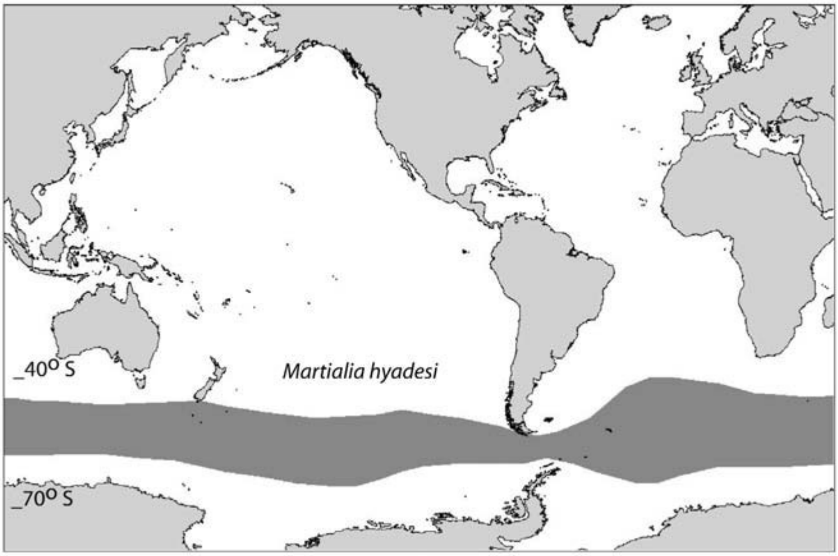


Fig. 17.9 The distribution of *Martialia hyadesi* in circumpolar waters of the Atlantic, Pacific and Indian Oceans (after Roper *et al.* 1984).

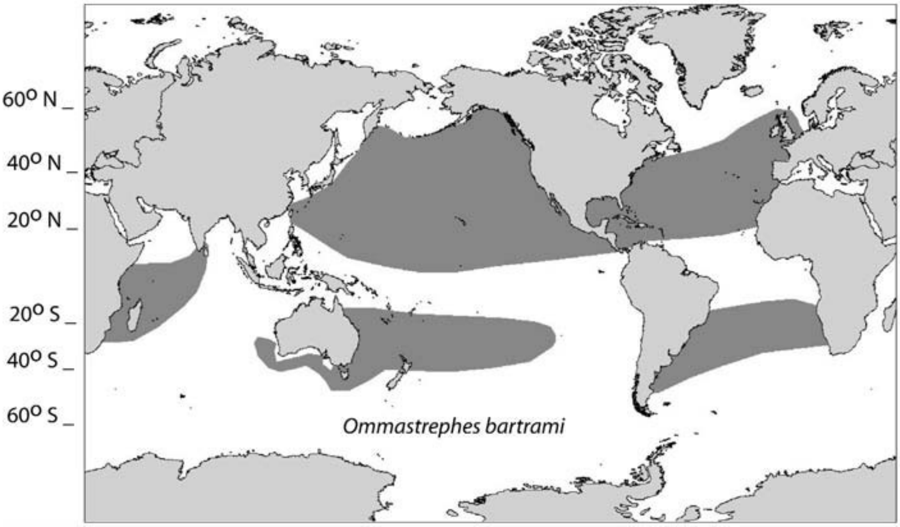


Fig. 17.10 The distribution of *Ommastrephes bartrami* throughout the northern and southern hemispheres (after Roper *et al.* 1984).

Dosidicus gigas (Fig. 17.11) is distributed in the eastern Pacific from 35°N off California to southern Chile, extending westwards furthest in the tropics to about 120°W. It is largely an off-shelf species. The major fisheries for *D. gigas* are off Peru and in the vicinity of the Costa Rica Dome off central America (Costa & Costa Fernandes 1993; Ichii *et al.* 2002). This species is exploited by local South American artisanal vessels and also by far-seas jiggers from Japan and Korea, which also operate in the south Atlantic fishery earlier in the year (Kuroiwa 1998; Yamashiro *et al.* 1998),

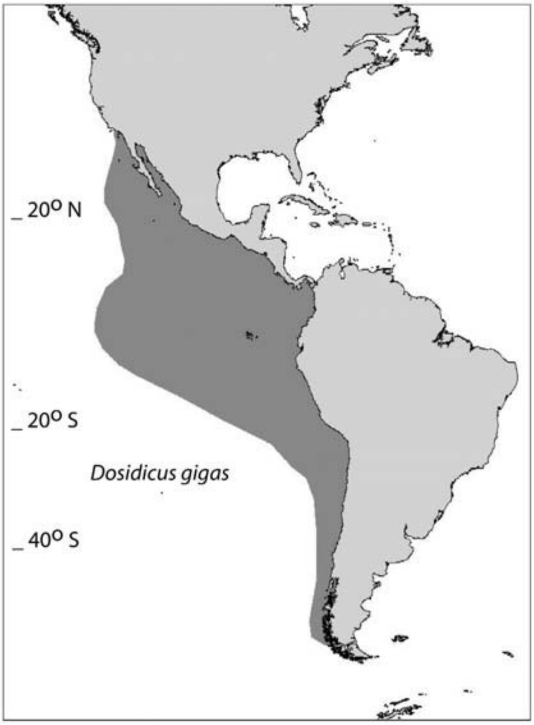


Fig. 17.11 The distribution of *Dosidicus gigas* in the western Pacific Ocean (after Roper *et al.* 1984).

and it had previously been exploited by vessels from the former Soviet Union (Nigmatullin *et al.* 2002).

Todarodes sagittatus (Fig. 17.12) is an eastern Atlantic species occurring from the Arctic off northern Norway to about 13°S, and westwards to approximately 40°W. It is an occasional by-catch of trawlers, although in the early 1980s it occurred at sufficient densities in coastal Norway to generate a short-lived, targeted fishery on a significant scale (Wiborg 1986). The fishery was based on a seasonal migration of juvenile animals into coastal waters. The source population for this movement, presumably located off the shelf in the eastern north Atlantic basin, has not been located.

The most important loliginid squid identified in the world catch is *Loligo gahi*, (Fig. 17.13) which is distributed in coastal and shelf waters around the coast of South America from southern Peru to northern Argentina. Most of the catch is caught in waters to the south and east of the Falkland Islands (Malvinas) by trawlers.

Loligo pealei (Fig. 17.14) is a western Atlantic species in coastal and shelf waters along the eastern seaboard of the USA, and Central and South America from 50°N to 5°N which is also caught by trawlers. *Loligo reynaudi*, as recorded by Roper *et al.* (1984), is a southern African squid, the distribution of which is poorly known. Augustyn and Grant (1988) have subsequently shown that on the basis of morphology, meristics and allozymes, *L. reynaudi* and *L. vulgaris* are in fact two sub-species (*L. vulgaris reynaudi* and *L. vulgaris vulgaris*). The fishery for *L. vulgaris reynaudi* (Fig. 17.15) is largely pursued by small jigging vessels (ski boats).

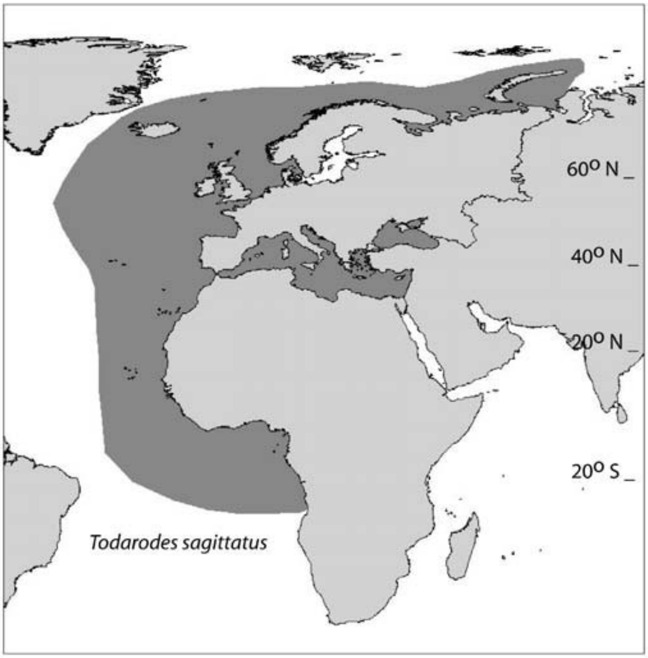


Fig. 17.12 The distribution of *Todarodes sagittatus* throughout the eastern Atlantic Ocean and Mediterranean Sea (after Roper *et al*. 1984).

Fig. 17.13 The distribution of *Loligo gahi* around South America in the southeast Pacific and southwest Atlantic Oceans (after Roper *et al*. 1984).

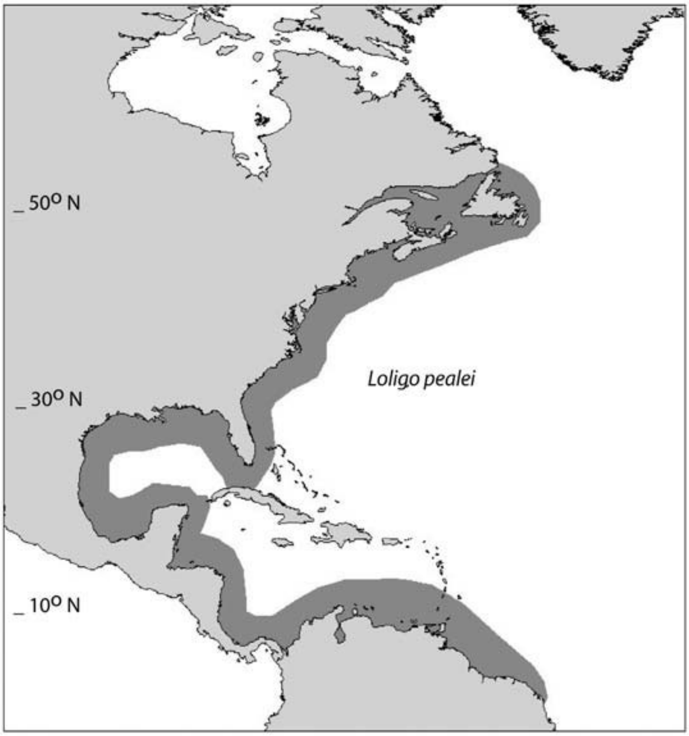


Fig. 17.14 The distribution of *Loligo pealei* in the western Atlantic Ocean (after Roper *et al*. 1984).

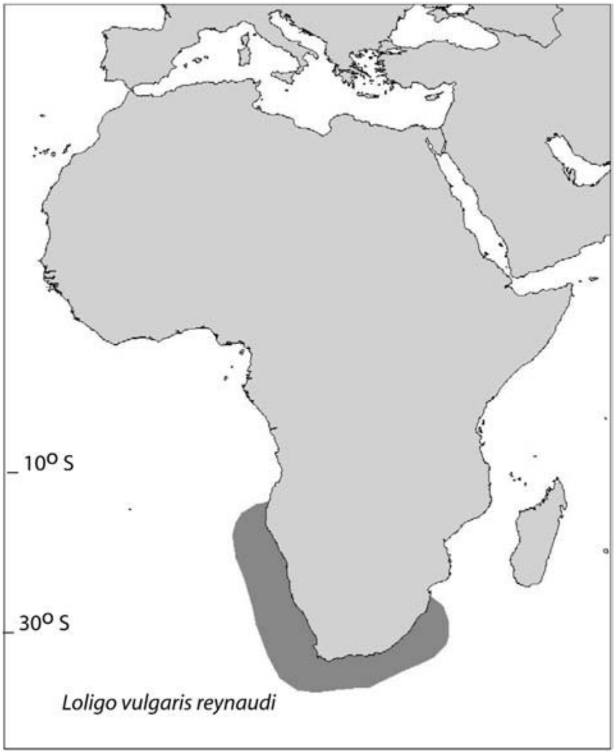


Fig. 17.15 The distribution of *Loligo vulgaris reynaudi* in the southeast Atlantic Ocean off South Africa (after Roper *et al*. 1984).

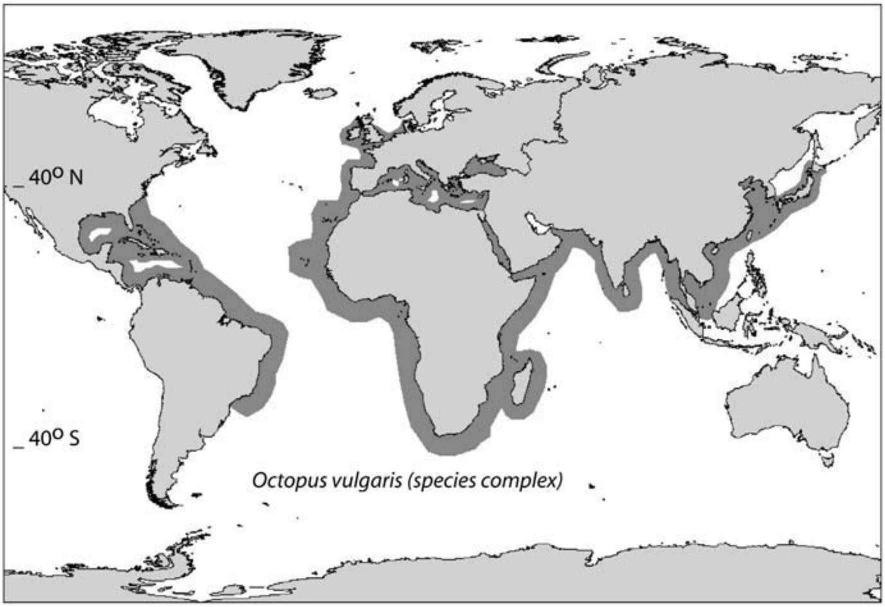


Fig. 17.16 Global distribution of the *Octopus vulgaris* species complex (after Roper *et al.* 1984).

17.2.3 Octopus

Octopus vulgaris is the only octopus identified to species level in the FAO Yearbook. This coastal and shelf species has an apparently world-wide distribution in temperate and tropical waters (Fig. 17.16). Most of the reported catch, which amounted to a total of 34 262 tonnes in 1999, is taken in areas 31, 34 and 37, the western and eastern central Atlantic and the Mediterranean, respectively.

Roper *et al.* (1984) identify 31 species of octopus, from several genera, of interest or potential interest to fisheries. These and other octopuses occur throughout the shelf seas of the world from the tropics to the poles, and are targeted by a great many coastal communities world-wide. The argonaut or paper nautilus (*Argonauta argo*), which is in fact a pelagic octopus, turns up in fish markets in India and Japan, and although there are probably no fisheries that target the species, catches of several hundred kilograms are sometimes landed.

17.3 Interpreting the unidentified catch

Although the FAO Yearbook provides information about a relatively small proportion of the global cephalopod catch identified to species level, the scientific literature on the cephalopod fauna enables us to interpret, to varying degrees, the catches from the statistical areas that are reported but are not identified. This is the category ‘not elsewhere included’ (NEI) used by FAO.

Of 153 740 tonnes included as 'cephalopods NEI' (not even broken down to the level of octopus, cuttlefish or squid) caught in 1999, some 62% (95 688 tonnes) are reported as having been caught in the Indian Ocean (areas 51 and 57). However, the bulk of this is taken from the western Indian Ocean (area 51), and in fact the contribution reported from India alone was 80 226 tonnes, or 84% of the total Indian Ocean catch. The cephalopod fauna in this area is not well studied, but the catch probably consists of a mixture of cuttlefish, octopus and loliginids, and some oceanic squids such as *Sthenoteuthis oualaniensis*, which is a common oceanic ommastrephid in the region. Jothinayagam (1987) lists at least 10 sepeiod species, 6 loliginid squid and 11 octopuses from the inshore coast of Madras alone, and it is likely that in mixed artisanal fisheries some or all of these are caught, as well as other species.

17.3.1 Cuttlefish

Globally, a total of 452 188 tonnes of cuttlefish and bobtail squids NEI were caught in 1999 (Fig. 17.17). For comparison, the total catch of *Sepia officinalis*, which is the only species of cuttlefish identified among this group, was a mere 14 638 tonnes in 1999. Of those in the NEI category, 309 839 tonnes came from the western Pacific (areas 61 and 71). This covers the seas from the Arctic through Kamchatka, Japanese waters and the China Sea to the Sunda–Arafura shelves region of Indonesia, the Philippines and Australasia. While the cephalopod fauna, especially the exploited species, of the northern parts of the western Pacific has been well documented, the Sunda–Arafura shelves region is an area where the cephalopod fauna is poorly known. This region is one of the hot spots of global marine biodiversity, so there is a need for more information on the taxonomy of the fishery species in this area. Nevertheless, there is information from the fishery in Thailand which accounts for the largest proportion of cuttlefish, etc., from area 71. Vessels here catch *Sepia aculeata*, *S. recurvirostra*, *S. pharaonis*, *S. lycidas, S. breviamana* and *Sepiella inermis* (Chotiyaputta 1993).

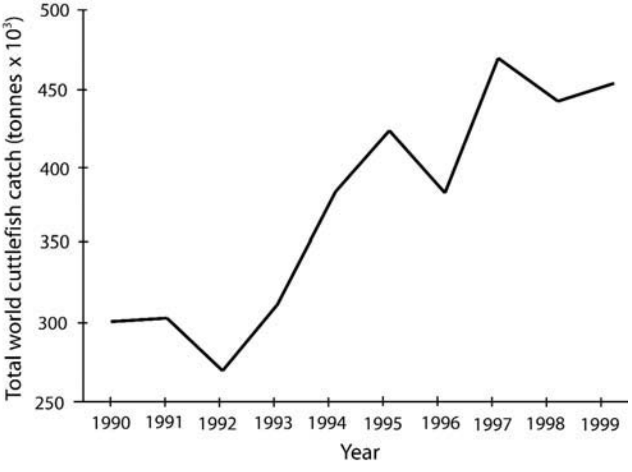


Fig. 17.17 Total world cuttlefish catch (tonnes × 10^3) between 1990 and 1999. Data from the Food and Agriculture Organization of the United Nations (after FAO Fisheries Department 2001).

17.3.2 Squid

The total catch of squid from the family Loliginidae in the NEI category in 1999 amounted to 213 317 tonnes. This compares with a total of 68 423 tonnes for the three identified *Loligo* species in the data (see Table 17.1). The largest proportion of loliginids NEI (68%) is taken in area 71, and of this, most is reported by Thailand. This is the same geographical region of high marine biodiversity discussed above in relation to cuttlefish and bobtail squids. The loliginids caught by the Thai fishery are well documented, and include *Loligo chinensis*, *L. deuvauceli*, *Sepioteuthis lessoniana*, *Loliolus sumatrensis* and *Loliolus affinis* (Chotiyaputta 1993).

Another point to be made about the unidentified catch of loliginids is that there is a category of 'various squids NEI' with a total catch of 313 259 tonnes. This will include both the Loliginidae and Ommastrephidae, but for reasons given below the majority in this category are likely to be loliginids. The largest proportion of this category (131 188 tonnes in 1999) comes from area 61, which includes catches by China, Japan, Korea and Russia. The second largest proportion (91 017 tonnes in 1999) comes from area 77, mostly from the USA. This is presumably *L. opalescens*, which is not recorded by species elsewhere. Nor is it included in the general loliginids NEI category, as no catch is reported by the USA for loliginids from area 77.

It is not possible to say anything about the relative proportions of ommastrephids identified in the FAO statistics because there is no 'ommastrephids NEI' category in the data. However, it is highly likely that ommastrephids are included in the 'various squids NEI' category, which must also include members of the loliginidae and probably some other families as well, such as the Thysanoteuthidaa (*Thysanoteuthis rhombus*) and Enoploteuthidae (*Watasenia scintillans*), which are known to be caught by Japan and probably other nations. The total catch for the 'various squids NEI' category was 313 259 tonnes in 1999. This compares with a total of named ommastrephids in 1999 of 1 804 057 tonnes, predominantly of *Illex argentinus* and *Todarodes pacificus*. It is also likely that ommastrephids are included in the 'cephalopods NEI' category, but the total for this, which includes a mix of cuttlefish, squid and octopus, is only 153 740 tonnes. Thus, of the ommastrephids, by far the greater proportion of the total catch is identified to species level in the FAO statistics. This presumably reflects the lower biodiversity of the family, the geographical separation of the species, and the more sophisticated nature of the high seas, deep-water fisheries which exploit the members of this family.

17.3.3 Octopus

The total octopus catch reported under the 'octopuses NEI' category was 318 146 tonnes in 1999. This compares with 34 262 tonnes of *Octopus vulgaris* in 1999 and 1433 tonnes of eledonids (mostly *Eledone cirrhosa* and *E. moschata*). Most of the 'octopuses NEI' were caught in two areas in 1999. A total of 77 113 t was from area 61 and 171 126 tonnes was from area 34. In the latter area, this was probably largely *O. vulgaris*, which is caught by a total of 28 countries on the Saharan Banks. It is well worth noting, however, that the octopuses are particularly difficult to identify, and there is possibly substantial incorrect reporting of this taxonomic group.

17.4 State of exploitation and production potential

It is not possible to make detailed predictions about the potential for growth in the cephalopod fisheries, but some broad statements can be made based on a combination of trends in the global statistics and knowledge of the ecology of the cephalopod fauna where exploitation is currently slight or non-existent.

17.4.1 Cuttlefish

The global cuttlefish catch increased over the decade between 1990 and 1999 from about 296 to some 467 thousand tonnes (see Fig. 17.17), and the continuing upward trend indicates that there may be further potential for increased catch in the future. However, it should be noted that these increases in cuttlefish catches have probably been made as a result of expanding trawl fisheries into previously unfished areas. Where these have exploited the spawning areas of the species concerned, there is evidence that populations such as *Sepia pharaonis* in the Arabian sea have been damaged and are now below their maximum potential, so the overall increases observed over the last decade may not be sustainable in the medium or even the short term. Lack of identification of most of the world catch of cuttlefish makes it difficult to interpret these statistics any further.

17.4.2 Squid

In the decade between 1990 and 1999, the world squid catch ranged between 1.7 and 2.5 million tonnes per year (see Fig. 17.18). Catches of identified squid are dominated by ommastrephids, and mostly by *Illex argentinus* and *Todarodes pacificus*, but between 1991 and 1997 *Dosidicus gigas* made a substantial contribution, totalling

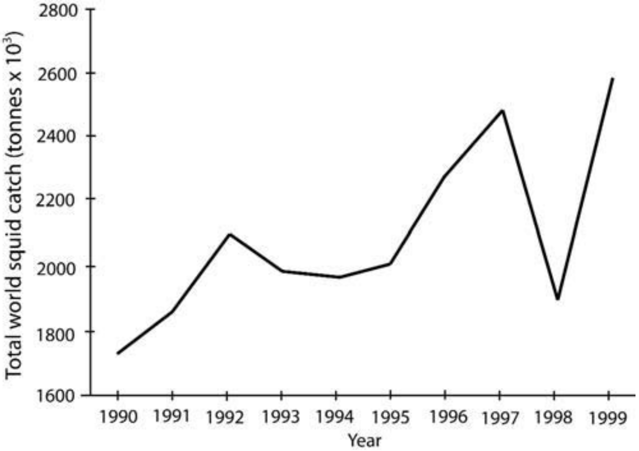


Fig. 17.18 Total world squid catch (tonnes × 10^3) between 1990 and 1999. Data from the Food and Agriculture Organization of the United Nations (after FAO Fisheries Department 2001).

about 200 000 tonnes in 1994. Among the unidentified loliginids, *Loligo* spp. have consistently contributed nearly 250 000 tonnes per year, and in most years *Loligo gahi* has dominated the identified catch by a considerable margin. Records of unidentified squid have declined substantially over the decade (by a factor larger than three). This is because the proportion of squids that remain unidentified in catches and landings is decreasing, and hence a larger proportion is now properly documented and identified to species level. Although there has been considerable variability in catches of all species and in the total squid catch over the decade, there does not appear to be any consistent trend. It seems likely that the species currently exploited, which with the exception of *Ommastrephes bartrami* have continental shelf or near-shelf distributions, are all fully exploited, and variations in catch rate are driven by environmental variability (see above).

On the other hand, there is some evidence that stocks of the oceanic squids could make a substantial contribution to increased catches of cephalopods. *Ommastrephes bartrami* is only exploited systematically in the north-west Pacific, although its distribution is global in the subtropical and temperate regions. Other ommastrephids, particularly *Sthenoteuthis oualaniensis* in the Indo-Pacific (Yatsu *et al.* 1998c) and *Todarodes filippovae* and *Martialia hyadesi* in the Southern Ocean (Rodhouse 1997, 1998a) have also been identified as having potential for supporting fisheries. Squid from other families also have potential which is only just being developed. The gonatid *Berryteuthis magister* in high-latitude Pacific waters and *Thysanoteuthis rhombus* in tropical/subtropical waters of all the oceans are lightly exploited and do not appear in FAO data, but could probably stand increases in exploitation rate and both have desirable qualities for human consumption (Dunning & Brandt 1985; Nesis 1998a; Kawasaki & Kakuma 1998).

Estimates of cephalopod predation by global populations of higher predators, especially sperm whales, have led to very high estimates of the potential for fisheries. Data from the former Soviet Union on deep ocean resource exploration, based on sampling by nets, provided more modest estimates of fishery potential, but still suggest that cephalopods, especially squid, could support catches of up to 5–10 million tonnes per year (Nigmatullin 1990). Increases of this order would involve exploiting families such as the Histioteuthidae and Octopoteuthidae, for which no markets currently exist, but which may be palatable for human consumption.

However, it should be noted that exploiting squid from the deep ocean, which themselves are known to feed largely on poorly understood mesopelagic fish and crustaceans, would pose both scientific and political management problems. Little is known about the biology of these communities or their productivity, and since these ecosystems largely fall outside the Exclusive Economic Zone (EEZ) of nation states as presently constituted, they are hardly considered for management.

17.4.3 Octopus

The global octopus catch has remained remarkably consistent over the decade from 1990 to 1999 (Fig. 17.19). This strongly suggests that, at least in the areas currently exploited by the fisheries, there is little scope for increased catch. There may be cur-

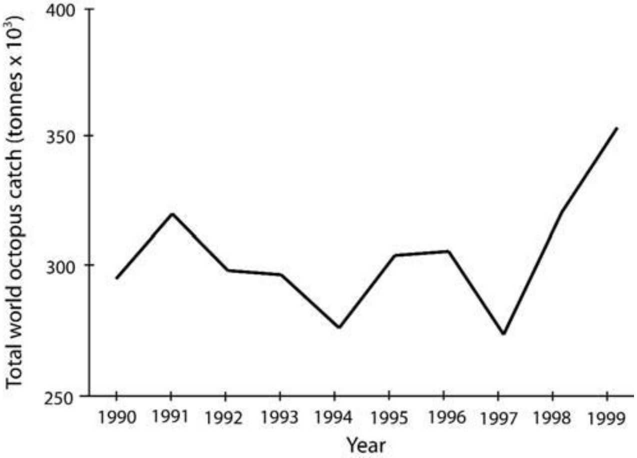


Fig. 17.19 Total world octopus catch (tonnes × 10^3) between 1990 and 1999. Data from the Food and Agriculture Organization of the United Nations (after FAO Fisheries Department 2001).

rently unexploited areas, such as the polar regions, where catches might increase in the future, but the high-latitude seas are unlikely to be particularly productive because rates of growth and reproduction in octopuses are slowed at low temperatures (Daly & Peck 2000).

Chapter 18

Fisheries oceanography

Summary: The largest cephalopod populations, including those exploited by fisheries, mostly inhabit one of the three types of large oceanic ecosystems: the high-velocity current systems mainly associated with the western boundaries of the world's oceans, the major coastal upwelling systems and the continental shelves. The large-scale squid fisheries which use lights to attract the squid can be seen in satellite images gathered by the US Defense Meteorological Satellite Programme. Large fleets of vessels can be visualised in the Kuroshio Current in the western Pacific, on the edge of the Patagonian Shelf in the Falkland (Malvinas)/Brazil Current system, on the New Zealand shelf, in the coastal upwelling system off Peru (Humboldt Current), on the China Sea shelf and in the Sunda–Arafura shelves system. In the ommastrephid fisheries, squid are often concentrated in the vicinity of meanders, eddies, core rings and jets of oceanic frontal systems. Because cephalopods are ecological opportunists, their populations are highly labile and changes in abundance are driven by large-scale oceanographic variability. Understanding short-term distributional changes linked to mesoscale processes and longer term (≤1 year) abundance changes associated with larger-scale processes holds out the possibility of predictive operational fisheries oceanography drawing on oceanographic satellite imagery from various sources.

The major cephalopod fisheries, as well as some of the large unexploited populations of cephalopods, are mostly associated with one of three different types of large marine ecosystem. These are the high-velocity oceanic current systems (the western boundary currents (WBCs) and the Antarctic Circumpolar Current (ACC)), the major coastal upwelling systems and the large, relatively shallow and flat, continental shelves.

18.1 Large-scale ocean systems

18.1.1 Western boundary currents and the Antarctic circumpolar current

The largest single fisheries are for ommastrephid squids and these are, with one exception, located in the WBCs of the Atlantic and Pacific oceans and in the boundary between the extension of the East Australia Current and the northern limits of the high-velocity circumpolar current system off New Zealand (Fig. 18.1).

Western boundary currents comprise the western periphery of the major gyres of the world's oceans, they mark the limit of coastal/shelf waters on the eastern seaboard of the continents, and they act as dynamic barriers retaining the internal waters of the oceanic gyres. The WBCs carry large amounts of heat away from the equatorial regions, and they are characteristically turbulent and variable systems in which the physical structure and velocity changes constantly (Mann & Lazier 1991). Eddies and meanders are typical features of the frontal systems at the peripheries of the WBCs, and these may reach up to 150 or 200 nautical miles across. Pockets of warm water

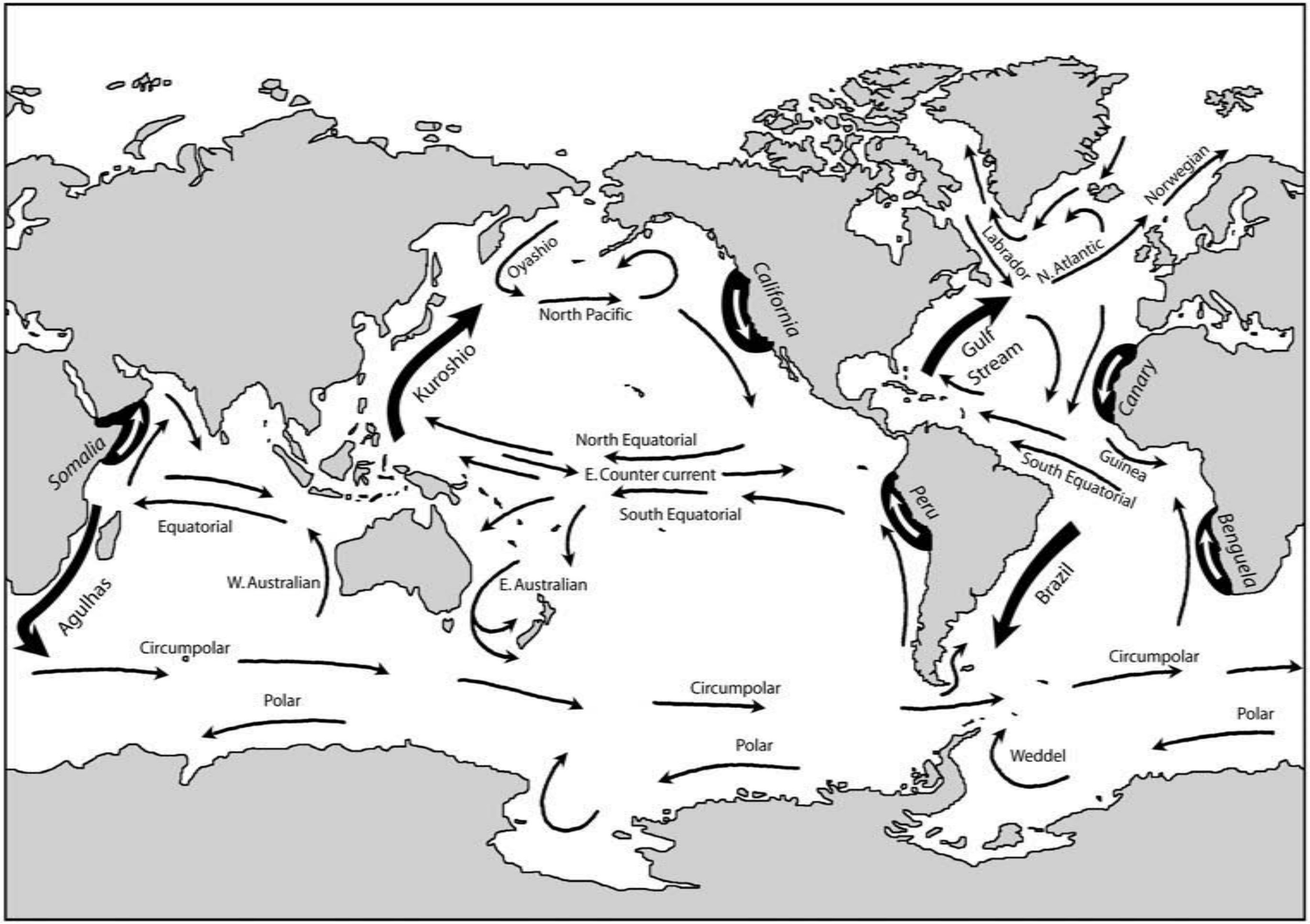


Fig. 18.1 The principal surface currents of the world's oceans, with the Western boundary currents emphasised by black arrows (Kuroshio, Gulf Stream, Brazil, Agulhas). Major coastal upwellings shown in black with their associated Eastern boundary currents in white arrows (California, Humboldt, Benguela, Canary, Somalia).

(warm core rings) detach and become embedded in cooler coastal waters and, conversely, pockets of cool water (cold core rings) detach and become embedded in the warm waters of the WBCs. These are clearly visible in infrared satellite imagery of sea-surface temperatures (Plate 1).

The large ommastrephid squid species inhabiting the WBCs have evolved life histories that enable them to utilise the current systems for the transport of the planktonic stages of their life cycle, and this enables the squid to exploit secondary production over large latitudinal ranges whilst reproducing in warm subtropical waters (O'Dor 1992). Both warm and cold core rings support enhanced primary production, giving rise to increased biomass at higher trophic levels, and this is also exploited by the squids (Mann & Lazier 1991). Warm core rings are also thought to contribute to the transport of paralarvae, and it has been suggested that recruitment success or failure in *Illex illecebrosus* in the north Atlantic may be critcally dependent on the timing, location and number of Gulf Stream front eddies and warm core eddies developing when larvae and juveniles are present (Rowell *et al.* 1984). Similarly, recruitment of *Illex argentinus* in the south Atlantic may be enhanced in a year when large numbers of paralarvae become entrained into a warm core ring at the confluence of the Brazil and Falkland (Malvinas) Currents forming at a critical time in their life cycle (Parfeniuk *et al.* 1992).

Although the Antarctic Circumpolar Current (ACC) is not a WBC, it shares similar characteristics. It has a high velocity, driven by the prevailing westerly winds of the Southern Ocean north of the Antarctic continent. At its northern extent there are well-defined frontal systems, the Antarctic Polar Front (previously known as the Antarctic convergence) and the subtropical front, which are characterised by the presence of eddies, meanders and core rings. Squid fisheries are associated with the northern limits of the ACC in the south Atlantic and off New Zealand.

18.1.2 Coastal upwelling systems

Coastal upwelling ecosystems are located off the western coasts of the continents, and in the Indian Ocean upwelling is also associated with the monsoon system (Fig. 18.1). Three large cephalopod fisheries are located in major coastal upwelling systems associated with low-velocity eastern-boundary current systems. These fisheries exploit the ommastrephid squid *Dosidicus gigas* in the Peru Current, the loliginid squid *Loligo opalescens* off the coast of California and octopus *O. vulgaris* off northwest Africa (Demarcq & Faure 2000). The eastern boundary currents are characterised by wind-induced upwelling mediated by a mechanism known as Ekman transport. Wind blowing over the surface of the sea generates a surface current which moves in the same direction as the wind. The Coriolis force, derived from the Earth's rotation, then causes the current to turn towards the right in the northern hemisphere and to the left in the southern hemisphere. When this Ekman transport is away from the coast (on the western side of the continents), surface water moving away from the coast is replaced from beneath by deep, cool, nutrient-rich water. When this reaches the sunlit (photic) zone, pimary production is stimulated by the presence of high concentrations of plant nutrients which accumulate in deep water through the mineralisation of organic

Fig. 18.2 Deck of a Japanese squid-jigging vessel at night showing the rows of incandescent fishing lights and fishing gear in place.

matter sinking from the epipelagic productive zone. This stimulates intense primary production providing the basis for high levels of secondary production, which in turn generates rich fishing grounds for finfish and cephalopods (Faure *et al.* 2000).

In the Indian Ocean upwelling system there are large stocks of the ommastrephid squid *Sthenoteuthis oualaniensis* that are recognised to have fishery potential, but which are not commercially exploited (Yatsu *et al.* 1998a; Chesalin & Zuyev 2002) at present. Upwelling in the Indian Ocean differs from that described above for coastal systems. In the north Indian Ocean, the upwelling uniquely occurs on the western side of the ocean but only during the summer when the southwest monsoon causes Ekman transport to carry surface water away from the coasts of the Arab states and Somalia. During winter, when the prevailing wind pattern in the northern Indian Ocean reverses, the upwelling ceases.

18.1.3 Large shelf systems

The other major cephalopod fisheries, mostly exploiting a mix of loliginid squid, cuttlefish and octopus, are located on the extensive, flat and relatively shallow (<200 m) shelf systems of the China Sea, the Sunda–Arafura region of southeast Asia and on the Patagonian Shelf off the southeast coast of South America. Primary production in these systems is driven by input of nutrients from river discharge, together with a seasonal turnover of the water column which recycles nutrients into the photic zone during winter and which subsequently supports the spring bloom.

18.2 Defence meteorological satellite programme (DMSP) imagery

In several of the major fisheries, squid are attracted towards jigging vessels at night by means of powerful incandescent lights (Chapter 16). Large fleets of jiggers, mostly from east Asia, use lights for fishing in various parts of the worlds oceans, especially in the western Pacific, the southwest Atlantic and around New Zealand. Where large fleets concentrate, the lights from these fisheries appear at night in satellite imagery from the United States Defence Meteorological Satellite Programme (DMSP) Operational Linescan System (OLS). The recent availability of archived data from the DMSP has provided a novel means of monitoring whole fleets of light-fishing vessels almost in real time (Cho *et al.* 1999; Rodhouse *et al.* 2001), and also provides a record of the distribution of the squid jigging fleets in relation to the major oceanographic features of the regions in which they occur.

The DMSP OLS detects low levels of visible and near infrared radiance (VINR) at night. Algorithms have been developed to identify and geolocate VNIR emissions in night imagery, allowing the production of an inventory of light sources from over the whole of the Earth's surface (Elvidge *et al.* 1997a, b). The wide swath of about 300 km allows global coverage four times per day, at dawn, day, dusk and night. The squid fishing fleets are only observed in night-time images, and are best seen when the moon is not full and when cloud cover is absent or thin. The sensors that measure radiance in the visible band are more than four orders of magnitude more sensitive than the VNIR bands of other sensors used for oceanographic applications such as the NOAA AVHRR (National Oceanic and Atmospheric Administration (US Department of Commerce) advanced very high resolution radiometer). DMSP imagery was originally collected for military purposes, but the data were declassified in 1972 and have been archived in digital form at the NOAA National Geophysical Data Center since 1992.

Light-fishing vessels which can be detected by the DMSP satellites are the squid-jiggers (Fig. 18.2) described in Chapter 16. Small artisanal vessels may deploy a single lamp, whilst large industrial vessels which operate offshore use an average of about 150 lamps. Typically, the lamps are 2 kW and are usually white with a small number of green lamps interspersed (Inada & Ogura 1988). A typical east-Asian far-seas jigger of 70 m overall length operating in the southwest Atlantic, off Peru or New Zealand, fishing with about 150 lamps would thus use a total of 300 kW. It would also operate 110 jig lines carrying 25 jigs per line (total 2750 jigs), and would expect to catch 25–30 t of squid (exceptionally up to 100 t) per night, usually with a crew of about 20 people. Experiments in Japan using sonar to detect squid attracted to fishing lamps have shown that in seawater of optical type 'oceanic III' (Jerlov 1964) squid (*Todarodes pacificus*) are concentrated in a depth layer between 30 and 70 m, in spectral irradiance levels (at 510 nm) of $1.8 \times 10^{-2} - 5.4 \times 10^{-5}$ W cm^{-2} nm^{-1} (Arakawa *et al.* 1998).

DMSP imagery has revealed the geographical extent of the global light fishery, and has been used to interpret the relationship of the species being targeted to the bathymetry and physical and biological oceanography of the regions where they operate (Rodhouse *et al.* 2001).

18.3 Distribution of the major cephalopod fisheries in relation to large-scale oceanography

18.3.1 Western boundary current systems and the Antarctic circumpolar current

18.3.1.1 Kuroshio Current

There are more squid fishing vessels using lights in the Kuroshio Current system in the western Pacific than anywhere else in the world's oceans. High densities of lights are visible in DMSP imagery in the Tsushima Strait between the Korean Peninsula and Japan, throughout the southern part of the Sea of Japan, and in the Pacific to the west of Japan off northern Honshu and Hokkaido (Plate 3). Japanese, Korean, Chinese and Taiwanese vessels fishing for the Japanese flying squid, *Todarodes pacificus*, make up the largest squid fishery in the world. Catches have been variable over decadal time scales, decreasing from high levels in the 1960s to low levels in the 1980s and increasing again in the last decade of the twentieth century. These changes have apparently been due to regime shifts associated with decadal changes in sea temperature (Minobe 1997).

To the east of Japan, in oceanic waters, the east-Asian light-fishing fleet exploits another ommastrephid, the neon flying squid *Ommastrephes bartrami*. Catches peaked at nearly 400×10^3 t/year in the 1980s (Murata & Nakamura 1998) during the drift-net fishery that was subsequently banned by a UN moratorium in 1991 because of unacceptable by-catches of marine mammals, seabirds and other non-target species. Since the ban on drift-nets, the fishery for *O. bartrami* has been re-established using lights, and Japanese jiggers were catching 70×10^3 t/year by the mid-1990s, with Chinese and Taiwanese vessels catching another 80×10^3 t/year (Rodhouse *et al.* 2001).

The Kuroshio Current is the western boundary current of the north Pacific. It originates off the east coast of the Philippines at about 15°N and flows northwards to 35–40°N, where an eddy field is created at the confluence with the cold southwards-flowing Oyashio Current, and where both currents are deflected eastwards (Longhurst 1998). The confluence is an area of highly seasonal primary production with strong spring blooms (Saijo *et al.* 1970), and it is here that the *O. bartrami* fishery operates.

A branch of the Kuroshio, the Tsushima Current, flows through the Tsushima Strait to the east of Honshu into the deep basin of the Sea of Japan. Within the Sea of Japan there is a gyre-like cyclonic flow which generates many warm- and cold-core mesoscale eddies. It is in the Tsushima Current that the most intense light-fishing for squid takes place, and this is primarily for *Todarodes pacificus* (see Plate 3). The continental shelf in the Sea of Japan is narrow, and strong phytoplankton blooms supporting large zooplankton concentrations are initiated by upwelling caused by eddy vorticity along the shelf edge and in the margins of warm core rings (Yamamoto & Nishizawa 1986).

18.3.1.2 Brazil/Falkland current system (Patagonian Shelf)

In the southwest Atlantic, fishing lights can be seen in DMSP imagery extending in a line closely following the Patagonian Shelf edge from about 40°S southwards to the

Falkland Islands (Malvinas), and spreading widely over the southern part of the shelf to the north of the islands (see Plate 2). The fishery is primarily targeting the winter spawning stock of the ommastrephid squid *Illex argentinus*, but it also catches variable amounts of another ommastrephid, *Martialia hyadesi*. The fishery biology of the genus *Illex* in the Atlantic has recently been reviewed (Rodhouse *et al.* 1998a), and the fishery for *I. argentinus* is well documented (Haimovici *et al.* 1998). The fishery began in the early 1980s, when east-Asian squid-jiggers shifted their effort from the north Atlantic, following the collapse of the *I. illecebrosus* fishery off eastern Canada. Catches in the southwest Atlantic are variable and linked to annual recruitment, which is apparently driven by oceanographic factors which affect the early-life phase of the squid before recruitment into the fishery (Waluda *et al.* 2001). The fishery operates from December to June, with peak catches from March to May.

There is also the large fishery for *Loligo gahi* in the southwest Atlantic, largely over the Patagonian Shelf to the south and east of the Falkland Islands (Malvinas) (Hatfield *et al.* 1990). Since 1987, annual catch rates have been between 44 and 89×10^3 tonnes, but this species is caught by trawlers which do not use fishing lights and so are not visible in DMSP imagery.

The *I. argentinus* fishery is associated with the southwest Atlantic western boundary current system and the Patagonian Shelf and Falklands plateau, which is one of the widest and flattest areas of continental shelf in the world's oceans (Longhurst 1998). The oceanic circulation here is complex. A shelf-break front extends almost the entire length of the shelf and separates the sub-Antarctic water of the northwards-flowing Falkland (Malvinas) Current, which is part of the Antarctic Circumpolar Current, from shelf water (Glorioso & Flather 1995). It is this frontal zone where much of the light-fishing visible in Plate 2 is concentrated. To the north of the region is the confluence of the Falkland (Malvinas) Current and the Brazil Current. At the confluence, the Falkland (Malvinas) Current is retroflected back southwards, and the Brazil Current separates from the shelf and is deflected into the oceanic interior (Olson *et al.* 1988). The confluence is characterised by a zone of intermediate surface water filled with eddies where the winter spawning stock of *I. argentinus* spawn (Haimovici *et al.* 1998). The latitude of the confluence is variable, and is determined by the relative strength of flow of the two currents. The shelf-break front is characterised by the consistent presence of chlorophyll associated with dynamic eddying at the front, and there is also a strong chlorophyll feature associated with tidal mixing in shallow water over the inner shelf and around the Falkland Islands (Malvinas), where the *I. argentinus* fishery spreads widely across the shelf.

The *Loligo gahi* fishery occurs on the extreme southern edge of the Patagonian Shelf. The shelf-break front here separates shelf water from oceanic sub-Antarctic water at the southern origins of the Falkland (Malvinas) Current, a branch of the Antarctic Circumpolar Current . The main concentrations of squid are located in the shelf water just to the north of this dynamic system.

18.3.1.3 Gulf Stream

No fishing lights are visible in the northwest Atlantic in recent DMSP imagery. The fishery for *Illex illecebrosus* was developed by Far-Eastern jiggers in the 1970s, but the catch rate fell dramatically in the early 1980s, the East Asian fleet shifted to the southwest Atlantic and the fishery has never become re-established. *Illex illecebrosus* is associated with the Gulf Stream system, and is caught near the shelf edge of the eastern seaboard of the USA and Canada. The highest catches were taken in the late 1970s off the Canadian shelf. At this latitude, the squid grow to a larger size but recruitment to the stock is more variable than further south off the coast of the USA, where there is a relatively stable trawl fishery (O'Dor & Coelho 1993). The ecology of the species in relation to the Gulf Stream system is very similar to that of *Illex argentinus* in relation to the WBC system in the south Atlantic.

18.3.1.4 Antarctic Circumpolar Current

Squid-fishing lights are visible in DMSP imagery on the shelf around New Zealand off the west coasts of North and South Island extending into the Taranaki Bight between the two islands of New Zealand, and on the shelf to the southeast of South Island (Plate 4). These vessels are targeting two ommastrephid squid species, the Wellington flying squid, *Nototodarus sloanii*, which is the major species in the New Zealand fishery, and Gould's arrow squid, *Nototodarus gouldi*. These are very similar species, which can only be separated on the basis of hectocotylus morphology in males, and sucker counts, which are not very reliable taxonomic characters. Otherwise, they can be distinguished using molecular genetic markers (Smith *et al.* 1981, 1987; Smith 1985) and they have different levels of infestation by parasites (Smith *et al.* 1981). *N. gouldi* is a subtropical species which occurs off Australia and New Zealand to the north of the Subtropical Convergence Zone (SCZ), and *N. sloanii* is distributed in cooler, sub-Antarctic New Zealand waters to the south of the SCZ (Gibson 1995; Uozumi 1998).

The fishery is located on the edge of the New Zealand continental shelf. The shelf is widest around North Island and off the southeastern part of South Island, including the area of shelf around the Snares Islands. New Zealand lies in the latitude of the subtropical convergence and the sub-Antarctic front. The regional oceanography is complex. The West Auckland and East Auckland Currents flow southwards along the shelf on the west and east side of North Island, respectively, and there are three major eddies off the shelf on the east of the island. Off the west coast of South Island, the gyral circulation of the Tasman Sea bifurcates at about 44°S. The southern branch flows south along the coast, rounds the south of the Island, and then forms the inshore component of the northward flowing Southland current off the east coast of South Island. The northern branch, the Westland Current, flows northwards to the west coast of North Island. The D'Urville Current flows into Taranaki Bight through Cook Strait, which separates North and South Island. Surface chlorophyll is especially enhanced over the shallow bathymetry off southern New Zealand.

The *N. sloanii* fishery is concentrated along the southeast coast of South Island and all over the Snares shelf in the Southland current system. There is also a trawl fishery on the Auckland Islands Shelf . The species is caught in both subtropical front and sub-Antarctic water at temperatures of <13°C, and the squid fishery is associated with elevated chlorophyll levels. In the mainland/Snares shelf area, the fishery mostly occurs over water depths of 40–140 m, but there is some fishing beyond the 200 m isobath.

The *N. gouldi* fishery is mainly concentrated around the north-west coast of South Island and the south-west coast of North Island over a broad area of shelf in subtropical water (>18°C) of the Westland/D'Urville Current system (Jackson *et al.* 2000b). The distribution of paralarvae and juveniles of both species of *Nototodarus* is similar to that of the adults, and spawning probably takes place over the continental shelf (Uozumi 1998).

In the southwest Atlantic, the ommastrephid species *Martialia hyadesi*, which is distributed in the Antarctic Circumpolar Current system, is taken as a variable by-catch in the *Illex argentinus* fishery. It is present in the Antarctic polar frontal zone (APFZ), apparently sometimes at high densities. The Falkland (Malvinas) Current represents a northwards flowing loop in the APFZ, bounded by the sub-Antarctic front (SAF) and retroflecting back towards the south at the confluence with the Brazil Current in the latitude of the northern Patagonian Shelf. The SAF on the western boundary of the Falkland (Malvinas) Current corresponds to the shelf-break front on the eastern edge of the Patagonian Shelf, and it is here that the jigger fleet targeting *Illex argentinus* catches *Martialia* in years when it is abundant. The high concentration of fishing lights at about 46°S, shown in Fig. 18.3, is the jigger fleet in 1995 which was catching

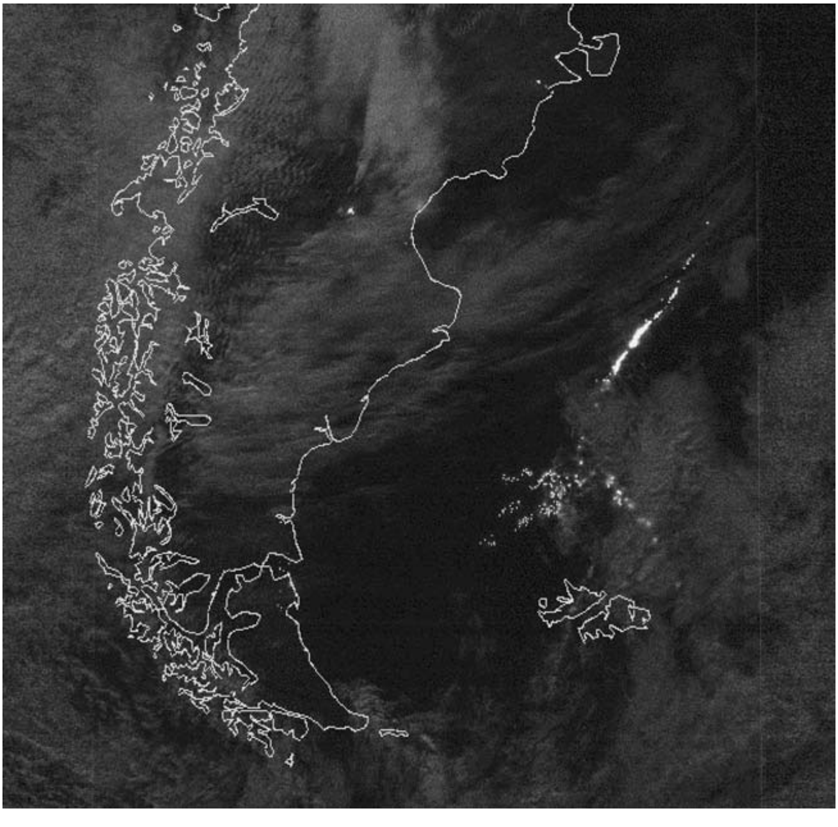


Fig. 18.3 A sample of the fishing lights in the south Atlantic visible from space by DMSP-OLS satellite imagery for the single night of 23 May 1995, showing the fishing fleet distribution on a wide area of the Patagonian Shelf north of the Falkland Islands (Malvinas), and concentrated northwards along the 200-m contour of the shelf edge (coastal outlines shown in yellow; fishing lights shown in white).

Martialia, which was especially abundant in that year (Gonzalez *et al.* 1997). In exceptional years the *Martialia* stock extends shorewards over the Patagonian Shelf, where it is caught more widely by the jigger fleet. This is an important species in the diet of seabird and seal predators in the Southern Ocean (Rodhouse 1997). Its distribution is circumpolar (Rodhouse 1998a), with observations such as strandings (O'Sullivan *et al.* 1983) indicating that it occurs elsewhere in the Southern Ocean.

18.3.2 Coastal upwelling systems

18.3.2.1 Humboldt Current

Concentrations of light-fishing vessels are visible in DMSP imagery off the Peruvian shelf extending from northern Peru between about 4°S and 9°S (Plate 5). The Humboldt Current system in which the *Dosidicus gigas* fishery is located is the eastern boundary current of the southeastern Pacific (Longhurst 1998). This region has a very narrow continental shelf, and is characterised by extensive and highly productive coastal upwelling features which are disrupted by periodic ENSO events. The distribution of *D. gigas* is mostly off the shelf edge in areas of high, but not maximum, primary production (Nesis 1983). It is likely that these visual predators are unable to forage effectively in the low visibility conditions of the densest phytoplankton blooms.

The fishery has been described by Yamashiro *et al.* (1998), and the jigging vessels are exclusively targeting the jumbo flying squid *Dosidicus gigas*, the largest member of the family Ommastrephidae, which was virtually unexploited until the mid-1990s. Until 1990, catches had been very low and limited to the Peruvian artisanal fleet, apart from some activity by Soviet Union trawlers in the late 1980s. Then in 1990, Japan and the Korean Republic started fishing on a large scale in the region. Annual catches have been variable, apparently in response to the ENSO cycle, with generally reduced catches in cold (La Nina) periods. This may be because eggs and the planktonic early life phase are entrained in surface water, carried away from the shelf towards the central Pacific and are lost from the population (Anderson & Rodhouse 2002).

In response to reduced catches off Peru associated with cold conditions, the light-fishing vessels sometimes move their activities further north, to the vicinity of the Costa Rica Dome, and catches there have considerably exceeded the catch off Peru in some years. Fishing effort and catches in the Peruvian fishery are greatest between June and December, and the fishery is pursued largely by jiggers that also fish in the southwest Atlantic, mainly between February and May, and then move round to the eastern Pacific.

This is also a large fishery for *D. gigas* in the Gulf of California (Baja California) (Morales-Bojorquez *et al.* 2001a, b). The fishery is pursued by small artisanal vessels that emit insufficient light to be visible in DMSP imagery.

18.3.2.2 California Current

In the California Current the fishery exclusively targets *Loligo opalescens*, which is caught on the spawning grounds along much of the Californian coast from central to southern California. The fishery differs from most other squid fisheries using lights in that a single boat with lights attracts and concentrates the squid, allowing one or more purse seiners to catch them using lampara nets. The large-scale image in Plate 6 shows small groups of fishing lights operating close inshore around the Channel Islands off the coast of Southern California.

The California Current is the eastern boundary current in the north-east Pacific. It originates to the north from the bifurcation of the eastwards flow of the north Pacific, and it flows south to the convergent front at the root of the north equatorial current off the southern tip of Baja California (Longhurst 1998). The shelf is narrow and characterised by upwelling fronts and also fronts associated with meanders in the coastal jet and cyclonic eddies. As in the Humboldt system, ENSO events occur when the north-westerly trade-wind stress relaxes. The coastal upwelling system is complex, and the enhanced productivity supports a low diversity diatom/copepod pelagic system (Mann & Lazier 1991). The highly variable fishery for *L. opalescens* in the California Current appears to be influenced by ENSO events in the wider Pacific system (McInnes & Broenkow 1978).

18.3.2.3 Canary Current

The Canary Current is the eastern boundary current of the north Atlantic, and is analogous with the California Current in the Pacific. It is characterised by coastal upwelling on the Saharan Bank off the west coast of Africa. The major cephalopod resource in the region is the *Octopus vulgaris* stock, which supports one of the largest octopus fisheries in the world. Squid, mostly loliginids (*Loligo vulgaris*) and cuttlefish, are also caught, mostly by trawling. No light-fishing vessels are apparent in DMSP imagery.

18.3.3 Large shelf systems

18.3.3.1 China Sea Shelf

There is an area of extensive light fishing for cephalopods along the whole continental shelf of China from the Yellow Sea in the north to the coast of Vietnam in the south (Plate 7). The highest density of lights is in the southern and central part of the Yellow Sea, near the shelf edge to the northeast of Taiwan, off the north coast of Taiwan, around the Peng-Hu Islands (Pescadores) to the west of Taiwan and in shelf waters to the west of Hainan. Substantial quantities of loliginids, cuttlefish and other unspecified cephalopods are reported to the FAO by Taiwan. The cephalopod fauna of this region, which includes the exclusive economic zones (EEZs) of China, Taiwan, Vietnam and Korea, has recently been described by Lu (1998) and Kubodera & Yamada (1998). Cephalopod catches by Vietnam are relatively small, not exceeding about 10 000 tonnes per year. The most abundant species caught by fisheries in the region is *Loligo chinensis* (Wu *et al.* 1989; Dong 1991). In the Yellow Sea there is probably some light-fishing with purse seine nets for finfish such as small clupeids, and these lights probably contribute to the fleet which is visible in Plate 7.

The China Sea continental shelf extends from the Yellow Sea in the north to the East China Sea in the south, together with the narrow shelf area of the western Sea of Japan. This is one of the largest areas of shallow shelf in the world, and is characterised by the discharge of freshwater and sediments by the Yellow and Yangtse rivers. The high sediment load is consistent with the predominance of myopsid squid in the catch which, because they possess a corneal membrane, are adapted to the presence of high concentrations of suspended particles. The shelf is bordered to the east by the shelf edge and the flow of the Kuroshio Current. The Kuroshio flows around the south of Taiwan and into the East China Sea, generating a northwards drift of warm water over the shelf which retroflects in an area of intense light-fishing in the DMSP-OLS image. There is a return flow of coastal water southwards from the western Yellow Sea which is reinforced by fresh water discharging from the Yellow and Yangtse rivers, and is associated with a persistent mesoscale eddy about 150 km south of Cheju Island. The Kuroshio meanders along the margin of the continental shelf off China, generating mesoscale eddies. Cool streamers advect cold shelf water seawards, and warm eddies move in across the shelf and are propagated northwards. There is upwelling near the Peng-Hu Islands where the squid fishery is located, and off the northeast coast of Taiwan, which are both areas of intense light-fishing activity which has been described by Lu *et al.* 1987. There is also upwelling off Shanghai and in the eddy system south of Cheju Island where there are high levels of primary production, but these are not areas of particularly high light-fishing activity, probably because of the low salinity and high sediment load in the discharge of the Yellow and Yangtse rivers.

18.3.3.2 Sunda–Arafura Shelves

Large concentrations of vessels using fishing lights are visible in DMSP imagery in the Gulf of Thailand, the Andaman Sea and in the coastal waters of the Philippines (Plate 8). There is little information on cephalopod fisheries in the Philippines, but substantial catches of common squid (*Loligo* spp.) are reported to the FAO, and the annual catch approximately doubled between 1987 and 1996. The Thai fisheries for cephalopods, in both the Andaman Sea and the Gulf of Thailand, are pursued by a mixed fleet of light-fishing vessels, trawlers and other vessels to catch loliginid squid, cuttlefish and octopuses (Chotiyaputta 1993). Although light-fishing is the most effective means of catching squid (*Loligo chinensis* and *L. duvauceli*), a proportion of the light-fishery also catches pelagic fish.

Taken together, the tropical Sunda–Arafura Shelves region, which includes the shelf areas of the South China Sea, Sulu Sea, Gulf of Thailand and Andaman Sea, is the largest shelf area in the world ocean. It is unusually shallow, and has complex tidal dynamics and high sediment input from rivers. The dominant oceanographic influence is the reversal of flow between the Pacific and Indian Oceans driven by the seasonally reversing monsoon winds. Little is known about the interactions between the large-scale oceanography of the region and the cephalopod stocks.

18.4 Interactions between mesoscale oceanography and fisheries

As discussed above, biological productivity is directly affected by the mesoscale physical structure of the ocean (Mann & Lazier 1991). In particular, meanders, eddies, core rings and jets associated with frontal systems, especially in the high-velocity WBCs, give rise to increased primary production, advection of zooplankton, especially into warm core rings, and enhanced secondary production. These productive features are important in influencing the distribution of squid, especially ommastrephids. Examples include *Todarodes pacificus* and *Ommastrephes bartrami* in the Kuroshio system (Sugimoto & Tameishi 1992), *Ommastrephes bartrami* in the East Australia Current (Brandt 1983; Wadley and Lu 1983), *Illex argentinus* in the south Atlantic (Waluda *et al.* 2001), *Illex illecebrosus* in the Gulf Stream (Rowell *et al.* 1984) and *Martialia hyadesi* in the Antarctic polar frontal system (González *et al.* 1997).

The same mesoscale features are also important in attracting concentrations of higher oceanic predators of squid such as sperm whales (Waring *et al.* 1993). The distribution of swordfish (*Xiphias gladius*), skipjack tuna (*Katsuwonus pelamis*) and albacore tuna (*Thunnus alalunga*) have been shown to be related to frontal features off the coast of California (Laurs *et al.* 1984; Fielder & Bernard 1987; Podestá *et al.* 1993). Bluefin tuna (*Thunnus maccoyii*) and albacore have also been found in association with mesoscale features off the east coast of Tasmania (Reddy *et al.* 1995), and Pacific saury (*Coloabis saira*) have been located in association with warm-core rings in the Kuroshio Current system (Saitoh *et al.* 1986; Sugimoto &Tameishi 1992).

18.4.1.1 Todarodes pacificus and Ommastrephes bartrami

Warm core rings and streamers are characteristic features of the Kuroshio Current system at its confluence with the Oyashio Current off the east coast of Japan and the warm Tsushima Current and the cold Liman Current in the Sea of Japan. Core rings can be up to 200 km in diameter, although smaller, more short-lived, rings of about 100 km diameter also develop. These rings move in the prevailing direction of the current and have a lifetime of from a few months to 1–2 years. Detailed analyses of the relationships between these features and the fisheries for *Todarodes pacificus* and *Ommastrephes bartrami* have been carried out by Sugimoto & Tameishi (1992), who overlaid spatial data from the fisheries on to Mercator projections of NOAA AVHRR satellite images of sea surface temperatures. In each case, the squid fishery developed in the warm, not the cold, structures, and once a fishery had developed in a core ring the vessels continued to catch squid in the feature for up to 2 months.

18.4.1.2 Illex argentinus

The fishery for *I. argentinus* on the Patagonian Shelf operates in coastal and shelf waters, particularly near the edge of the shelf north of 52°S. A large proportion of the catch is taken over the southern Patagonian Shelf, in the vicinity of the Falkland

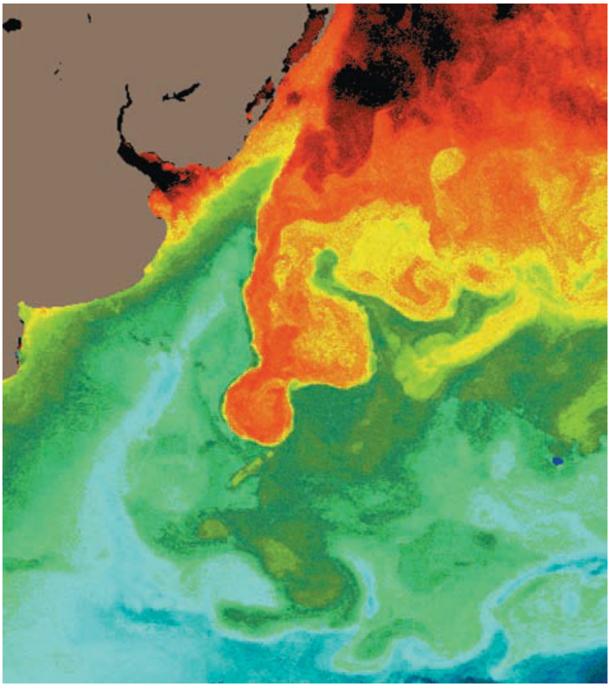


Plate 1 Infrared image of core rings associated with the frontal system of a western boundary current (Brazil Current).

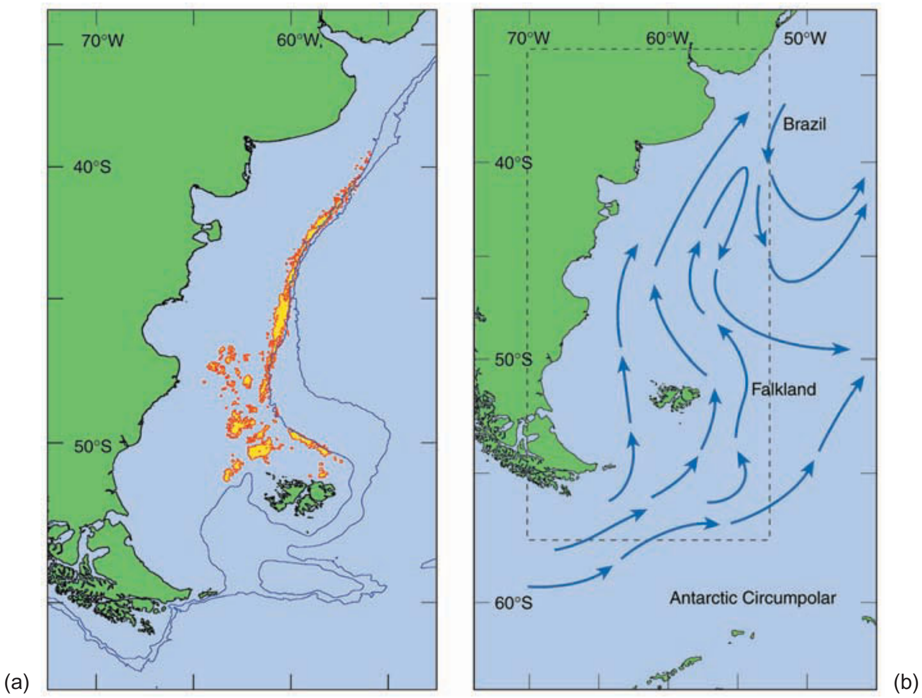


Plate 2 (a) Composite satellite image of the fishing lights on the Patagonian Shelf off the coasts of Argentina and the Falkland (Malvinas) Islands for the period October 1994 to March 1995 (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline) from fleets fishing for *Illex argentinus*. (b) The main track of the Falkland and Brazil Currents along the shelf edge are shown by blue arrows.

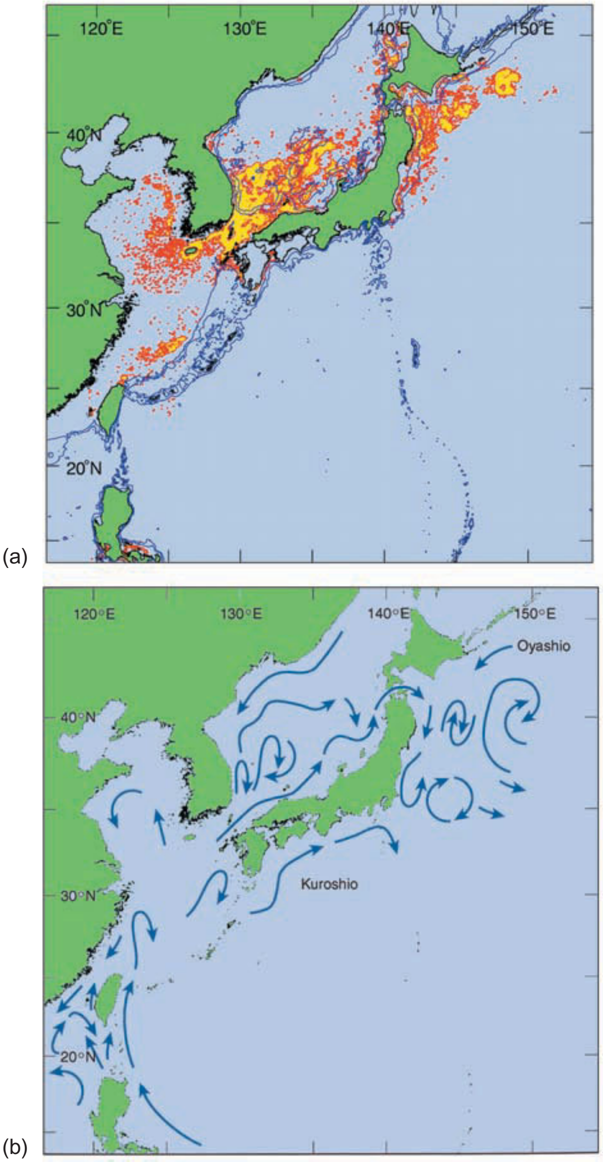


Plate 3 (a) Composite satellite image of the fishing lights of vessels fishing primarily for *Todarodes pacificus* off the coasts of Japan for the period October 1994 to March 1995 (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline). (b) Main current patterns the Kuroshio and Oyashio and the Sea of Japan are shown by blue arrows.

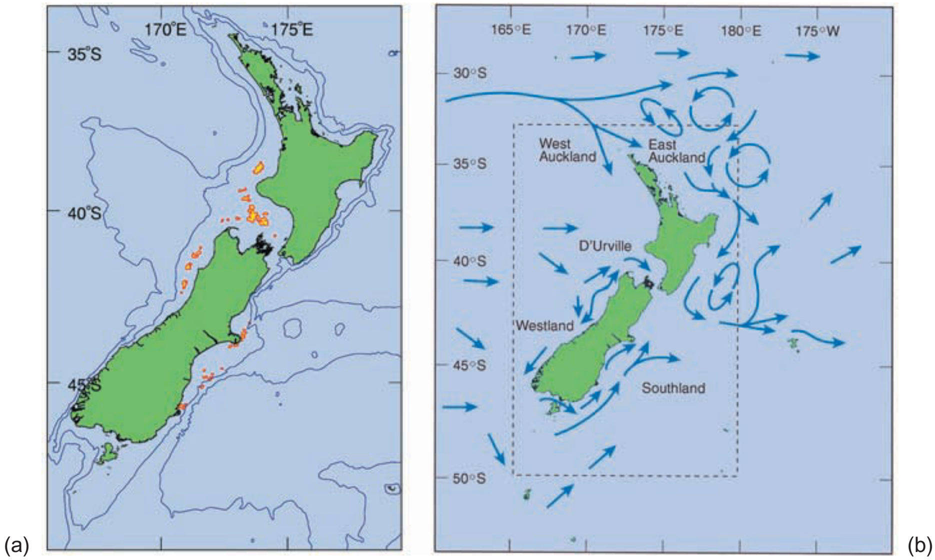


Plate 4 (a) Composite satellite image of fishing lights off New Zealand for the period October 1994 to March 1995 from vessels targeting the southern arrow squids *Nototodarus* spp. (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline). (b) Some of the principal component currents of the regional oceanography are shown by blue arrows.

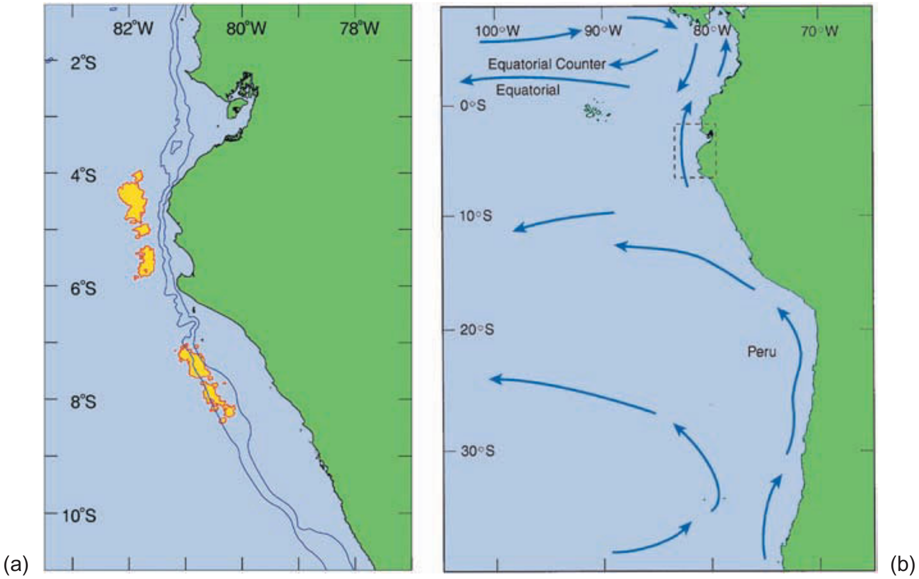


Plate 5 (a) Composite satellite image of fishing lights off Peru in the Humboldt Current (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline) for the period October 1994 to March 1995. (b) The northward upwelling flow of the Humbolt Current and westwards drift of the Equatorial counter current are shown by blue arrows.

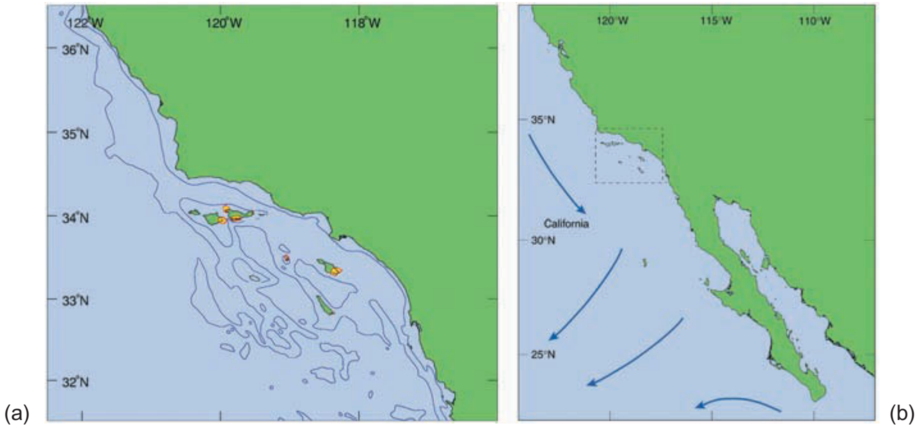


Plate 6 (a) Fishing lights off the coast of California from March 1996 to January/February 1997, visualised by composite satellite imagery (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline). (b) The southward flow of the California Current is shown with blue arrows.

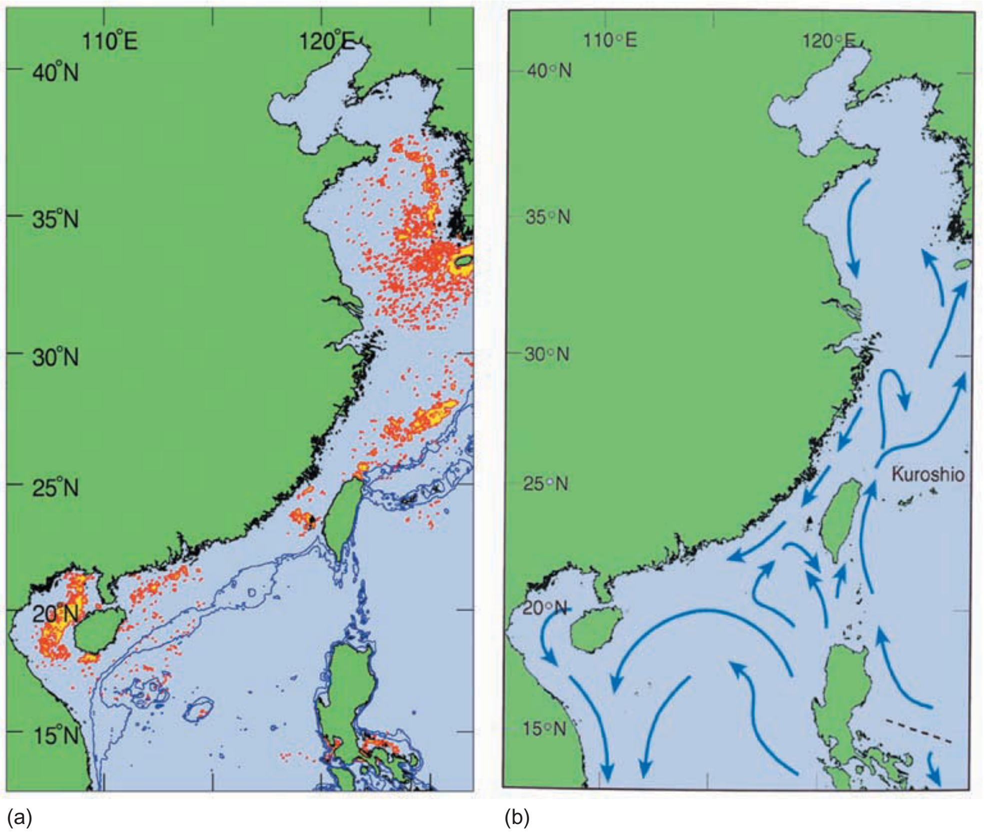


Plate 7 (a) Fishing lights visualised by satellite imagery for the period October 1994 to March 1995 in the China Sea Shelf province from the Yellow Sea and coasts of Vietnam (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline). (b) Some of the current patterns of the Kuroshio and associated currents over the shallow shelf are shown by blue arrows.

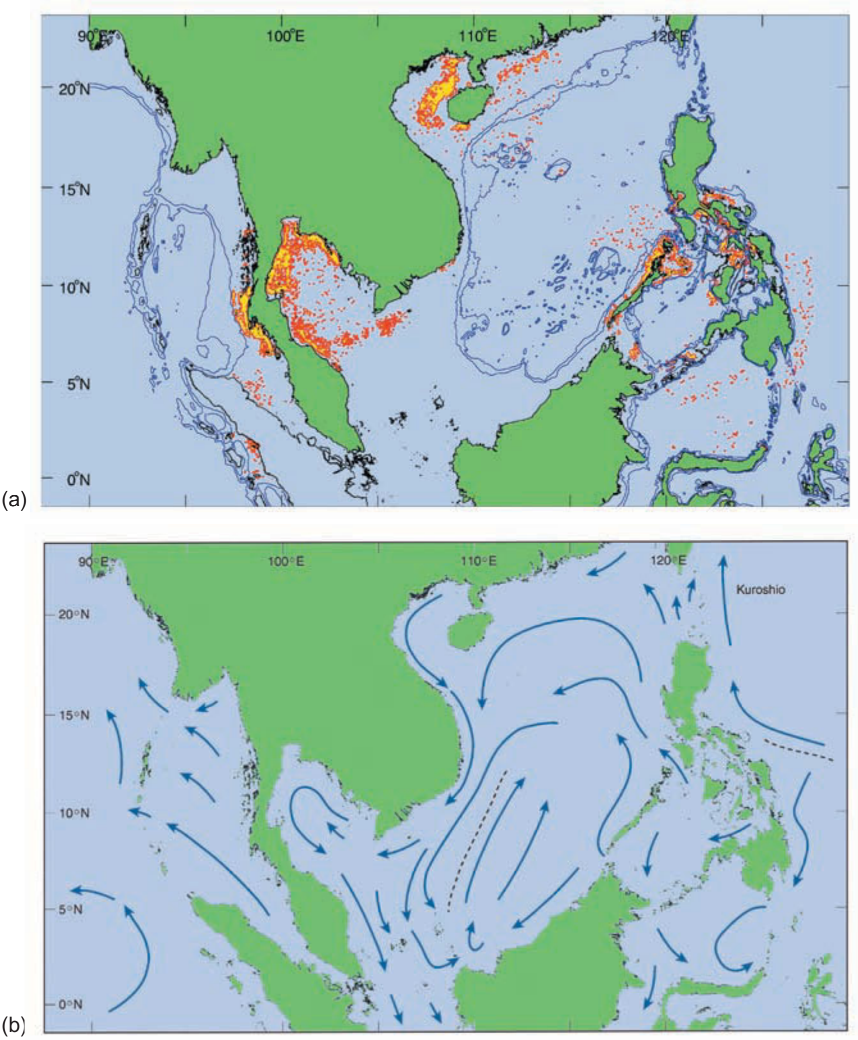


Plate 8 (a) Composite satellite image of intensive fishing with lights, mostly for cephalopods of many species, on the Sunda–Arafura Shelf for the period October 1994 to March 1995 (200 m and 1000 m bathymetric contours shown in blue; area lit by fishing lights shown in yellow with a red outline). (b) Some of the dominant current patterns of this complex region bounded between the Indian and Pacific oceans are shown by blue arrows.

Plate 9 Squid traps on the beach in Thailand (photograph courtesy of Jaruwat Nabhitabhata).

Plate 10 A successful fisher of octopus (*Octopus cyanea*) in Tanzania (photograph courtesy of Martin Guard).

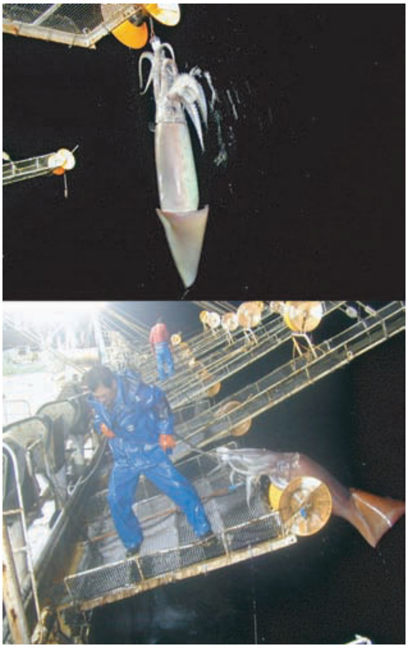


Plate 11 The Humbolt Current squid (*Dosidicus gigas*) caught off Peru (photograph courtesy of Carmen Yamashiro).

Plate 12 Prepared octopus for the market in Fiji (photograph courtesy of Martyn Gorman).

Islands. In a study by Waluda *et al.* (2001), an analysis of SST images of the southern Patagonian Shelf suggested that mesoscale oceanography in the area was reasonably consistent over a 4-year period, and was dominated by the presence of warm Patagonian Shelf water and cooler water from the Falkland (Malvinas) Current. The boundary between cold Falkland current water and warmer Patagonian Shelf coastal water was clearly visible on all the images and was the location of easily identified thermal gradients which could be located automatically using a geographical information system (GIS). Thermal gradients in the surface oceanography are thus consistent features in the seas around the Falkland Islands, and a correlation analysis demonstrated that the location of vessels and the catch rates of *I. argentinus* were associated with the presence of these gradients. The higher squid abundance in these mesoscale features is probably related to high food availability. *I. argentinus* is an opportunistic predator, and in the southern Patagonian Shelf feeds primarily on small crustaceans such as euphausiids and amphipods which aggregate in productive frontal features.

18.4.1.3 Illex illecebrosus

The larvae and juveniles of *Illex illecebrosus* are concentrated mainly in a narrow extended ribbon of water centred along the frontal system separating the slope water off the continental shelf of the eastern seaboard of North America and the waters of the high-velocity Gulf Stream (Rowell *et al.* 1984). The physical environment is probably a major factor determining juvenile distribution in this species, as the Gulf Stream provides a rapid transport system (up to 1000 km per week) from the spawning grounds which lie off the southern states of the USA to the feeding grounds off the northern States and Canada, where most growth and sexual maturation takes place.

18.4.1.4 Martialia hyadesi

Information on mesoscale distribution of *M. hyadesi* comes from studies in the southwest Atlantic. This is an area with a high incidence of mesoscale eddies with dimensions measured in tens of kilometres (Peterson & Whitworth 1989), which are implicated in the generation of phytoplankton blooms and zooplankton concentrations. Shipboard research, which sampled squid using research and commercial nets, has demonstrated concentrations of *M. hyadesi* feeding on mesopelagic fishes and epipelagic crustaceans associated with an eddy structure in the APFZ (Rodhouse *et al.* 1996).

M. hyadesi concentrations also appear to be associated with mesoscale oceanographic features at the interface of the open ocean and the slope of the Patagonian Shelf. The unusually high catches taken on the edge of the shelf in 1995 were associated with mesoscale features where the SAF runs parallel to the north/south orientated continental slope (González *et al.* 1997). Similarly, in the austral winter of 1996, *M. hyadesi* was found in high densities close to the South Georgia shelf edge near the 1000 m bathymetric contour (González & Rodhouse 1998).

A common feature of these observations has been that the mesoscale features at the surface with which concentrations of *M. hyadesi* have been associated are found in the vicinity of bathymetric features at depth. In the case of the open ocean at the APFZ north of South Georgia these were deep features on the North Scotia Arc, while elsewhere they were associated with the rise of the continental slope. Records of *M. hyadesi* close to the sub-Antarctic Kerguelen Islands and Macquarie Island (Cherel & Weimerskirch 1995; O'Sullivan *et al.* 1983) suggest that concentrations may also be present in association with bathymetric features in the Indian Ocean and Pacific sectors. The implication of this apparent connection between bathymetry, mesoscale oceanography and *M. hyadesi* is that the squid may concentrate in more or less predictable areas when abundant.

18.5 Oceanic variability and recruitment processes

18.5.1.1 Ommastrephid squid

Bakun & Csirke (1998) have proposed a set of hypotheses about how the variability in ocean ecosystems might cause interannual variability in the stocks of ommastrephid squids that inhabit the major western boundary current systems of the world's oceans. They propose that recruitment may be dependent on one or more of: (a) wind effects, with onshore, wind-driven Ekman transport being favourable to both onshore transport of surface-dwelling larvae and offshore migration of pre-adults in the sub-pycnocline layers; (b) fluctuations in prey abundance; (c) 'match–mismatch' effects driven by temperature, as proposed for fish stocks by Cushing (1982); (d) variations in predation pressure; (e) disease.

In the South Atlantic, Waluda *et al.* (2001) have shown by analyses of remotely sensed sea-surface temperature (SST) data that about 55% of variability in recruitment strength in the Falkland Islands *Illex argentinus* fishery can be explained by the variation in the total area of surface water of putative optimum temperature for larval development on the spawning grounds during the spawning season prior to recruitment. The species spawns in the vicinity of the Brazil/Falkland (Malvinas) Current confluence off the edge of the continental shelf at the northern limit of the Patagonian Shelf. The SST conditions that predict strong recruitment are also associated with a reduced incidence of horizontal temperature gradients (3°C over 15 km) in the spawning area. Furthermore, SST variability in the South Atlantic has teleconnections with ENSO events in the Pacific, so it is reasonable to conclude that variability in the *Illex argentinus* population probably has links back to the ENSO (Waluda *et al.* 1999).

18.5.1.2 Illex illecebrosus

Dawe & Warren (1993) have shown that recruitment strength in *Illex illecebrosus* in the northwest Atlantic during the period of commercial fishing by jiggers in the 1970s–1980s was linked to oceanographic variability. They used sightings of icebergs by the Canadian Coastguard off Newfoundland as an index of the relative influence of the Labrador Current. They found that during years of greater influence of the current, recruitment of *Illex illecebrosus* into the Canadian fishery was reduced and catch rates were less than in other years.

Further analyses of decadal data sets (Dawe *et al.* 2000) have shown that the abundance of *Illex illecebrosus* has been positively related to a favourable oceanographic regime associated with a negative north Atlantic oscillation (NAO) index, giving rise to weak winter northwesterly winds, high sea temperatures off Newfoundland, and a southward shift in the position of the Gulf Stream and the boundary between the shelf waters and the offshore shelf waters. Furthermore, any increased meandering of the Gulf Stream appears to promote increased abundance, probably through enhanced shoreward transport of squid.

Environmental relationships with squid abundance thus appear to reflect the effects of broad-scale winter atmospheric circulation patterns in the dynamics of the Gulf Stream, which largely regulate the year-class strength of the dominant winter-spawning group of squid early in their life cycle.

18.5.1.3 Todarodes pacificus

Variability in abundance of *Todarodes pacificus* in the Sea of Japan has been shown to be driven by changes in the area of ocean at the optimum SST for larval development (Bower *et al.* 1999a; Sakurai *et al.* 2000). In this region, oceanographic variability occurs on a decadal time scale and is apparently linked to large-scale climate changes in the north Pacific. The ecosystem varies, in turn shifting from a regime dominated by squid (*Todarodes pacificus*) to one dominated by Japanese sardine.

18.5.1.4 Loliginid squid

In contrast to the ommastrephid squid discussed above, the life cycles of loliginid squid are not linked in the same way to basin-scale oceanic circulation, probably because their life-style is much more closely linked to the sea bed. Nevertheless, variability in *Loligo vulgaris vulgaris* in the English Channel has been shown to be correlated with inter-annual changes in SST conditions (Robin & Denis 1999), and in South Africa, variable abundance of another loliginid squid, *Loligo vulgaris reynaudi*, is apparently driven by storm events during the spawning season. Storms at this time (Sauer *et al.* 1991) reduce underwater visibility on the spawning grounds and reduce breeding success (Roberts & Sauer 1994; Roberts 1998). The explanation for this is that squid possess excellent eyesight and have evolved ritualised mating behaviour which is dependent on being able to read the ‘body language’ of potential mates (Sauer *et al.* 1997). After storm events, underwater visibility is poor so mating success is reduced, and this in turn has a negative effect on the spawning success of the population.

In another study of variable recruitment strength, Agnew *et al.* (2000) have shown that 66% of the variance in recruitment strength in *Loligo gahi* in the southwest Atlantic can be explained by sea-surface temperatures 6 months prior to recruitment. Furthermore, a model combining SST and size of spawning stock explained 77% of the variance, with very high spawning stock biomass apparently leading to a reduction in recruitment strength and suggesting a density-dependent effect. This seems paradoxical, because density-dependent effects, in fish stocks for instance, are caused by cannibalism, hence the Ricker stock recruitment model (Ricker 1954). However, in squid such as *L. gahi*, the parent generation dies after spawning and is therefore not present to cannibalise the next generation as the individuals grow, so the density-dependent mechanism must presumably be different.

The highly variable fishery for *L. opalescens* in the California Current system is apparently linked to ENSO events which have as profound an effect in this system as in the Peru Current of the western coast of South America (McInnes & Broenkow 1978).

18.6 Operational fisheries oceanography

The relationship between pelagic fish stocks and mesoscale oceanography is exploited by commercial and sport fisheries to aid the location of resources. Remotely sensed images with information such as sea-surface temperature and surface chlorophyll concentrations, with fitted contours and overlaid onto bathymetric charts, are available on the World Wide Web and can be downloaded by vessels fishing at sea and used to increase their efficiency. Given the information already available about the relationships between pelagic squid stocks (primarily the ommastrephids) and mesoscale oceanographic features that can be visualised in remote-sensing imagery, the opportunity undoubtedly exists to extend the use of remote-sensing technology to the cephalopod fishing industry for operational purposes.

Furthermore, the ability of environmental fishery models to forecast recruitment, at least in exceptional years (Bostanci 2002), suggests that in future it may be possible to set the level of fishing effort in squid fisheries on the basis of scientifically predicted levels of abundance in advance of recruitment of the squid into the fishery. Agnew *et al.* (1998b, 2002) have developed an approach which may allow for an increased catch while at the same time reducing the possibility of overexploiting the fishery.

Chapter 19

Assessment and management

Summary: The assessment and management of fished cephalopod populations is a relatively undeveloped field. An unresolved issue is whether cephalopods (especially squid) may be treated in the same way as fish for assessment purposes and thus become subject to the range of methods traditionally applied to finfish. As a consequence, most of the methods of assessment applicable to finfish fisheries have been tried out on cephalopods in one place or another, but no standard approach has resulted. The most obvious difficulty in treating cephalopods like most fish is their universally short lifespan and generally single year-class population, which is totally dependent on recruitment success in the fishing year. Fishing and acoustic surveys, egg and larval production estimates, and mark–recapture data have all contributed to assessment methods. Depletion of the stock during the fishing season, usually monitored from changes in the catch per unit effort (CPUE) throughout the season, has been consistently measured in a number of fished populations. These data have allowed the application of the Leslie–DeLury method to estimate the size of the stock at the beginning of each fishing season. Estimation by this method allows the introduction of management measures aimed at allowing a fixed proportion (40%), or an absolute quantity, of the stock to escape from fishing. Despite the obvious difficulties introduced by immigration to, and emigration from, the fished stock, the Leslie–DeLury method is currently the most widely used assessment approach for management. Long runs of catch information allow the development of empirical models predicting the availability in some fisheries from environmental information such as sea-surface temperature (SST), indices of coastal upwelling, and even large-scale climatic fluctuations such as the north Atlantic oscillation index (NAO) and El Niño–southern oscillation (ENSO) events. Indirect evidence of cephalopod abundance from predator diet is also being used for assessment purposes (*Martialia hyadesi*) and for the setting of catch limits for the species while maintaining their availability to top predators.

Controlled exploitation of any potential resource species by fishing requires knowledge of its basic biological characteristics, effective methods for the quantitative assessment of the population size, composition and distribution, and an understanding of the likely effects of exploitation.

Key features of the target species, such as growth rate, lifespan and the timing of reproduction and recruitment, are clearly important to the numbers and biomass of the stock. Exploited cephalopods show some consistent biological characteristics (high growth rate, short lifespan, single breeding) which are directly relevant to their availability to fishing. The varying physical environment and their biological interactions with other species in the sea are likely to cause wide fluctuations in populations of cephalopods. Environmental variability is critical, particularly as it affects recruitment and the relative success of the young stages in joining the adult population, and is always an important factor in assessment methodology on intra- and inter-annual timescales. Cephalopods, with their semelparous breeding pattern with little overlap between generations, are particularly vulnerable with respect to environmental factors affecting recruitment. A good year for survival and growth of the juveniles can lead to a massive increase in the population available for fishing; conversely a bad year results in a minimal stock and an apparent crash in yield from fishing. This exposure to environmental fluctuations undermines the value of straightforward stock assessment procedures for cephalopods.

The impact of the fishing activity itself must also be considered for its effect on the long-term health of the target population. This has to be measured firstly in terms of the direct result of subtraction by fishing on the natural population. Are the fished individuals surplus to the population? Do they represent sustainable production? Are the key individual stages at breeding and recruitment harmed? Evidence is available from most of the world's productive fishing areas that populations of many of the traditional fish and invertebrate resource species are significantly over-exploited. Finally, the method of fishing itself commonly impacts heavily on non-target species, i.e. those that are taken and killed accidentally (e.g. the marine mammal catch by drift netting for cephalopods, see Chapter 16). Even the structure of the environment itself may possibly be damaged by fishing operations, for example, the disruption of the sediment structure and its relationship with the macrofauna by heavy bottom trawling (Frid *et al.* 1999). These effects, in turn, impact on the fished target population through environmental degradation and their trophic links to other components of the ecosystem.

19.1 Assessment methods applied to cephalopods

For most of the history of scientific fisheries management, the overall aim has been simply to fish the stock at maximum yield, consistent with long-term availability and without obvious damage to other species or the habitat. The aim of assessment has been to provide population data sufficient to set the level of fishing effort. A series of reports, especially those arising from expert groups of the Food and Agriculture Organization of the United Nations (FAO), have reviewed the general and specific problems of fishery assessment and management for cephalopods (Caddy 1983a; Okutani 1977; Rathjen & Voss 1987; Rodhouse *et al.* 1998b; Saville 1987; Voss 1973, 1983). In the present day, the aims of fishery management extend to biological, environmental, economic, social and institutional sustainability.

The long history of fish stock assessment has meant that fishery scientists and managers, have tended to treat cephalopods, especially squid, in the same ways as fish. Adopting this approach has the advantage of allowing the application of several standard methods for the population assessment of exploited fish species (Pauly 1985). In his seminal review of the subject, Caddy (1983b) discusses many of the specific issues surrounding the assessment of cephalopod stocks and why they can be treated as other short-lived species. Compared with fish, of course, the general understanding of their biology and ecological roles is weak. Perhaps the most obvious difficulty in treating cephalopods in the same way as fish for the purposes of assessment is their short lifespan and single breeding. This means that the time available to assess and respond to changes in population biology is very short when compared with more conventional multi-age fish populations. The lack of overlap of generations, and the dependence of the fished population in any year on the annual recruitment, is also a problem because it reduces even further the chance of predicting the scale of future fishery success from the current catch. Controversially, there is little agreement as to the general form of cephalopod growth; specifically as to whether asymptotic or final adult size is reached (Forsythe & Van Heukelem 1987; Rodhouse 1998b), or even whether this matters

(Pauly 1998). Together with the weak estimation of 'size at maturity' in cephalopods, these uncertainties further undermine the usefulness of standard stock assessment methodologies.

Assessment methods applied to cephalopod stocks were reviewed by Pierce & Guerra (1994). Three general categories may be recognised based on the timing of their application in the fishing season:

- *pre-season assessment* using survey methods;
- *in-season assessment* makes use of (incomplete) data as they are collected and may be used to adjust levels of fishing activity during the fishing season;
- *post-season assessment* is based on complete data collected from the fishing season(s) and, especially when several years' data are available, may be used to examine the relationships between variables (e.g. environmental conditions, stock recruitment), to estimate stock size in the following season and to establish management goals.

The conventional approaches to the assessment of fisheries are based on the collection of supporting data of a variety of different forms (see Fogarty 1989; Hilborn & Walters 1992; Jennings *et al.* 2001). These data may be used either to give direct estimates of population abundance and availability to fishing, or to contribute to indices of the likely future success of the population.

Fishing surveys: These use actual or modified fishing gear to sample the population directly and estimate abundance. The sampling design of surveys may be random, throughout the fishing area; stratified, sampling within pre-determined areas and combining estimates; or systemic using a regular grid design. Each design has some inherent bias, and several approaches are often used for important finfish stocks. Examples of these direct approaches for cephalopods are the US National Marine Fisheries Surveys for *Loligo pealei* in the northwest Atlantic, and the *Illex argentinus* surveys in the south Atlantic. Use has also been made of data arising incidentally from surveys of bottom fish (Pierce *et al.* 1998; Robin *et al.* 1998).

Acoustic surveys: The application of acoustic survey methods to cephalopod stocks has been limited in the past, partly because they are not particularly strong targets for detection with echosounders. In recent years, experience with other invertebrates that have weaker target strength than cephalopods has shown that it is possible to use acoustics to survey them effectively, especially when the target species form dense aggregations (Starr & Thorne 1998). Squid have been detected acoustically in different geographical locations, and in surveys of the *Loligo gahi* fishery in the Falkland Islands (Malvinas), this species has been shown to be distinguishable acoustically from finfish present in the same area (Goss *et al.* 2001). When a species has been characterised acoustically, this technique permits rapid surveys of large areas to determine the biomass and geographic range of a population, both within the fishing grounds and in areas that are inaccessible to nets. There appears to be scope for expanding acoustic surveys of cephalopod populations, but more data collected with trawls in conjunction with echosounders are needed to confirm the acoustic properties of aggregations of different squid species.

Depletion by fishing: During the fishing season the abundance of the fished population is reduced. Over the short-term, the change in catch rate during the season may be used to predict the abundance in the fished stock at the start of fishing and its depletion over the season. This method, originally due to Leslie & Davis (1939) and DeLury (1947), is strictly applicable to 'closed' populations only, i.e. without immigration and emigration. When such a population is fished, the population at time $t(N_t)$ will equal the population at the beginning of the fishing season, time $t = 1(N_1)$ less the cumulative catch up to time $t(K_t)$.

$$N_t = N_1 - K_t$$

Because the Leslie–DeLury method is operable with data collected over the short time-periods of a single fishing season (Caddy 1983b), it has been applied to several cephalopod stocks, although the strict limitations of use to 'closed populations' introduces considerable uncertainty (see below).

Egg/larval surveys: Data on the abundance of eggs and larvae have been used to estimate the abundance of spawning animals. Based on detailed information on life history, fecundity and spawning, survey data are synthesised to provide estimates of daily or seasonal egg production and, in turn, to estimate spawning stock for assessment purposes. The biomass (B) of the spawning stock is calculated from the estimate of total egg production (P), the individual female fecundity (F) as number of eggs spawned per unit weight of female, and the sex ratio (R) of spawning females in the total population (all males and all females).

$$B = P/(FR)$$

Such surveys have been used in a modified form based on diver surveys of spawned egg masses for the squid *Loligo vulgaris reynaudi* (Sauer *et al.* 1993) and plankton tows of larvae for *Todarodes pacificus* (Okutani & Watanabe 1983) to estimate the early-season spawning stock.

The stock size of *Todarodes pacificus* historically available to fishing has shown large-scale fluctuations. Using catch per unit effort (CPUE) as the estimate of stock size, Okutani & Watanabe (1983) examined the larval abundance of the preceding year from 1960 to 1976. The results were contradictory and inconclusive; despite large stock size, larval production and recruitment were sometimes very low; in contrast, very low stock size has produced an exceptionally high larval abundance. Poor survival and recruitment led to continued low stock size and decreased larval abundance. The correlation between stock size (CPUE) and subsequent larval abundance was not consistent, and was apparently inconsequential compared with the vulnerability of the annual recruitment phase to environmental variability.

Mark–recapture data: Tags are used to mark individuals of the target species, and the marked animals are then released back into the source population. This approach is highly successful as a method of abundance estimation for terrestrial animals and fish in relatively enclosed areas. It is assumed that the tagged fish mix randomly with the untagged population, and that they all have the same mortality rates, migration characteristics and catchability. Re-sampling allows the abundance (N) to be estimated from the number of fish tagged (T) and recaptured (R) in the catch (C).

$$N = TC/R$$

Very extensive tagging and marking studies have been carried out on cephalopods, particularly in Japanese waters (Nagasawa *et al.* 1993) and elsewhere (Sauer *et al.* 2000), but generally the results of these surveys have been used for studies on distribution and migrations rather than population estimation.

19.1.1 Depletion estimates of stock size

The annual migratory habits of most of the larger fished stocks create special problems of fluctuating availability to fisheries and consequent uncertain assessment of populations. Caddy (1983b) laid the foundation for understanding the significance of these fluctuating population, and pointed the way to the use of one of the common assessment methods for cephalopod fisheries – the Leslie–DeLury depletion method, applied in real-time during the short fishing season.

The standard Leslie–DeLury approach is applicable only during the limited period of the main fishing season (Phase II, Fig. 19.1), and assumes that there is no immigration to or emigration from the target population, that mortality is only due to fishing, and that the catchability (catch per unit effort, CPUE) of the stock is proportional to population abundance. Generally these assumptions can only be met over rather limited geographic areas and timespans where there is reasonably complete monitoring of

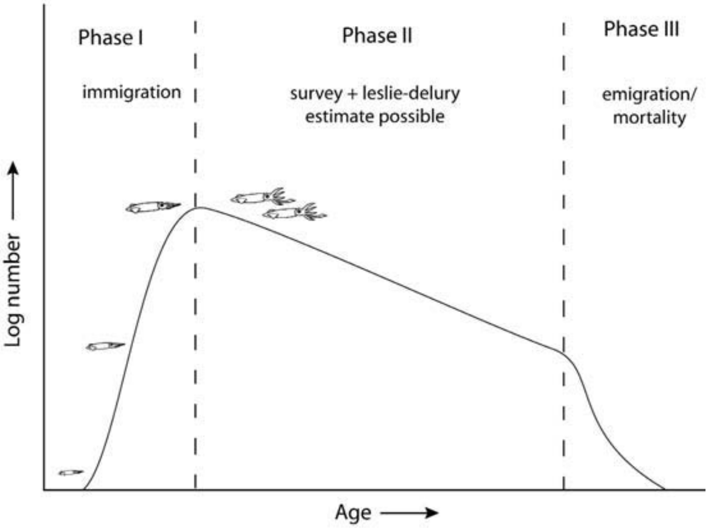


Fig. 19.1 Schematic diagram illustrating three phases of availability to fishing during the short life cycle of a migratory cephalopod species (after Caddy 1983b, 1991). Phase I: there is immigration into the fishing grounds supplemented by an increased selection of larger animals due to growth. Phase II: full recruitment to the fishing grounds has occurred, there is a steady decline in the population due to natural and fishing mortality. Phase III: emigration away from the fishing ground occurs and/or catastrophic post-spawning mortality.

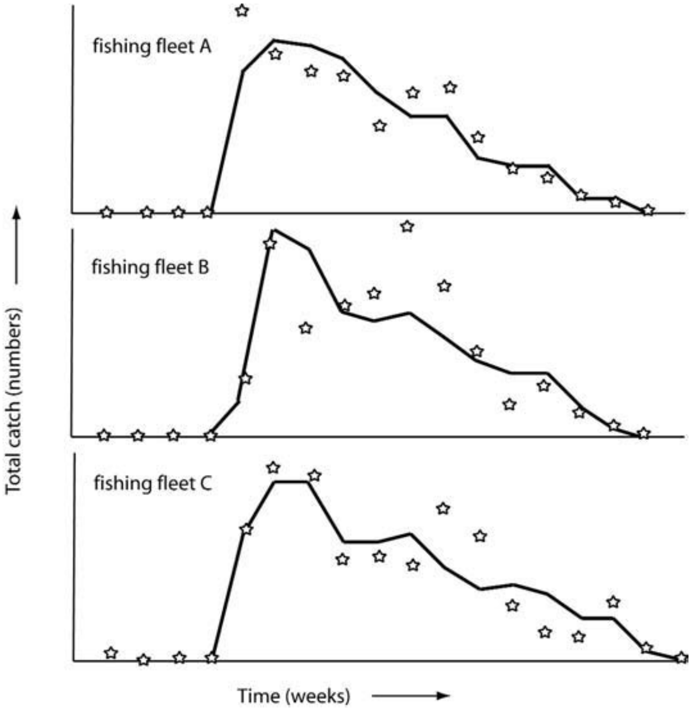


Fig. 19.2 Fitted (solid line) and observed (✩) catch (numbers) of *Illex argentinus* taken in the Falkland Islands fishery in 1987 for three major jig-fishing fleets (A, B and C) show good agreement (after Rosenberg *et al.* 1990).

fishing activity. Such conditions arose for the south Atlantic fishery for *Illex argentinus* in waters over the Patagonian Shelf surrounding the Falkland Islands (Malvinas) in 1987, when an interim conservation zone of 150 mile radius around the islands was declared (the FICZ). This situation allowed for the close monitoring of the catch and fishing effort of all vessels involved in jig-fishing for *I. argentinus* within this zone.

Specifically for this fishery, the Leslie–DeLury methodology was developed by Rosenberg *et al.* (1990) to include an estimate for natural mortality, as well as the accumulation of datasets from several fishing fleets in the FICZ. Provided each fishing fleet was relatively homogeneous in composition, the CPUE reached a peak a few weeks after the start of the fishing season and then entered a smooth decline, during which the assumption was made that the CPUE was proportional to absolute stock abundance (Fig. 19.2).

The use of depletion estimates has been examined in a few stocks of fished squid such as the inshore *Loligo pealei* fishery off Cape Cod (Brodziak & Rosenberg 1993). Perhaps because of the tight control of fishing in the Falkland Islands Interim Conservation Zone, the fisheries there for *Illex argentinus* and *Loligo gahi* (Hatfield & Des Clers 1998) remain the sole examples of cephalopod stocks where a consistent assessment method has been used over many years and applied directly to their management. Nevertheless, for one of the species, *Illex argentinus*, the approach is applied only within a sector of the total migratory route of the species (see below and

Chapter 18) and for part of the annual life cycle. For the rest of the life cycle, catches are made outside the zone managed by the Falkland Islands Government (Waluda *et al.* 2002).

19.1.2 Other stock assessment methods

Although the Leslie–DeLury depletion method of stock estimation has proved popular, almost every type of assessment methodology used for fish species has been attempted on cephalopod stocks. The applicability and value of some of these methods is concisely reviewed by Pierce & Guerra (1994), from which the following summary is drawn.

Stock–recruitment relationship: It is an underlying assumption of the most widely used stock–recruitment models (Ricker 1954; Beverton & Holt 1957) that a fixed relationship exists between the stock size in one year and recruitment in the following year. Measures of both parameters over several years are needed to establish any relationship, which, for an annual species, may be the only way of predicting stock size for the current year. Using proxy data for stock size (CPUE) for comparison with annual plankton larval surveys in *Todarodes pacificus*, Okutani & Watanabe (1983) reported inconsistent results (see egg/larval surveys above), although extending the pre-fishing surveys to include experimental jigging for juveniles strengthened the relationship (Murata 1989).

The reality is that for most cephalopod populations, any stock–recruitment model is usually so weak as to be useless for assessment purposes. However, there will be a point in any population at which the spawning stock becomes so low that recruitment is affected.

Surplus production models: Attempts have been made to identify the largest fishing mortality rate that can be sustained by growth in the population biomass. Alternatively termed ‘production models’, ‘stock production models’, ‘surplus yield models’ or ‘biomass dynamic models’ (Jennings *et al.* 2001), the principle is to determine the ‘surplus’ of production that can be harvested sustainably. Although fish populations fluctuate widely, the model can be applied using time-series data on catches and abundance (normally using catch per unit effort as the index of abundance). Pierce & Guerra (1994) refer to several applications of surplus production modelling to cephalopod populations. They point out, however, that a strong stock–recruitment relationships and density-dependent population dynamics are implied by the model making it of doubtful value in highly variable cephalopod populations in which recruitment depends to such a large extent on environmental conditions.

Cohort analysis: In conventional fisheries assessment there is an assumption that the population is composed of more-or-less discrete cohorts of animals of increasing size and in sequential age. Direct-ageing methods based on otoliths or scales can be used to generate a key to the age–length relationship. In cephalopods, as we have already seen, the short annual life cycle (see Chapter 6) means that most of the commercial fisheries exploit the single annual recruitment of that year, and there is no multi-annual population. Measurements of large numbers of individuals throughout the recruitment season, and the use of statolith ring counts to provide age estimates (days), allows the resolution of the population into a series of intra-annual microcohorts distinguished by size or age (see Chapter 13). This refinement does not routinely allow the application of cohort analysis and yield-per-recruit models, because estimates of initial recruitment (N_0), fishing mortality (F_t) and natural mortality (M) would be required for each of the microcohorts. The practicalities of the routine reading of statoliths which would be required for age estimates in real time during the characteristically short season in most cephalopod fisheries means this approach is not feasible in most situations.

Pierce & Guerra (1994) reviewed a number of cases in which length-based cohort analysis has been used for cephalopods stocks, but it is clear that doubts over the validity of the approach, such as lack of a reliable length/age relationship, disputed fit of the growth pattern to the asymptotic (Bertalanffy) assumption, seasonal changes in growth rate, lack of rigour in the statistical separation of complex length–frequency micro-cohorts and the artefacts due to immigration and emigration, presently undermine the general applicability of this approach in cephalopods.

Empirical models: The difficulties of population modelling with data from short-lived species and the high responsiveness of the population to environmental variables has led some authors to seek empirical models which can relate fishery abundance to environmental variables. Physical environmental variables, such as temperature and salinity, can be routinely measured and may exert a direct effect on the animals through key life-history stages such as time to hatching of eggs, hatching success or growth rate. More likely they are proxy indicators for other variables such as the relative strength of currents, or shifts in oceanographic boundaries which affect advection of larvae and juveniles, or food supply at appropriate times.

Correlations between environmental variables and abundance in squid fisheries have been described many times. Sea-surface temperature, which may be a useful predictor of annual abundance in *Illex illecebrosus* on the Scotian Shelf (Coelho & Rosenberg 1984; Rasero 1994), showed that an abundance of *Todaropsis eblanae* in Spanish coastal waters was related to an upwelling index of physical variables, and Waluda *et al.* (1999) showed that sea-surface temperature anomalies associated with El Niño in the Pacific may be linked to recruitment of *Illex argentinus* on the Patagonian Shelf between 2 and 5 years later. El Niño–southern oscillation (ENSO) events are also considered to be linked to the large fluctuations of *Loligo vulgaris reynaudi* in the coastal waters of South Africa (Roberts & Sauer 1994).

In a series of papers on the Scottish fishery for *Loligo forbesi*, researchers (Pierce *et al.* 1994a, d; Pierce 1995; Waluda & Pierce 1998; Bellido *et al.* 2001; Pierce & Boyle 2003) have progressively developed formal modelling of catch rates to show that abundance can be related both spatially and temporally to a series of environmental indices, including the winter north Atlantic oscillation index (NAO) and average sea-surface temperature (SST), and that future catches are predictable from pre-season environmental conditions (Fig. 19.3). Robin & Denis (1999) and Denis *et al.* (2002) have

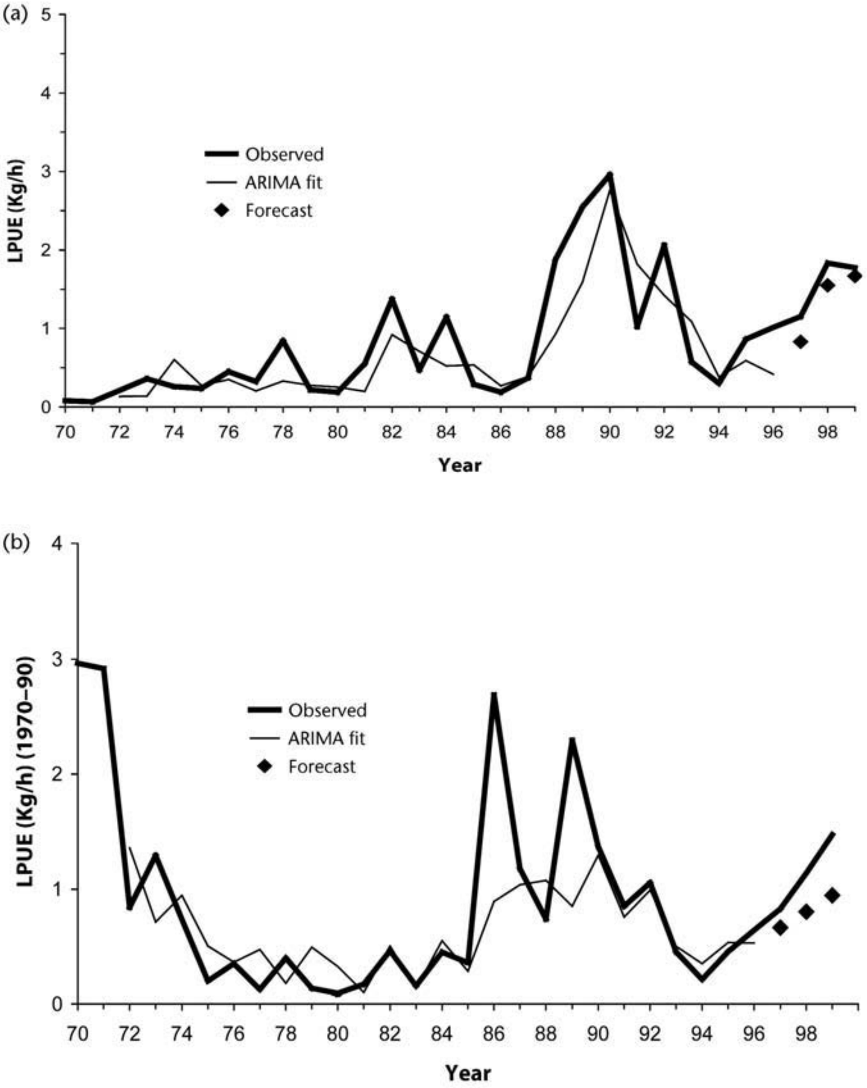


Fig. 19.3 Empirical models (ARIMA, autoregressive integrated moving average) fitted to an annual index of fishing abundance (LPUE, landing per unit effort) for *Loligo forbesi.* (a) In Scottish coastal waters (transfer function based on the May sea surface temperature in the northern North Sea with time lags of 0 and 1 year). (b) In all Scottish waters (transfer function based on the January sea surface temperature, time lag 1 year). The large error bars associated with the forecast values of LPUE for the years 1997–1999 are omitted for clarity. After Pierce & Boyle 2003.

shown that fishing-season indexes of abundance for the English Channel mixed fishery for *Loligo vulgaris* and *L. forbesi* were increased by warm conditions in the previous winter, suggesting improved early growth/survival leading to greater cohort success. The migratory pattern of *L. forbesi* into the English Channel has been shown by Sims *et al*. (2001) to be strongly influenced by climatic conditions. In years of warm (positive) phases of the NAO, the timing of peak squid abundance occurred earlier in the year and the migration advanced correspondingly further eastward. In the southwest

Atlantic, Agnew *et al.* (2002) have shown that 66% of the variance in recruitment strength in *Loligo gahi* can be explained by sea-surface temperatures occurring 6 months prior to recruitment. Furthermore, a model combining SST and spawning stock size explained 77% of the variance.

The *Loligo forbesi* fishery is a relatively small trawler by-catch, but the empirical modelling approach is beginning to be useful in larger fisheries such as that for *Illex argentinus*, in which the predictive variables are environmental conditions on the spawning grounds off the River Plate in the previous year (Waluda *et al.* 2002; Bostanci 2002). It is likely that this approach will predict years of poor recruitment better than years of strong recruitment. This is because when conditions for spawning and egg/larval survival are poor, this will inevitably lead to poor recruitment, but when conditions for the early life stages are good, there still remains the possibility that conditions affecting the later life cycle will modify the ultimate strength of recruitment.

Ecological approach: The important role of cephalopods in the food webs of higher predators leads to the possibility of using predator consumption data as a basis for stock assessment and consequential management. With a circumpolar distribution, in association with the Antarctic Polar Front, the ommastrephid squid *Martialia hyadesi* is known to be important in the diet of Southern Ocean predators, e.g. seabirds, seals and whales (see Chapter 15). For the Scotia Sea, quantitative studies on these predators has allowed estimates for the total annual consumption of the species from a conservative 245 000 tonnes to an upper estimate of 550 000 tonnes (Rodhouse 1997). As a precautionary approach, the annual permitted catch of this species has been set as a fixed proportion of the predator consumption. There is as yet no assessment or fishery for this species, but the precautionary limit set by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) is sufficiently low to ensure that any future fishery would have a negligible impact on dependent predators, and harmonises with the general ecosystem approach taken by CCAMLR.

19.2 Management of cephalopod fisheries

There is no consensus of management objectives for cephalopods. Such targets as are set are species- and location-specific, often with rather arbitrary or pragmatic quantitative limits. Most efforts at fishery management of the larger commercial stocks concentrate on the limitation or control of the period and scale of fishing effort in order to be consistent with sustainable catch levels (*Illex argentinus*, *Todarodes pacificus*, *Nototodarus sloanii* and *Loligo gahi*), although the prevention of fishing disputes and maintenance of catch prices are also motives (*Todarodes pacificus*). Spawning stocks and spawning grounds in coastal areas may be protected by closing areas to fishing for defined seasons (*Loligo vulgaris reynaudi*). A few attempts at positive habitat enhancement to promote egg deposition by benthic species can be found (*Octopus*, *Sepia*), but there is little scientific evaluation of these measures. Ecological approaches to management are beginning to emerge, in which target catches are set in relation to the resource value of the species to other components of the food web (*Martialia hyadesi*).

A range of management approaches is illustrated by the following case histories in which at least some assessment techniques and management measures have been attempted. In common with fisheries for other species, there is little evidence to suggest that the methods available are leading to catches which are sustainable over the long-term at predictable levels. These approaches should perhaps be viewed as precautionary measures intended to prevent fisheries reducing the population size to levels below which recovery is possible and which is able to absorb environmental effects.

19.2.1 Falkland Islands *Illex* fishery

The management system developed for the *Illex argentinus* jig-fishery within the Falkland Islands Conservation Zone (FICZ) and the FOCZ (Falkland Outer Conservation Zone, extending 200 miles to the north, east and south of the islands) is one of strict regulation of fishing effort aimed at ensuring a safe level of escapement of potential spawners (Beddington *et al.* 1990). Assuming that a stock–recruitment relationship exists, however variable, the objective is that sufficient spawners escape from the fishery in July to allow good recruitment into the next year's fishery the following January (Fig. 19.4).

To set the actual level of escapement to be targeted by management, two approaches were considered. A fixed level of spawner escapement (absolute numbers) at or above the level estimated to maintain recruitment in the following season, or a constant proportional level, defined as the number of spawners alive at the end of the fishing season as a proportion of those that would have been alive had there been no fishing

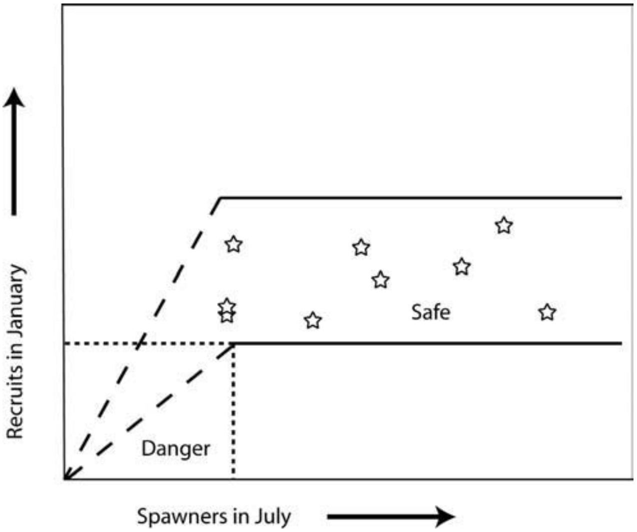


Fig. 19.4 Schematic relationship used to illustrate the relationship between the level of spawner escapement in July with the recruitment in the following January, and the setting of the safe level of escapement (after Beddington *et al.* 1990).

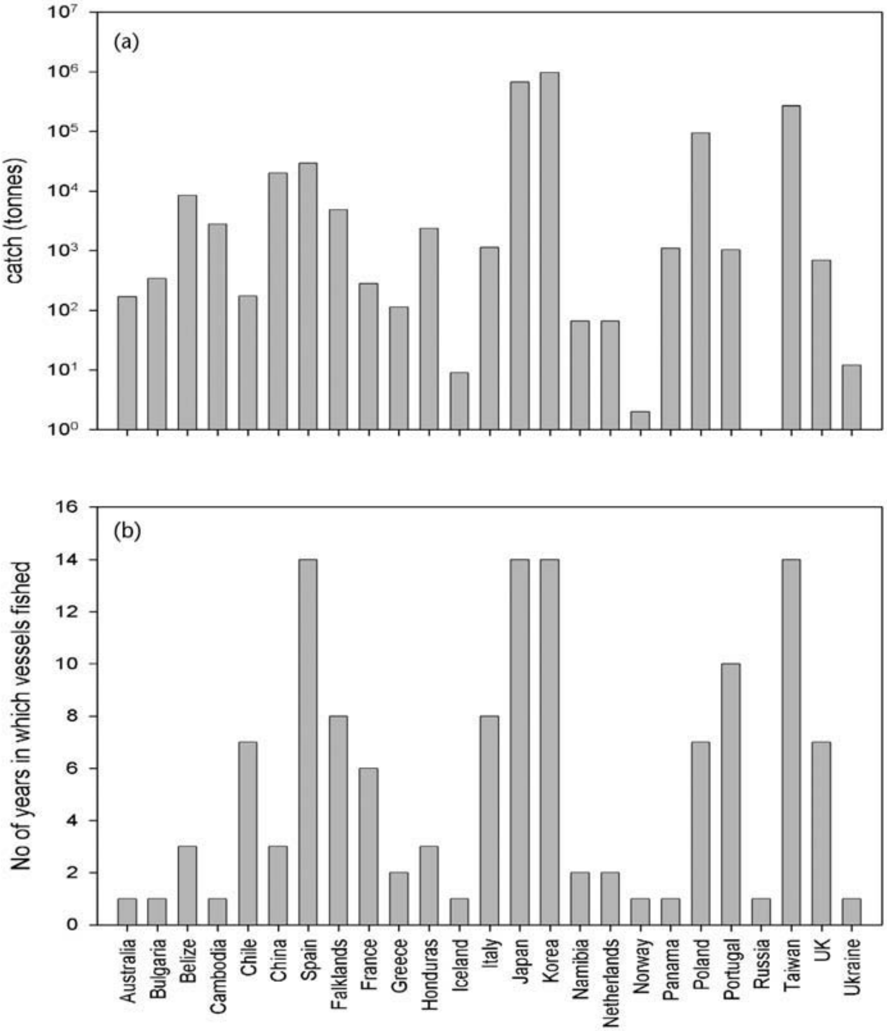


Fig. 19.5 Nationality of vessels targeting the *Illex argentinus* fishery in the Falkland Islands (Malvinas) for the years 1987–2000. (a) Total catch (tonnes). Note that the data for Russia records just 1 metric tonne of squid in 1994. (b) Number of years in which each fleet participated in the fishery. Data compiled from the Falkland Islands Government Fisheries Department Fishery Statistics (FIGFD) by Waluda (2000).

(Beddington *et al*. 1990). Principally because the year class size, and therefore the fishable stock on the Falkland Islands fishing grounds, varies widely between years, a proportional escapement target results in a constant harvest rate. Provided the harvest rate is sufficiently conservative, this is a policy which is much more feasible to administer and justify to fishermen than one based on quota alone. In a year of strong recruitment, the multi-national fleets (Fig. 19.5) take a higher catch.

The target adopted for escapement has been set at 40% of the estimated pre-fishing stock. This is an arbitrary figure based on convention in other fisheries (Beddington *et al.* 1990) and without particular biological significance. Because there is within-season monitoring of effort and catch, within-season adjustments in effort are possible, for example by early closure of the season. Because of the wide between-season variability in the size of the fishable stock, it is also probable that the licensed fishing effort in any year may under- or over-shoot the target of 40% escapement. However, the system of annual fishing licences, based on catching power, allows for adjustments to be made in the total fishing effort licensed in the following year. A later refinement of the 40% proportional escapement policy (Basson *et al.* 1996) introduced an absolute minimum target for escapement of 40 000 tonnes, a policy that sets a precautionary limit in a year of poor recruitment. In-season adjustment and joint management by Argentina and the UK ensures that the fishery is closed at around the escapement limit. Despite the management target of 40% annual escapement, a retrospective analysis of the data by Basson *et al.* (1996) suggested that the actual proportional escapement ranged from 32.1% in 1990 to only 8.7% in 1987. Moreover, the relationship between the estimated annual spawning stock biomass and the subsequent recruitment was not consistent. The lowest spawning stock biomass in 1989 resulted in the lowest estimated recruitment in 1990 and an only slightly higher spawning stock biomass in 1987, resulted in the highest estimated recruitment value in 1988.

19.2.2 Canadian Illex fishery

Lange & Sissenwine (1983), updated in O'Dor & Dawe (1998), described the early development of the management regime for the *Illex illecebrosus* fishery off Canada and the USA. Historically exploited only as a local bait fishery in Newfoundland and Nova Scotian waters, international catches of the species began to increase in the early 1970s due to increases in fishing effort in the area in response to the relative shortage of *Todarodes pacificus* in the western Pacific. Canada and the USA initially managed the squid fishery through ICNAF (International Commission for North Atlantic Fisheries) by setting pre-season quotas for the total allowable catch (TAC).

In 1977, both countries extended their jurisdiction to 200 miles, setting TACs for separate sub-areas based on pre-season indices of recruitment from spring and autumn bottom-trawl surveys. Fishing 'windows' based on spatial and seasonal restrictions were established. In addition to jig-fisheries offshore and inshore, the species was also caught offshore in targeted trawls for which a minimum mesh size of 60 mm was set. In later years, the TAC was partitioned between the national fleets, with a portion of the total held back for mid-season reallocation in years of high squid recruitment.

19.2.3 Eastern Pacific Dosidicus fishery

The jumbo flying squid (*Dosidicus gigas*) occurs in the eastern Pacific between about 35°N on the coast of southern California, southwards to the tip of South America at about 55°N. In the Gulf of California and off Peru, substantial commercial jig-fisheries for the species may exist, but the overall distribution and abundance is highly dependant on oceanographic conditions, especially the periodic El Niño phenomenon.

The *Dosidicus* fishery in the Gulf of California has historically been one of relatively unpredictable catches by locally based artisanal fishers. In the early 1980s there

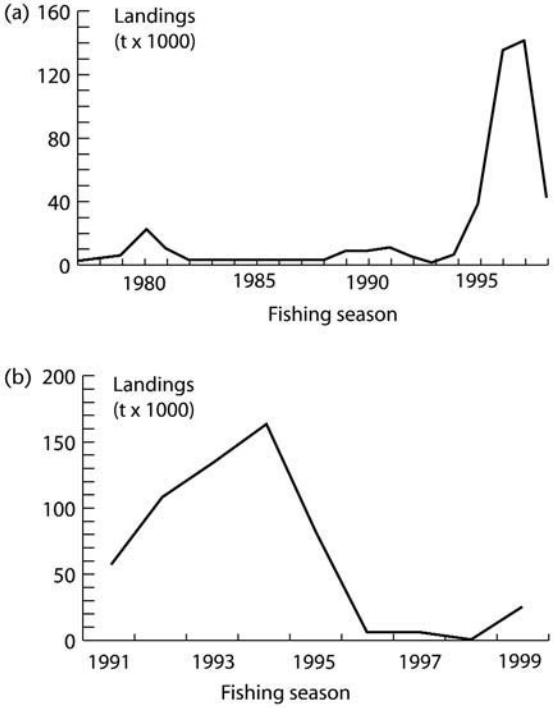


Fig. 19.6 Annual trends in landings for *Dosidicus gigas* from (a) the Gulf of California (after Morales-Bojórquez *et al.* 2001a), and (b) the Peruvian sector (after Taipe *et al.* 2001).

appeared to be a single stock of multiple cohorts migrating northwards into the Gulf in winter and spring, and returning southwards to the Pacific Ocean in summer/autumn (Ehrhardt *et al.* 1983). Stock assessment by cohort analysis, yield-per-recruit analysis and the DeLury methodology suggested that the maximum catches (22 000 tonnes in 1980) had reached the maximum sustainable yield, but no management regime was put in place. The fishery then collapsed, probably because of changed oceanographic conditions arising from the ENSO cycle. Landings resumed in 1994 (Fig. 19.6), when only a single cohort was present in the stock. Based on the system of management used in the Falkland Islands, the catch per unit effort data of the three commercial fleets were used to estimate the annual proportional escapement, and a management strategy was introduced. Landings rose to a peak in 1997 (120 000 tonnes), followed by almost complete collapse, again probably caused by environmental changes associated with the ENSO cycle. Using a biomass estimate of the squid from research cruises using the swept-area method and a retrospective analysis of catches, Hernández-Herrera *et al.* (1998) estimated that the proportional escapement actually achieved by the management method ranged between 27% and 40% of maximum biomass in 1996–1997.

In the Peruvian sector, the fishery for this species has been similarly unstable over many years, with some catches up to nearly 165 000 tonnes (1994). Landings and effort are closely monitored, and an observer is present on each vessel, but no overall management of the fishery is attempted (Taipe *et al.* 2001).

19.2.4 New Zealand Nototodarus fishery

The two commercially important ommastrephid squid species in New Zealand waters, *Nototodarus gouldi* and *N. sloanii*, are approximately separated in their distribution by the Subtropical Convergence Zone (Gibson 1995), with the *N. gouldi* attributed to the north of 41°55′S (generally a single cohort fishery) and *N. sloanii* to the south of 44°S (may be multi-cohort, but without biological information which could lead to their separate management). There is limited, but commercially insignificant, mixing of their distributions near and between their common boundaries. Fishing within the New Zealand EEZ involves a multi-national fleet using specialised squid-jigging vessels, as well as large-stern trawlers operating a mix of bottom and pelagic trawls.

The history of the fishery has been documented by Gibson (1995). Early control within the EEZ was by effort regulation, i.e. the licensing of foreign and domestic boats and controlling the number of annual licences. Foreign vessels could also gain access to the fishery through joint venture agreements with New Zealand companies. By 1983, the method of control for the trawl catch changed to the allocation of individual fishing company quotas; only the jig-catch was then controlled by vessel licences. By 1986, the system of individual transferable quotas (ITQs) was introduced throughout the squid fishery. The ITQ system, pioneered in New Zealand and Australian fisheries, promotes a more relaxed approach to the fishery. Fishers can catch at a rate that suits their business because they are effectively guaranteed a share of the TAC rather than having to fish in competition with the rest of the fleet (Jennings *et al.* 2001). The TAC is set annually and optimistically. Starting at 90 000 tonnes in 1986, it was increased progressively to 166 250 tonnes in 1989, and reduced to 122 875 tonnes in 1992 and 1993 (Gibson 1995). Throughout this period, the actual combined annual catch of the two species seldom exceeded 50 000 tonnes.

19.2.5 Japanese Todarodes fishery

Todarodes pacificus in Japanese waters is historically the largest single-species cephalopod fishery and has been the object of numerous scientific surveys and diverse approaches to management of the stocks. The basic description of the fishery, its assessment and management, is compiled in technical papers for the FAO (Okutani 1977; Caddy 1983a) and in the reviews of Okutani (1983), Murata (1989, 1990) and Suzuki (1990). The management regimes have been a complex interaction between fishing availability and market demand, aimed as much at maintaining price and market stability as at sustaining the stock. Much of the recent work on the assessment and management of this species is contained within internal reports, mostly in the Japanese language. Consequently, we are most grateful to Dr Hideaki Kidokoro and Dr Akihiko Yatsu (National Institute of Fisheries Science, Yokohama, Japan) for providing this summary.

Until 1998, effort control was put in place by the licensing of fishing vessels. Thereafter, the Japanese government introduced a TAC system for the management of the species, based on an estimation of the allowable biological catch. The total resource of *Todarodes pacificus* is divided into two stocks: the Japan Sea stock (the autumn group) and the Pacific stock (the winter group), which are based on different fishing areas and seasons. Pre-season scientific surveys assess the distribution of the stocks and the number of recruits, together with some biological parameters. Yield information from previous years is then used as the basis for the calculation of the allowable biological catch for the coming season.

19.2.6 Southern Ocean Martialia fishery

In the Southern Ocean and associated waters of the Antarctic Polar Front there has been no consistent commercial fishing for *Martialia hyadesi*. Sporadic catches by research vessels and the occasional commercial expedition have only amounted to a few tonnes annually. Exceptionally, there have been a few seasons in which higher catches up to 24 000 tonnes have been recorded (see Table 17.1), mostly over the Patagonian Shelf, attracting the interest of commercial fishers to the Southern Ocean and raising the prospect of unregulated fishing, potentially in competition for the food supplies of predators.

There are two potential areas for a *Martialia* fishery in the south Atlantic: the polar frontal zone and the Falkland (Malvinas) Current, which may be the same biological stock. Despite some commercial interest in the polar frontal zone, no continuity of fishing activity has materialised. Large catches have occasionally been taken in the Falkand current, although also sporadically. There is no assessment for the Falkland current and only an indirect assessment, based on consumption by higher predators, is available for the polar frontal zone. Using an ecological approach, Rodhouse (1997) estimated total higher predator consumption, and CCAMLR set a precautionary catch limit of 1% of this value. It is envisaged that pre-season stock assessment may be possible by monitoring seabird predation and using the information to set quota limits. The success of the most sensitive predator populations (albatrosses and petrels) could also provide evidence of the potential impact of fishing.

19.2.7 Falkland Islands Loligo fishery

Loligo gahi, a species widely distributed on the Pacific and Atlantic coasts of South America, and comprising a substantial trawl fishery on the Patagonian Shelf and in the waters surrounding the Falkland Islands (Malvinas), has been the subject of assessment and management measures within the Falkland Islands Conservation Zone (FICZ) and the FOCZ (Falkland Outer Conservation Zone). The Falkland Islands fishery is assessed annually using depletion methods (Agnew *et al.* 1998a). The population structure of the species is complex, there being two cohorts separated using biological data. In some years, the DeLury model does not fit, and in these cases a modification is used to achieve some consistency with previous years. These assessment methods have allowed the specification of stock–recruitment relationships. As with most squid, stock size does not explain much of the variance in the recruitment, most of which is explained by SST (Agnew *et al.* 2002). This work has allowed the definition of target escapement values of 10 000 tonnes for each cohort.

19.2.8 US east coast Loligo fishery

The early history of the fishery for *Loligo pealei* is of a series of small coastal fisheries, greatly expanded by the entry of distant water fleets in the 1960s and 1970s (Lange & Sissenwine 1983). Distributed from Cape Hatteras to Georges Bank, the squid are present in commercial quantities from New Jersey to Newfoundland. They are present in warmer waters over the continental shelf, and migrate to deeper water during winter. The fishery, by otter trawl and inshore trap, dates back to the late 1800s and, like that for *Illex illecebrosus* with which it partly co-occurs, was largely for bait to supply the lucrative cod-line fishery in the region. Although *Loligo* and *Illex* have very different life-history and breeding characteristics (see Chapter 6), problems in correctly reporting catches of the two species led to difficulties in setting separate management targets for them.

Activity by distant water fleets was first recorded in 1964, successively by Soviet, Japanese, Spanish and Italian vessels. In response to the rapid rise in catches of both species by these vessels (from 4 tonnes reported in 1964 to 57 000 tonnes in 1973) a combined preemptive quota of 71 000 tonnes was first set in 1975 by ICNAF (International Commission for North Atlantic Fisheries). In 1977, the US extended its jurisdiction to 200 miles, bringing into effect a new fisheries management plan for its resources and setting a 44 000 tonnes quota for *L. pealei* alone based on biomass estimates from research trawls. Classic fishery field models (multiple cohort yield model; yield per recruit analysis) have been applied to the fishery, but without really affecting the simple management by single quota.

Application of the Leslie–DeLury model to this population (Brodziak & Rosenberg 1993) for the years 1983–1990 showed a 10-fold range in the size of the initial (pre-fishing) population. Later use of statolith ageing data (Brodziak 1998) emphasised the 1 year age of the fished population and led to a precautionary downwards revision of the long-term potential yield for this species from 44 000 tonnes to 21 000 tonnes. On the basis of this downward revision of the long-term potential yield, the fishery was estimated to be fully exploited. Consequently, the annual domestic allowable harvest was revised down to equal the potential yield, entry to the fishery was limited, and in-season monitoring of landings and enforcement of the harvest level were implemented.

19.2.9 English Channel Loligo fishery

The Atlantic coasts of Western Europe support several loliginid species of modest commercial value, e.g. *Loligo vulgaris* and *L. forbesi*, with occasional catches of *Alloteuthis subulata*. The relatively small commercial value of these mixed stocks compared with demersal fish, and their exploitation by fleets of several nations, have not yet led to an overall stock assessment or management plan for European waters. Although the squid caught in these waters are a by-catch, its high value has led to good records of port landings, and several national fleets keep records of catch distribution in the form of catch-by-square data. This has allowed the trial application of DeLury estimates to the stock during the fishing seasons to selected ICES sub-areas of the range. For some sub-areas (North Sea, Rockall) there was a reasonably good fit to data, but others (West of Scotland, English Channel) were very sensitive to the choice of input parameters (Pierce *et al.* 1996).

19.2.10 South African Loligo fishery

The coastal squid of South Africa, *Loligo vulgaris reynaudi*, is distributed over the continental shelf from southern Namibia to the Cape Province. Prior to 1984 it was a by-catch of demersal trawlers, but the fishery developed to an inshore hand jig-fishery operated from small boats with annual catches of up to 10 000 tonnes. Careful handling and packaging of the catch made it a valuable export to the countries of southern Europe, and considerable attention has been given to stock assessment and management approaches (Augustyn *et al.* 1992; Augustyn & Roel 1998; Lipinski 1998). Hydro-acoustic surveys are initially used to locate inshore concentrations of spawning squid, and experimental trawl and jig surveys are then undertaken, together with diver surveys of the spawning beds (Sauer *et al.* 1993). Management measures for the fishery developed as a strict control effort by limiting entry to the fishery by licence, coupled with a closed season (November) to protect spawning beds. Comparable trials in Tasmania, of a seasonal closure to fishing to protect the inshore spawning beds of the southern calamary *Sepioteuthis australis* gave variable results. One closure period resulted in a greatly increased density of spawned eggs, a result not repeated by a second closure (Moltschaniwskyj *et al.* 2003).

The dynamics of the coastal oceanography limit the optimum habitat for this species to between the low oxygen levels of the inner shelf water and the low temperatures of the upwelling cold Atlantic ocean central water (Roberts & Sauer 1994). This preferred zone concept (Fig. 19.7) limits the distribution of high-density fishable concentrations of squid and makes them particularly vulnerable to targeted fishing and activities such as trawling, which would damage the spawning beds.

Using jig-fishery catch data, application of the Leslie–DeLury method suggested that fishing mortality has a large impact on the population compared with natural

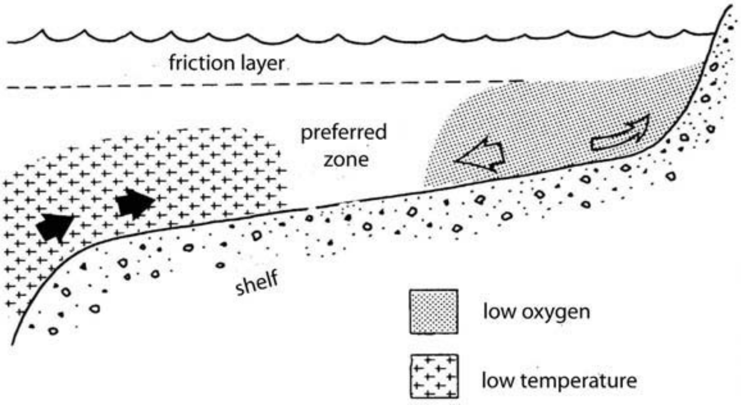


Fig. 19.7 Schematic diagram of the 'preferred zone' for spawning aggregations and breeding of *Loligo vulgaris reynaudi* lying between low-temperature offshore upwelling water and low-oxygen coastal water (after Roberts & Sauer 1994).

mortality during the time that the species comes inshore to breed. A trawl fishery for this species is operating offshore on the Agulas Bank, but the catches are in decline (Roel *et al*. 2001).

19.2.11 Saharan Bank Octopus fishery

The extensive shelf area of the Saharan Bank (West Africa 21°N to 26°N latitude) has provided rich fishing grounds since the fifteenth century. Typically, the fishing for finfish (families Sparidae, Serranidae and Sciaenidae) was by hand-line from small boats supported from the shore or by larger mother ships. As well as local fishers from the coastal states, the fishery has attracted fleets from elsewhere, notably Spain (mainland and Canary Islands), Portugal, France and Italy. Following World War II, north Atlantic fleets from these countries moved on to the Bank, establishing bottom trawling as the main commercial fishing method.

The catches of cephalopods (*Octopus vulgaris*, *Sepia officinalis hierredda* and *Loligo vulgaris*) were very small until the 1960s when spectacular increases were observed, which in turn attracted a further great influx of trawlers. Concurrently, the years between 1960 and 1972, the period of heaviest trawling activity, saw a steep decline of the traditional finfish catches (Fig. 19.8). The apparent replacement of the originally dominant finfish by cephalopods has been interpreted as resulting from ecosystem disturbance due to over-fishing of groundfish (Caddy 1983b; Fig. 19.9). The general thesis is that fish and cephalopods are in competition for food, and that each group preys on juveniles of the other. When the fish population was artificially suppressed by fishing, the release of predation pressure and competition for food allowed a great increase in the cephalopod biomass. The cephalopods, particularly the octopus stocks, with their short generation time and high growth rates, have remained the major fishery resource. Surplus production models have been applied to the octopus, cuttlefish (Sato & Hatanaka 1983) and squid catches (Bravo de Laguna 1989) of the Saharan Bank, and they suggested that each stock was over-exploited.

Using fishing survey data and independent of the commercial catch, Balguerias *et al*. (2000) re-evaluated the history of these fisheries and concluded that species-replacement due to overfishing is not the whole story. Their data suggest that while there may have been some compensatory adjustment of communities, factors such as oceanographic variation and market demand have also contributed to favouring the benthic cephalopod populations. Balguerias suggests that it is more likely to be the incidental effects of fishing, such as the discarding of dead material, rather than population interactions between cephalopods and fish which may have been influential (Fig. 19.10).

19.2.12 Japanese Octopus fishery

The coastal octopus resources around Japan have been exploited and managed for over a century for the benefit of local communities. Most of the catch is identified as *Octopus vulgaris*, with *O. dofleini* in the north and only small quantities of other species. The total catch, which can exceed 100 000 tonnes, is taken mainly by potting, with

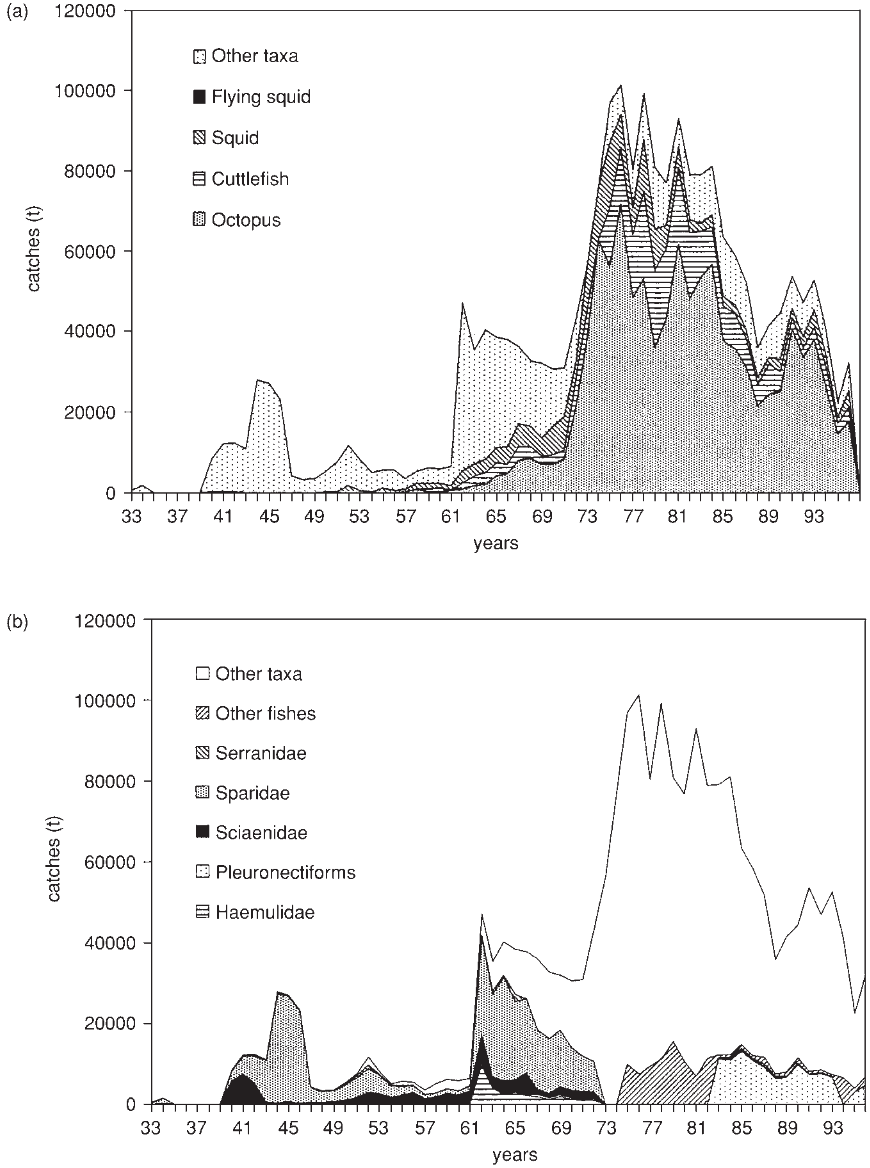


Fig. 19.8 The composition of Spanish landings from the Saharan Bank. (a) By major cephalopod taxa. (b) By major fish taxa. (After Balguerias *et al.* 2000.)

significant catches by small trawlers and long-lines (Takeda 1990). The management of these resources is highly sub-divided into local areas with cooperative arrangements between fishermen to agree access, methodology and catch limitation. Regional schemes are also in place to provide protection for spawning grounds and spawn by the placing of rocks or concrete blocks on the substrate and the provision of tethered pots as spawning sites for the octopus.

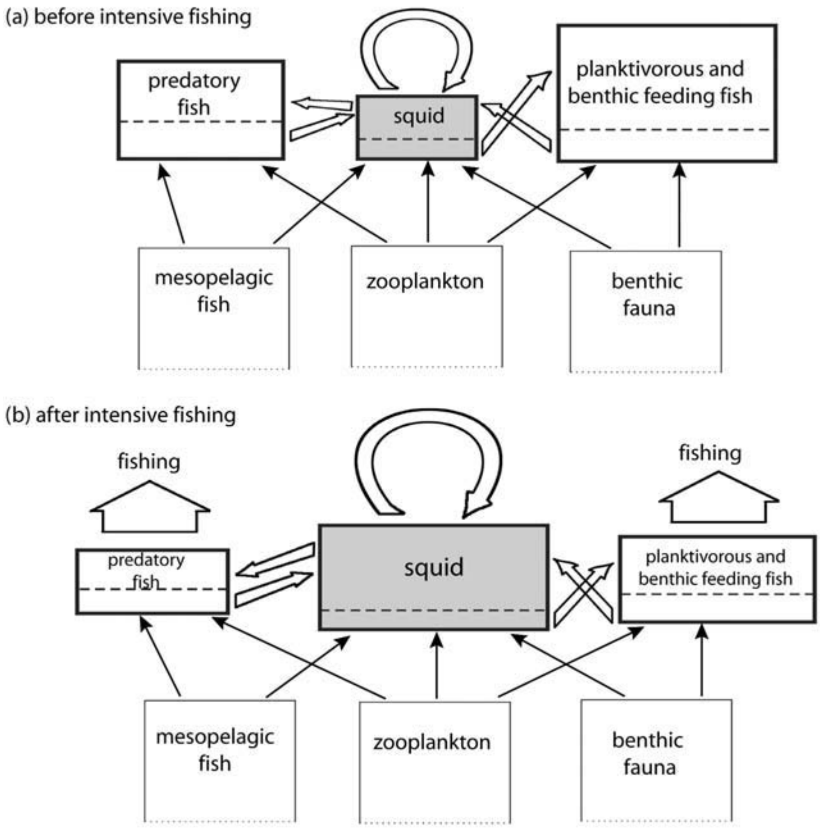


Fig. 19.9 Hypothetical trophic relationships of neritic squid (*Loligo*) in the marine ecosystem of the Saharan Bank (a) prior to intensive fishing on any of the components, and (b) after intensive fishing on fish and prior to an intensive squid fishery (after Caddy 1983b). Outlined arrows indicate the direction of the flow of biomass; the three basal components are left open to imply that they are probably large in biomass, and relatively independent of all but major changes in the upper components. The circular arrow above the squid box implies cannibalism.

19.3 Cephalopod fisheries – is management needed?

The most consistent interpretation that might be drawn from the diverse efforts at the management of many cephalopod stocks is that we really have no objective evidence that any of them actually work!

The interaction between cephalopod life cycles and environmental variability due to physical factors has been consistently emphasised throughout these case history examples of management policies. These variables operate on a variety of scales; some are broadly predictable (e.g. winter conditions will be cooler than summer), others quite unpredictable (e.g. at a given locality whether the temperature range or cumulative temperature to which a brood of eggs is exposed will permit hatching to coincide with optimum conditions for the larvae). The significance of the effect of these stochastic variables on annual species is extreme, and is the main reason why it has proved difficult to establish reliable assessment and management procedures for cephalopods.

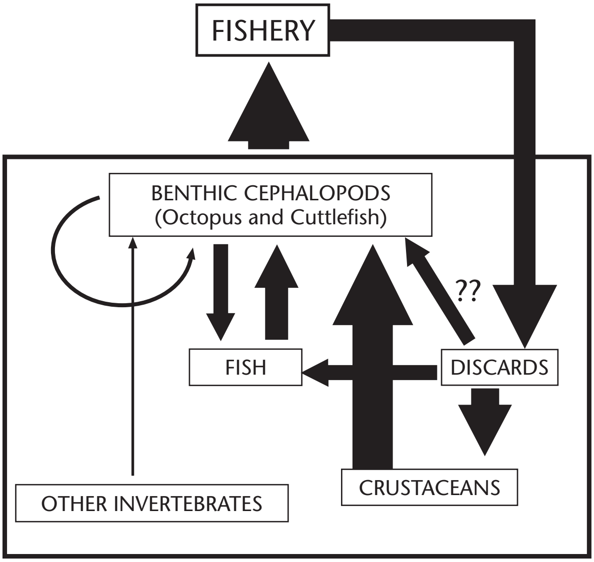


Fig. 19.10 Proposed trophic relationships between benthic assemblages on the Saharan Bank favouring increased production of benthic cephalopods through the influence of the discarding practices of the fishing industry (after Balguerias *et al.* 2000). The possible direct consumption of discarded trash fish by cephalopods is suggested.

We have almost no estimates of natural mortality at different stages and in different conditions and, as a consequence, cannot clearly quantify the significance of fishing mortality.

A precautionary approach should always argue for the best assessment procedures possible and propose a minimum management regime capable of responding should the fishery appear to be suffering from over-exploitation. A very clear case of where strong management is needed is where trawl fisheries could target a species laying eggs on the bottom. Trawling through the spawning aggregation directly subtracts the spawners, detaches the spawn masses and damages the spawning ground. The elimination of *Sepia pharaonis* from much of the coastal Indian Ocean was probably from such a cause, although we are not sure whether to call this over-exploitation or simply environmental damage.

On theoretical grounds there must be a minimum spawning stock of any species which is sufficient to ensure that there is a sufficient supply of eggs and larvae to provide for the annual population recruitment. It is therefore a valid objective of management to ensure that this minimum spawning stock is protected. The unpredictability of the environmental conditions to which the output of that breeding stock will be subjected provides a strong reason for setting any minimum estimate of spawning biomass sufficiently high to allow for adverse conditions.

Clearly there is a pressing need to improve methods of population assessment for cephalopods of all types, and to gain a better understanding of the interactions between the various life-cycle stages and factors of the physical and biological environment leading to natural mortality. As this steady accumulation of knowledge proceeds, we can expect that management methods will be progressively improved.

Chapter 20

Conclusion

The trend from descriptive zoological studies to quantitative ecosystem work is apparent in most of the areas covered in this book. Although the bulk of the information presently available is rooted firmly in traditional approaches to animal biology, the introduction to cephalopods of techniques developed in other disciplines is advancing rapidly, increasing the pace of new discovery and promising further rapid advances in understanding. Molecular genetics, satellite observation, GIS methods, acoustic tracking and the increased availability of underwater observations from submersibles and remotely operated vehicles are all having an impact. Our purpose in this final section is both to pick out these advancing areas and to indicate some of the many outstanding issues deserving attention.

Form and function in cephalopods is covered in a major body of literature exploring their anatomy, physiology and behaviour. The classical approaches of comparative zoology establishes their status as highly evolved and specially adapted molluscs, and simultaneously describes the many ways in which they have evolved biological systems which are comparable to those of fish in many instances, but by quite different routes. The principles by which cephalopod biology is governed can therefore be largely understood in the context of comparative studies. Despite this general knowledge, there are many capabilities of the cephalopods that have been evolved to an exceptionally specialised degree, or may even be unique, and where a full understanding of the mechanisms involved is incomplete. Topics such as the production and control of complex surface patterns by the chromatophores and other skin elements, the production and control of light, the biochemistry and specificity of digestive and prey-handling enzymes, the roles of social behaviour and the significance of the brain to the incorporation of learned, experience-based, components of behaviour are very imperfectly understood.

As a result of the persistence of the hard shell of the ancestral cephalopods in fossils, the history and evolution of the cephalopods from their early molluscan ancestry is a matter of detailed record. The evolution of neutral buoyancy by the containment of low-pressure gas spaces seems to have been the key step that allowed occupation of three-dimensional space instead of the primitive benthic habitat. Progressively, the heavy, protective external shell was reduced, perhaps as a result of competition from fish and reptiles, and the modern soft-bodied forms (some with a vestigial internal shell) arose. During these later evolutionary stages, the characteristically active, high-energy lifestyle evolved, as did the short semelparous strategy. Due to the nature of the fossil evidence, it is inevitable that most of the comparisons made between the modern and fossil forms are strictly speculative. This problem is made worse because both palaeontologists and biologists tend to work within their respective spheres of reference, allowing little scope for critical comparisons of living and fossil material.

Most of the fossil lines of evolution appear to have become dead ends, not giving rise to any forms surviving to the present. A much better biological interpretation of the fossil forms is needed in order to make sense of the evolutionary trends leading to the present distinctive cephalopod characteristics.

The modern nautiluses are the only living relatives of the many forms of ectocochleate (external shelled) cephalopods found in the fossil record. Their known biological characteristics are the only reliable means of interpreting the likely biology of the extinct species. In addition to the external shell, these animals have different morphological and biological characteristics, including multi-annual breeding and much longer life spans. Nautiluses can reduce their metabolic rate substantially in low oxygen levels, allowing them to operate occasionally within deep-sea environments. Whether this ability was shared with ancestral forms or was a later adaptation allowing the relatively slow nautilus to avoid predation and competition from fish is a matter of speculation. Despite their clear relationships to the ancestral and the modern cephalopods, nautiluses do not share many of the key life-cycle characteristics with the coleoids. Biological studies on living nautilus, and details of their feeding, growth, reproduction and lifespan, potentially offer great insight into the evolutionary significance of the common characteristics of the modern forms as well as the lives of those in the palaeo-historical record.

Once the trend towards shell loss, and the themes of coleoid mobility, predation, growth, reproduction and life history, became established, the cuttlefish, squid and octopuses radiated into all of the major marine habitats, but never penetrated into fresh water or estuarine conditions. Distinct patterns of biodiversity and zoogeography have become apparent. The greatest range of cephalopod forms and the greatest number of families are found in the highly dispersed and relatively unproductive environment of the oceanic mesopelagic zone (500–1000 m depth). Many of these families include few genera, 50% of those genera are monospecific, and as many as 85% contain fewer than five species. In contrast, the relatively few genera typically colonising shelf waters, notably *Octopus*, *Sepia* and *Loligo*, are the most speciose, with *Octopus* and *Sepia* each having over 100 species. There is no clear answer as to how this imbalance arises, but a plausible suggestion is that the shelf colonists have evolved more recently, fully exploiting the active lifestyle and use of three-dimensional space to compete with teleost fish for the most productive habitats.

The capacity of cephalopods to migrate over large distances has allowed many species (from the family Ommastrephidae in particular) to exploit the highly productive boundary currents and upwelling systems of the edge of the continental shelf, and it is these populations that provide some of the major fisheries. Despite the relatively low number of established cephalopod species, 650–700 in total, and the importance of species identification for the international cephalopod fisheries, the taxonomy and systematics of cephalopods are still in a state of flux. Conventional morphological approaches to species identification leave many questions unanswered. New techniques of molecular genetics are beginning to have an impact at several taxonomic levels, but are already giving rise to differences from the traditional interpretation. It is likely, therefore, that these different approaches to species identification will be needed in combination for some time before the biodiversity and zoogeography of the group can be comprehensively revised.

It is the life-cycle characteristics of the living cuttlefish, squid and octopus that determine much of our thinking about their ecological roles in the ocean. The single-breeding (semelparous) habit and short lifespan of the coastal forms, which is well established and consistent across many species, sets a pattern of high dependence on environmental conditions for recruitment and of strong seasonal changes in abundance. These generalisations must increasingly be qualified:

(1) to account for the high degree of interannual plasticity in the timing and phasing of breeding activity found in coastal species;
(2) to account for the developing field of information on the mesopelagic and deep-water oceanic species where the dispersed populations, low productivity and relatively aseasonal environment result in greater divergence from the simple general model.

Even among the well-known coastal species, detailed population studies uncover many aspects which are difficult to resolve, such as the apparent alternation between 1- and 2-year cycles, the mismatch of timing between breeding and recruitment in some loliginids, and the inconsistent influence of daylength, among other environmental factors, in stimulating maturation and breeding in loliginids and cuttlefish with northern and southern hemisphere distributions. We might wish that the rapid development of molecular markers might enable generation tracking in future, in which the timing and success of successive generations of localised breeding poplations could be followed, and would possibly throw more light on the evolutionary significance of terminal spawning in cephalopods.

Evidence from aquarium-held animals, and field studies on populations or tagged cephalopods have established that remarkably high growth rates are possible for coleoid cephalopods. The keys to this performance are their high feeding rate and high conversion efficiency of food into somatic growth. These capabilities underpin the rapid biomass growth of cephalopod populations, and allow some species to attain body sizes comparable to the largest fish and greater than any other known invertebrate. The discovery of incremental lines in the statolith and the gladius has provided an important tool for the ageing of cephalopods and an investigation of the growth rates in field-caught animals. The technique also gives rise to some problems; for example, it apparently shows that giant squid, *Architeuthis*, grow and reach adult body size at more or less the same rates as many smaller species. If true, this is an astonishing finding and serves to emphasise the urgent need to conduct more critical studies on these proxy indicators of age. We need to have a better understanding of the causal mechanisms of statolith increment formation, more data validation studies through the matching of increment counts to known age, a better understanding of the embryonic and peri-natal events at the starting point for age estimation, a knowledge of any changes in the rate of increment production with age and, in particular, whether increment formation could cease at some time before the end of the natural life of the animal, and to develop a methodology for species such as the octopus that lacks a gladius, and in which the meaning of statolith increments is obscure. Reliable and universally applicable methods for ageing would contribute greatly to our understanding of the growth of cephalopods in the field.

As poikilothermic animals, the energy transformations of cephalopods controlling their rates of metabolism, growth and reproduction are dependent on the temperature and their body size. A 10°C change in temperature alters these rates up or down by a factor of two or more (Q_{10}), and relative rates of feeding and growth decline at larger body size. Another way in which cephalopods achieve a large body size is by deferring the allocation of energy to gonad production until a late stage in their life. The formation of yolk reserves for the eggs of cephalopods involves the sequestration of energy, largely as protein, into the lumen of the egg. Some cephalopods are known to utilise the energy and nutrient stores of their somatic tissues to fuel this process, and this results in loss of muscle mass at the time of gonad maturation and poor physical condition after breeding, and may contribute to their post-spawning death. Males apparently invest less energy into gonad production than females, but this is less reliably estimated because the male reproductive output is usually spread over a longer fraction of their lifespan, and males probably expend greater energy resources on locating and competing for mates. Consistent with their lifestyle, benthic forms such as cuttlefish and octopus are more efficient converters of energy to somatic growth than squid because less is allocated to the active swimming needed by squid to remain in the water column. Despite these generalisations, there is currently no cephalopod for which all of the components of the energy budget have been estimated, and comparative studies are needed to extrapolate to the less active lifestyles of deep-water and neutrally buoyant species. The biochemical and physiological mechanisms involved in the apparently exceptional food conversion efficiency are almost unknown.

With separate male and female sexes (no hermaphroditism is known), the process of mating and reproduction in cephalopods underlies many aspects of the ecology of individuals and populations. The wide availability of shallow-water SCUBA diving has encouraged much greater study of behaviour patterns at breeding sites and the development of concepts of communication and social organisation in shallow-water cephalopods. Increasingly, the complexity and adaptability of reproductive behaviours has been shown to have the potential to profoundly influence individual reproductive strategies, and hence influence the life-cycle parameters of different broods of offspring. Competition for mates, mate choice and sperm competition all play a role. Here, especially, molecular techniques have already proved powerful in showing that multiple mating behaviour can result in multiple paternity among batches of hatchlings from a single female, and even of hatchlings from within a single egg string. Moreover, these batches of different genotypes within the brood may have significant differences in phenotypic characters such as size at hatching. These findings are opening up use of the tools of molecular genetics to begin the process of linking the reproductive strategies of individuals with the success of individual broods and the maintenance of sufficient diversity within the population to ensure survival through the unpredictable conditions for annual survival and recruitment.

Post-hatching development in cephalopods is a simple process of growth, with associated changes in the allometry of the body proportions and often a progressive ontogenetic change in habitat and food supplies. There are no radical transitions in body form or metamorphoses. For the bulk of the annually reproducing cephalopods, the larval stages are the essential link between successive generations and ensure the continuity of species distributon. In common with most marine animals with planktonic larval stages, these small and delicate animals are difficult to capture and maintain, and there is little work directed specifically at the living larvae and juveniles. Exceptions are found in selected coastal species where there is a potential for commercial aquaculture. A number of cuttlefish, squid and octopus have been reared in captivity throughout the life cycle, with special attention to their nutritional requirements and the prospect of feeding them on manufactured pelleted food. The utility of these studies as a basis for commercial aquaculture is as yet unrealised for a combination of reasons: the high costs of pumped water systems for tank maintenance, the availability and low cost of products from wild fisheries, and the difficulty and costs of providing live food of a range of types and sizes to satisfy the requirements of the growing larvae. Technically, full culture of many species is feasible, but it has not yet proved commercially attractive on any scale. In the long term, however, the value of cephalopod cultivation for food production is questionable in principle because as predators several levels up the food chain, and dependent on high-quality protein food whether natural or artificial, there are clear energetic and ecological inefficiencies in the process.

Knowledge of the ecology of cuttlefish, squid and octopus endemic to the continental shelf and coastal zone has had the greatest influence in shaping ideas about cephalopod biology in general. Here, there are the most physically diverse and biologically productive habitats available to cephalopods and where they are most accessible for study. Although they make use of the water column, the shelf species are typically associated with the sea bed for shelter or feeding and for the attachment of egg masses. Genera such as *Sepia*, *Loligo* and *Octopus* are among the best known of all cephalopods, and will continue to provide model species and material in most areas of study. Also exploiting the productivity of the shelf break and coastal upwellings are squid of the family Ommastrephidae. Characteristically oceanic in distribution, with a life cycle completed with entirely pelagic egg and larval stages, shoaling genera such as *Todarodes* and *Illex* travel the shelf-break contours and make major feeding incursions over the shelf itself. Again owing to their relative availability for study and also their importance as global fisheries, the abundance and distribution of these species are the objects of considerable scientific and commercial interest, but owing to the logistical difficulties of live capture and holding of large but delicate pelagic species, we have almost no comparative studies on captive animals.

The scale and extent of the oceanic and deep-sea environment encompasses the greatest biomass of cephalopods and includes all the familial diversity. These are species that show many special adaptations to the deep-water environment, including neutral buoyancy and luminescence, coupled with a general loss of muscularity and activity. It is self-evident that, in common with other deep-water species, our direct knowledge of the biology of these forms is very limited. Complete life cycle information for any species is lacking, but the available information suggests that growth rates may also be high and that their lifespan is short. Although a greater range of breeding mechanisms is described, including the continuous egg production of cirrate octopods and the pelagic brooding of eggs by gonatids, for some species at least it seems that the typical cephalopod characteristics of reduction in muscle tone at reproduction and synchronous post-spawning mortality still apply. New technology in the form of exploratory deep-diving submersibles and ROVs are adding significantly to knowledge of these species, but for reasons of quantification of the pelagic biomass and annual production, a greater certainty about their biology and life cycles is needed.

Cephalopod populations, whether coastal or oceanic, are studied with the full range of techniques available for any marine population. Compared with most marine fish, it is the annual recruitment and short lifespan of cephalopods that introduces difficulties in the application of the common population demographic methods, which are the basis of conventional fisheries assessment. Instead of a population size structure composed of annual year-class cohorts, cephalopod populations are dominated by a single annual size mode within which a sub-structure of intra-annual microcohorts may or may not be recognisable. Many of the main cephalopod populations of interest to fisheries are highly migratory, and this also introduces major difficulties in the use of demographic methods where the population is changing owing to the effects of immigration and emigration. The concept of the constitution of a population or stock in fisheries terminology is conventionally still based on criteria of species identification, and the spatial and temporal location of fishable quantities. Molecular methods, particularly micro-satellite markers, are beginning to be applied which, in combination with a clearer recognition of breeding localities and migratory routes, may supply a more reliable basis for population studies. Progress in the development of molecular genetic markers for population studies would be a great asset to fundamental approaches to the dynamics of populations and to its practical application to fished stocks.

The universal carnivory of cephalopods places them several steps along the food chain. All are highly capable predators and they have many special evolutionary adaptations specific to prey capture, and a high degree of cannibalism within populations is probably normal. A major problem in identifying and quantifying the diet of cephalopods is that they chop up captured prey, injesting only bite-size pieces of flesh. Consequently, visible evidence of the identity of prey species and the numbers of individuals in stomach contents is rarely complete. Some biochemical approaches to diet analysis using serological methods or lipid signatures have been helpful in specific instances, but more generic and readily applicable methods of diet analysis are required. To marine ecology generally, the particular importance of improving the methods of diet analysis relates to establishing the quantitative role of cephalopods as predators and reconciling, on theoretical grounds, the apparently massive biomass of cephalopods with the secondary production available to them as prey.

The beaks (mandibles) of cephalopods are chitinous and largely untouched by the digestive systems of their predators. The discovery that the beaks could be identified to taxa and that body size could be predicted from beak size opened up a wide field of work identifying and quantifying the consumption of cephalopods by the higher vertebrate predators, large fish, seals, whales and birds. Although there are some qualifications about the possible over-estimation of cephalopod consumption from beak evidence, there is ample evidence that cephalopods are a central food resource for marine top predators over the shelf and in oceanic waters. The scale of the current estimates is so great that there is a major task to be undertaken in matching predator consumption and the catch by human fisheries with the productive capacity of predatory cephalopods themselves. This further emphasises the overall role of cephalopods in the trophic structure of the oceans that should contribute to a more comprehensive cohesive modelling of energy and material flow in marine ecosystems.

Traditional and commercial methods of fishing for cephalopods are characterised by the degree to which they are selective for the target species. In this respect, the use of jigs for squid and the various pots and traps for octopus differ greatly from general fishing methods such as trawls and seines, which still catch cephalopods in multi-species as well as targeted fisheries. Fishing effort by these selective methods can be precisely quantified, the catch is in first-class condition, and there is neglible impact on the physical environment and non-target species. The questions for fishing are focussed on the location of fishable stocks and the timing of their availability. These are major issues for species with wide inter-annual fluctuations in abundance, but the use of acoustic survey methods and predictive models based on environmental conditions are increasingly of value. The greatest problem in using fisheries data for ecological purposes remains that of correct species identification and recording. As long as much of the commercial catch is not reliably allocated to species, or the area of catch is unkown, these data will be of limited scientific use.

Considerable uncertainty is attached to the degree to which the capture of non-commercial species by scientific trawling is representative. The composition of the cephalopod fauna recorded by open-ocean and deep-water scientific sampling techniques differs substantially from that implied from predator diet analysis, and leads to the conclusion that the present methods may be producing unrepresentative results. This is an area in which we might expect that the rapidly increasing use of new underwater technology (submersibles, ROVs, autonomous landers, acoustic detection, photo- and chemical detection) will soon yield new results.

The exploited resources of cephalopods have steadily increased in significance since the early 1970s. This has arisen partly by the global expansion of fisheries into new ocean areas, partly because increased market demand has led to increased utilisation of cephalopod catches for human consumption rather than as bait for other fisheries, and partly because the abundance of cephalopods in some areas has apparently increased relative to fish. This last point has led to some speculation as to whether ecosystem perturbations caused by intensive fishing generally are leading to changes in the trophic structure in favour of these short-lived opportunistic species. There is evidence from many fields of marine ecology to suggest that changes are taking place in the ecosystems, especially in the interrelationships of the main food-web components. The effects of global fishing and the roles of cephalopods are part of this changing scene.

The use of earth observation systems for surface oceanography (satellite monitoring) has great potential. Because powerful lights are used fishing for the main pelagic stocks of cephalopods, mapping the fleet distribution from space has shown just how closely the fishing activity, and by implication the target fished stocks, are linked to large scale and mesoscale oceanographic features. Much of the commercial fishing for migratory squid stocks takes place on the high seas, outside national jurisdictions. As the fishing nations increasingly seek to extend their monitoring and control of fishing activity into international waters, it is inevitable that space observations will become an important tool for monitoring and management. The overview of the cephalopod fleets that can be achieved from space offers a model that may be more widely applicable to other fisheries resources.

The modelling and management of fishing on cephalopod stocks is at an early stage. The methods available have largely been adapted from those used for finfish, and most of them involve assumptions that are not completely appropriate for cephalopods. There are intrinsic difficulties in modelling short-lived, single-year-class populations that are highly responsive to environmental fluctuations, and these are made more difficult by immigration and emigration effects in migratory species. Advances in the use of large relational databases for mapping catch and environmental data together have begun to offer approaches to predictive modelling which is independent of population data. Increasingly, the use of environmental information available on large geographic scales will become an integral tool for modelling pelagic stocks and for providing a framework for fisheries management. The other new approach arises directly from ecological information from cephalopod predators. In addition to conventional fishery survey methods, a start is being made on using data on cephalopod consumption by other marine predators to track their location, abundance and availability to the predator populations, and to model the impact of fishing activity. These data can then be used to estimate the effects of fishing and to derive management measures. This concept, that of the management of fisheries in their ecosystem context, is already in operation in the Southern Ocean and under active consideration elsewhere for other species. With exploited marine stocks under pressure world-wide, and increased awareness of the dynamics of marine ecosystems, the results of these new approaches will be followed with considerable interest.

The importance of interdisciplinary studies to further progress in cephalopod ecology and fisheries can hardly be overestimated. Combining traditional taxonomic skills with the technologies of molecular biology, relating satellite earth observation techniques to conventional oceanography and fisheries statistics, and exploration of the pelagic fauna with high-technology underwater vehicles are all producing new ideas and pointing to future discoveries.

Appendix A

Classification of cephalopod families

A summary classification of cephalopod families together with brief information on extinct groups mentioned in the text (shown in italics). The terminology used is consistent with that proposed by Sweeney & Roper (1998), but there are differences in the taxonomic rank assigned to some groups. Alternative names and common names for some of the groups are shown in parentheses (see explanation below). We are grateful to Dr Louise Allcock for suggesting this version of the classification.

A long-standing problem of inconsistency in the names used for the higher classification of cephalopods arises from differences in the use of taxon word-endings of ordinal and subordinal ranks (Clarke & Trueman 1988). To standardise the terminology, and to bring in consistency of practice between biologists working with modern forms and palaeontologists dealing with fossils, Sweeney & Roper (1998) propose the ending of orders to be 'ida' and of suborders 'ina'. Despite the benefits of a wholly consistent naming system, these word endings are not yet in common usage, nor are they universally accepted (Boletzky 1999). We have attempted to harmonise all ordinal and subordinal terms to the new system in this classification and the following Synopsis of Families (Appendix B), but because of their familiar use in English and throughout most of the scientific literature, we have mostly retained the earlier usage in the text. Thus, for the suborders of squid the terms Oegopsina = Oegopsida and Myopsina = Myopsida, are interchangeable and are used in their earlier form in the text of the book. The order Octopodida = Octopoda in the text, and for the suborders of octopods Cirrina = Cirrata and Incirrina = Incirrata. The specialist reader, however, should be aware that a fully consistent system of naming is available, and we have used that standard format wherever possible in the more systematically rigorous parts of the text. Illustrations of a member of most families are provided with A-prefix numbers, or a reference is given to figures in the text. The figures are NOT to scale; extinct groups are in italics.

Class: Cephalopoda

Subclass: Ammonoidea (ammonites)

Subclass: NAUTILOIDEA Agassiz 1848
    Order: NAUTILIDA Agassiz 1848
        Family: NAUTILIDAE Blainville 1825 (pearly nautiluses)
Subclass: COLEOIDEA Bather 1888
  Division BELEMNOIDEA – includes BELEMNITIDA (belemnites), AULERACIDA, DIPLOBELIDA

- Division NEOCOLEOIDEA
  - Superorder: DECABRACHIA Boettger 1952
    - Order: TEUTHIDA Naef 1916 (TEUTHOIDEA, squid)
      - Suborder: OEGOPSINA Orbigny 1845 (OEGOPSIDA)
        - Family: ANCISTROCHEIRIDAE Pfeffer 1912
        - Family: ARCHITEUTHIDAE Pfeffer 1900
        - Family: BATHYTEUTHIDAE Pfeffer 1900
        - Family: BATOTEUTHIDAE Young & Roper 1968
        - Family: BRACHIOTEUTHIDAE Pfeffer 1908
        - Family: CHIROTEUTHIDAE Gray 1849
        - Family: CHTENOPTERYGIDAE Grimpe 1922
        - Family: CRANCHIIDAE Prosch 1847
        - Family: CYCLOTEUTHIDAE Naef 1923
        - Family: ENOPLOTEUTHIDAE Pfeffer 1900
        - Family: GONATIDAE Hoyle 1886
        - Family: HISTIOTEUTHIDAE Verril 1881
        - Family: JOUBINITEUTHIDAE Naef 1922
        - Family: LEPIDOTEUTHIDAE Pfeffer 1912
        - Family: LYCOTEUTHIDAE Pfeffer 1908
        - Family: MAGNAPINNIDAE Vecchione & Young 1998
        - Family: MASTIGOTEUTHIDAE Verrill 1881
        - Family: NEOTEUTHIDAE Naef 1921
        - Family: OCTOPOTEUTHIDAE Berry 1912
        - Family: OMMASTREPHIDAE Steenstrup 1857
        - Family: ONYCHOTEUTHIDAE Gray 1849
        - Family: PROMACHOTEUTHIDAE Naef 1912
        - Family: PSYCHROTEUTHIDAE Thiele 1920
        - Family: PYROTEUTHIDAE Pfeffer 1912
        - Family: THYSANOTEUTHIDAE Keferstein 1866
        - Family: WALVISTEUTHIDAE Nesis & Nikitina 1986
      - Suborder: MYPOSINA Orbigny 1841 (MYOPSIDA, long-finned squid)
        - Family: LOLIGINIDAE Lesueur 1821
        - Family: PICKFORDIATEUTHIDAE Voss 1953 (placed within the Family Loliginidae by Brachionecki 1996)
    - Order: SEPIOIDEA Naef 1916 (cuttlefish)
      - Family: IDIOSEPIIDAE Appellöf 1898 (pygmy squid)
      - Family: SEPIADARIIDAE Fischer 1882 (bottletail squid)
      - Family: SEPIIDAE Keferstein 1866 (cuttlefish)
      - Family: SEPIOLIDAE Leach 1817 (bob-tail squid)
      - Family: SPIRULIDAE Owen 1836 (ram's horn squid)
  - Superorder: OCTOBRACHIA Fioroni 1981 – *includes Loligosepiina, Teudopsidae, Trachyteuthidae*
    - Order: VAMPYROMORPHIDA Pickford 1939 (VAMPYROMORPHA, vampire squid)
      - Family: VAMPYROTEUTHIDAE Thiele 1915

- Order: OCTOPODIDA Leach 1818 (OCTOPODA, octopuses)
  - Suborder: CIRRINA Grimpe 1916 (cirrate octopuses)
    - Family: CIRROTEUTHIDAE Keferstein 1866
    - Family: OPISTHOTEUTHIDAE Verrill 1896
  - Suborder: INCIRRINA Grimpe 1916 (incirrate octopuses)
    - Family: AMPHITRETIDAE Hoyle 1886
    - Family: BOLITAENIDAE Chun 1911
    - Family: IDIOCTOPODIDAE Taki 1962
    - Family: OCTOPODIDAE Orbigny 1840
    - Family: VITRELEDONELLIDAE Robson 1932
    - Division: Argonaut families
    - Family: ALLOPOSIDAE Verrill 1881
    - Family: ARGONAUTIDAE Tryon 1879 (paper nautiluses)
    - Family: OCYTHOIDAE Gray 1849
    - Family: TREMOCTOPODIDAE Tryon 1879

Appendix B

Synopsis of living cephalopod families

A summary of the characteristics of living cephalopod Families, typical genera and species listed alphabetically by Family. As in Appendix A, the Order and Suborder (where given) of each Family is shown in square brackets except where indicated, but higher order classifications (super-order, division) and sub-families are omitted. This synopsis is based mainly on information and figures in Nesis (1987), supplemented and modified from Clarke (1966), Roper *et al.* (1969, 1984) and Guerra (1992), as well as from the literature cited in the text. We also acknowledge original sources in Joubin (1895, 1900, 1920, 1924), Chun (1910), Pfeffer (1912) and Naef (1928), and the revisions proposed by Drs Louise Allcock and Martin Collins. Family names, their authorities and the list of recognised genera are consistent with Sweeney & Roper (1998) and the Integrated Taxonomic Information System (ITIS http://www.itis.usda.gov) except where specifically noted. An explanation of some of the difficulties associated with consistent terminology is given in the Classification (Appendix A).

The depth distributions given are approximate and relate to individual species; the larger families may include species with widely differing depth ranges. Where maximum depth ranges are given, it should be noted that these often arise from non-closing nets and are likely to exceed the actual maximum. Diurnal and regional variation is also present in many species, but is not described. Illustrations of a member of most families are provided with A-prefix numbers or reference is given to figures in the text.

The figures are NOT to scale, and many include an enlarged detail of the tentacular club.

Alloposidae Verrill 1881: large (<2 m overall) benthic or epibenthic gelatinous octopuses. Appear in the diet of North Atlantic sperm whales (Santos *et al.* 1999), Fig. A1. *Haliphron* Steenstrup 1861 [Octopodida, Incirrina]

Amphitretidae Hoyle 1886: a single genus and species of colourless, semi-transparent octopuses, almost enveloped by a layer of gelatinous tissue and with the mantle fused with the funnel. Mesobathybenthic, with juveniles also found in the epipelagic zone, Fig. A2. *Amphitretus* Hoyle 1885 [Octopodida, Incirrina]

Ancistrocheiridae Pfeffer 1912: a single genus and species of squid, widely distributed by depth in tropical and sub-tropical waters, numerous photophores, considered to be largely mesopelagic and slow-growing (Arkhipkin 1997). Placed within the Enoploteuthidae in earlier classifications. *Ancistrocheirus* Gray 1849 [Teuthida, Oegopsina]

Architeuthidae Pfeffer 1900: the giant squids of legend (Lane 1957; Ellis 1998), and certainly the largest mollusc and invertebrate, with authenticated specimens <2 m mantle length and <5 m overall length and 450 kg in weight (Roper & Boss 1982). Only known from dead or moribund single specimens cast ashore (Brix 1983; Boyle

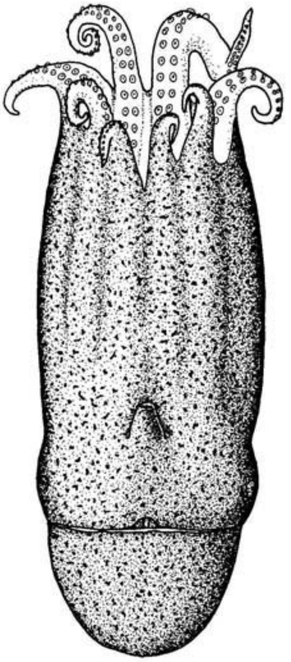


Fig. A1 Alloposidae (*Alloposus*).

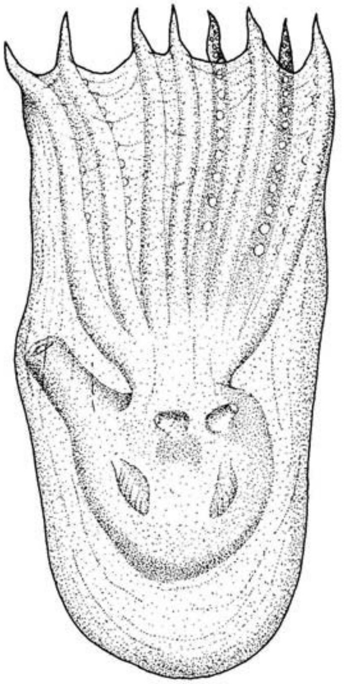


Fig. A2 Amphitredidae (*Amphitretus*).

1986d; Collins 1998; Ré *et al.* 1998, González *et al.* 2002b), caught in fishing nets, or retrieved from the stomachs of sperm whales, the true distribution and population biology of these animals is yet to be discovered, but they are thought to occupy the upper mesopelagic. Present in all oceans, but rarely found in the tropics and Antarctica, one genus with 15 nominal species is described, but the lack of specimens leaves doubt over these names (Roeleveld 2000), Fig. A3. *Architeuthis* Steenstrup 1857 [Teuthida, Oegopsina]

Argonautidae Tryon 1879: tropical and sub-tropical seas. Great sexual dimorphism; females characteristically secrete a thin laterally compressed calcareous shell moulded from two large flaps of tissue on the dorsal arms. Although not attached to the shell, it acts as a shelter and as a brood chamber for egg-laying (see Fig. 12.8). A small gas bubble possibly has a buoyancy function in life, and empty shells, commonly called ‘paper nautilus’, drift and are cast ashore. Occasional mass strandings of living animals are known (Norman 2000). Males are tiny (<15 mm total length), planktonic and with the relatively very large hectocotylised arm coiled within a thin pocket. After mating, the arm is cast off and remains within the female mantle cavity. Although very common in tropical waters and known since the writings of Aristotle, little is known of the biology of these animals, and these are only limited observations on movement and feeding (Guerra *et al.* 2002b; Voss & Williamson 1971; Young 1959). Probably feeding normally on planktonic heteropods and pteropods, Heeger *et al.* (1992) describe an association with the jellyfish *Phyllorhiza punctata* Von Lendenfeld 1884 in which *Argonauta* is apparently feeding on particles

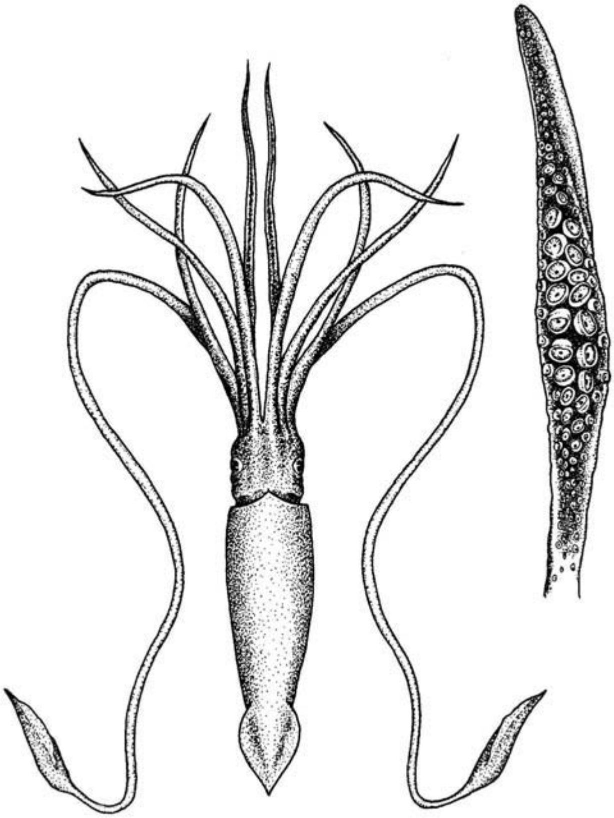


Fig. A3 Architeuthidae (*Architeuthis*).

in the gastric cavity of the jellyfish, as well as its tissues, while using its body as protection or camouflage against predators, Fig. A4. *Argonauta* Linnaeus, 1758 [Octopodida, Incirrina]

Bathyteuthidae Pfeffer 1900: a single genus with three species of small (<8 cm mantle length) gelatinous squid. *Bathyteuthis abyssicola* Hoyle 1885 is a cosmopolitan species, usually found in the depth range 1000–2500 m, Fig. A5. *Bathyteuthis* Hoyle 1885 [Teuthida, Oegopsina]

Batoteuthidae Young & Roper 1968: a monospecific genus of sluggish bathypelagic squids (*Batoteuthis skolops* Young & Roper 1968, <27 cm mantle length) from the southern Pacific, Scotia Sea and Falkland Islands (Malvinas), Fig. A6. *Batoteuthis* Young & Roper 1968 [Teuthida, Oegopsina]

Bolitaenidae Chun 1911: gelatinous, pigmented octopuses with short arms in the meso- and bathypelagic zones. Small stalked eggs with larvae covered with a sticky, gelatinous buoyant envelope (*Japatella diaphana* Hoyle 1885). Eggs carried on the arms by female *Bolitaena microtyla* Steenstrup in Hoyle 1886 until hatching, Fig. A7. *Bolitaena* Steenstrup 1959; *Japatella* Hoyle 1885; *Eledonella* Verrill 1884 [Octopodida, Incirrina]

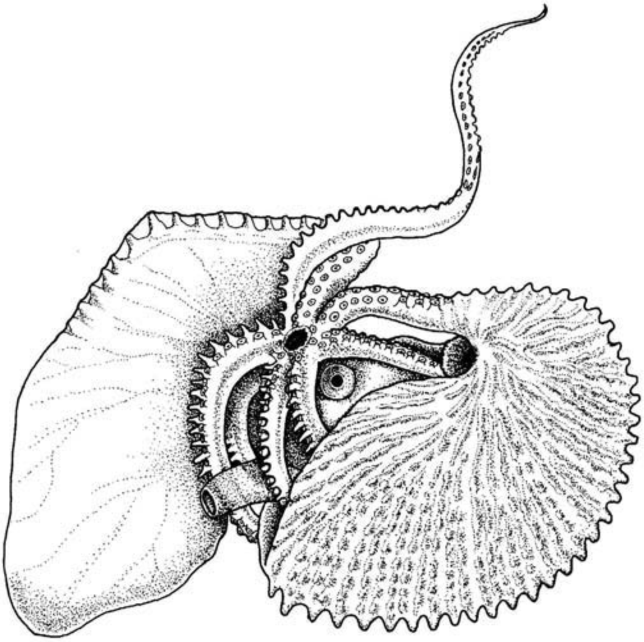


Fig. A4 Argonautidae (*Argonauta*).

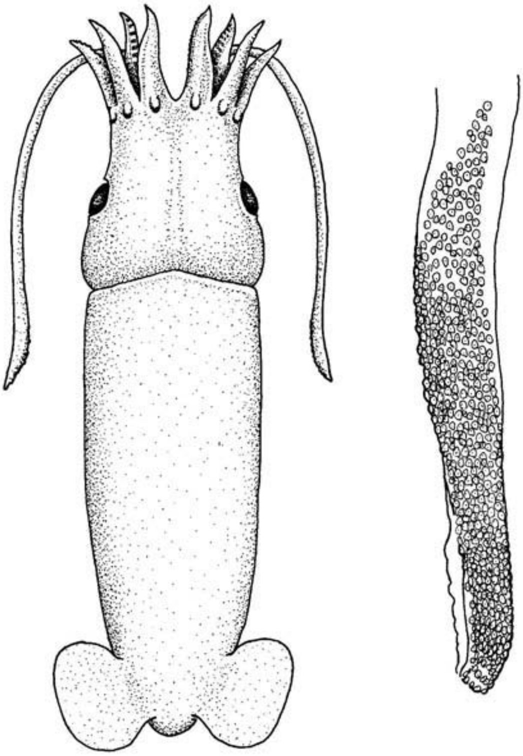


Fig. A5 Bathyteuthidae (*Bathyteuthis*).

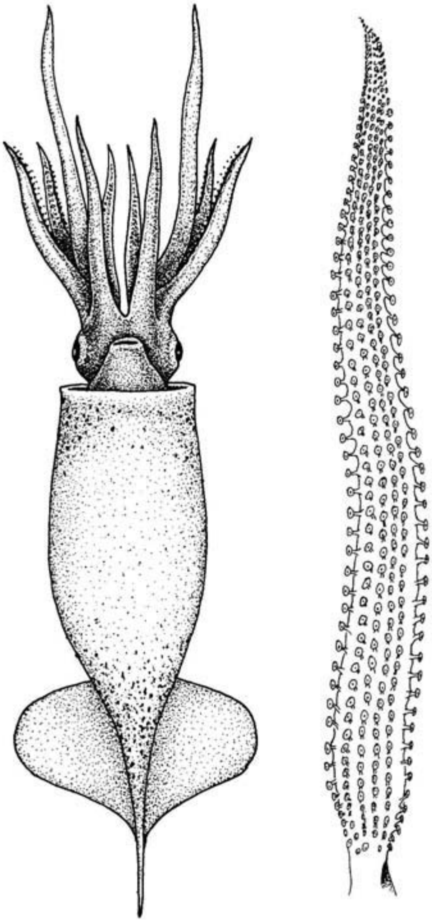


Fig. A6 Batoteuthidae (*Batoteuthis*).

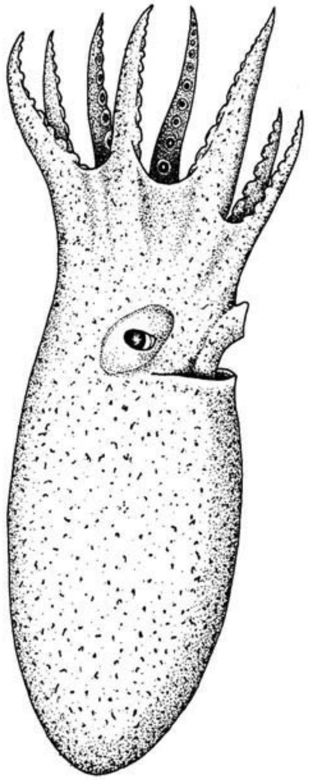


Fig. A7 Bolitaenidae (*Japatella*).

Brachioteuthidae Pfeffer 1908: small (<17 cm mantle length) weakly muscular squids, some cosmopolitan species (*Brachioteuthis riisei* (Steenstrup 1822)). Adults mainly mesopelagic and bathypelagic, young frequently epipelagic, Fig. A8. *Brachioteuthis* Verrill 1881 [Teuthida, Oegopsina]

Chiroteuthidae Gray 1849: bathypelagic or mesopelagic squid, four genera with 14 species. Medium-to-small sized (20–40 cm mantle length) with gelatinous tissues, photophores present in some, others covered with small cartilaginous tubercles. The larval forms are often strangely shaped with a very extended 'neck' between mantle and head that may be the only described form of a species (e.g. '*Doratopsis*'). *Grimialditeuthis*: gelatinous, medium-sized squids (one species) of meso- and bathypelagic depth distribution in the tropical and subtropical Atlantic and northern Pacific. Tentacles are completely lost, even in juveniles, with only short rudiments remaining, Figs. A9, A10. *Chiroteuthis* Orbigny 1841; *Asperoteuthis* Nesis 1980; *Grimalditeuthis* Joubin 1898; *Planctoteuthis* Pfeffer 1912 [Teuthida, Oegopsina]

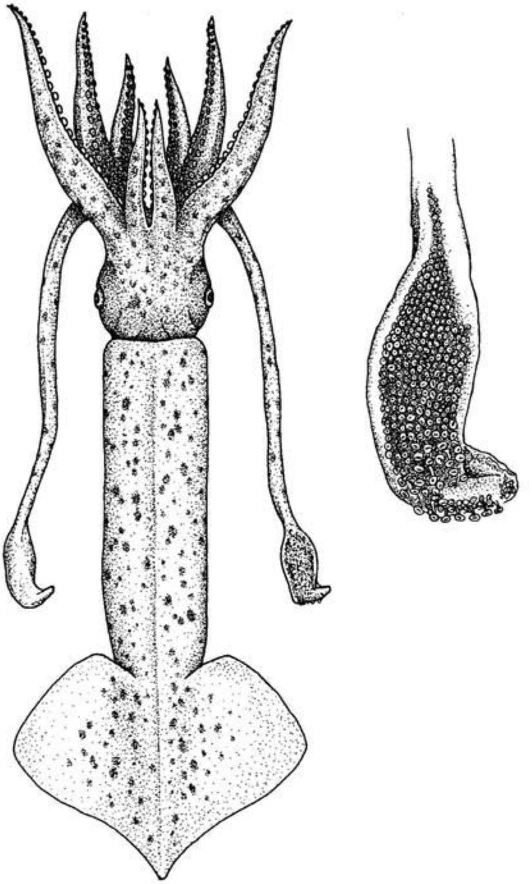


Fig. A8 Brachioteuthidae (*Brachioteuthis*).

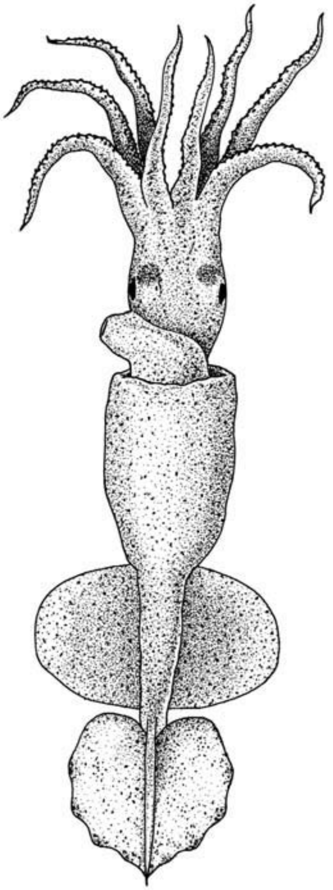


Fig. A9 Chiroteuthidae (*Grimalditeuthis*).

Chtenopterygidae Grimpe 1922: a single genus with two species of small (<9 cm mantle length) squids living in tropical to sub-tropical regions. Mesopelagic to bathypelagic in depth, with juveniles in the epipelagic. They are unusual animals in which the fins are sub-divided into a series of soft ‘rays’, but they share with all oegopsids the lack of a corneal covering to the eye. Based on other morphological features such as the presences of accessory nidamental glands and fused axons in the giant fibre system, coupled with evidence of relatedness from enzyme electrophoresis (Brierley *et al.* 1996b), it has been proposed to reclassify these squid as loliginid myposids, Fig. A11. *Chtenopteryx* Appellöf 1890 [Teuthida, Oegopsina]

Cirroteuthidae Keferstein 1866: medium to large octopuses some with secondary web and extremely long cirri, with bathyal to abyssal depth distribution. *Cirrothauma murrayi* Chun 1911 (1500–4500 m), *Cirrothauma* spp. (2900–4100 m; 4000–6200 m), *Cirroteuthis* n spp. (1300–2000 m; 2500–5200 m), *Stauroteuthis syrtensis* Verrill 1879 is broadly distributed in the North Atlantic at depths of 700–4000 m, with peak abundance at 1500–2500 m (Collins & Henriques 2000). This group of genera may be divided into separate families, the Cirroteuthidae

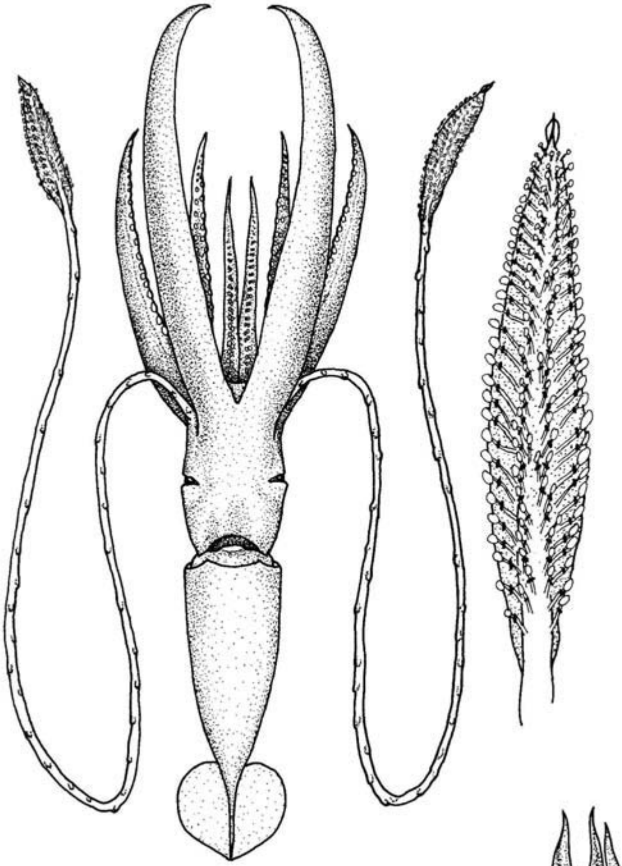


Fig. A10 Chiroteuthidae (*Chiroteuthis*).

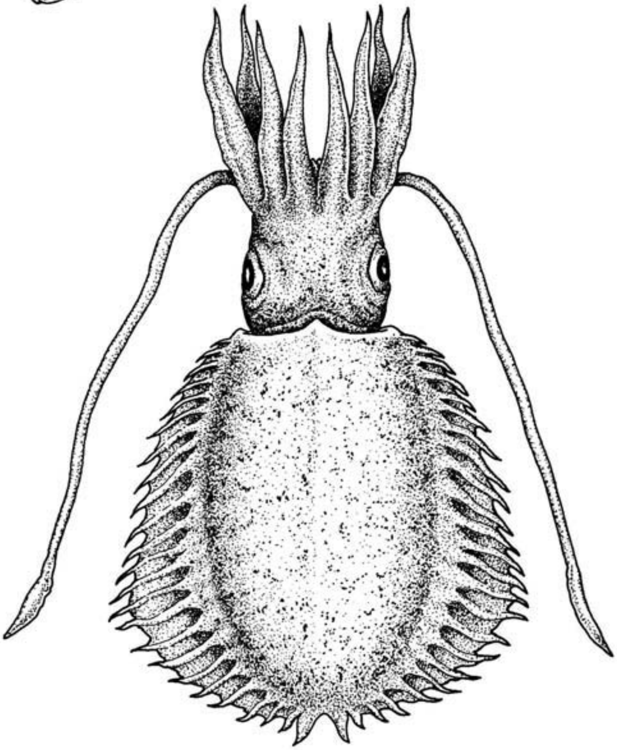


Fig. A11 Chtenopterygidae (*Chtenopteryx*).

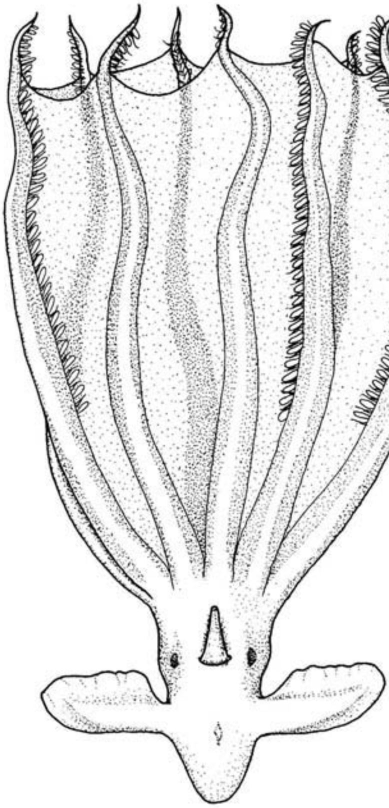


Fig. A12 Cirroteuthidae (*Cirrothauma*).

(*Cirrothauma*, *Cirroteuthis*) and Stauroteuthidae (*Stauroteuthis*), but molecular evidence suggests that they should be combined in Cirroteuthidae. Chunioteuthis Grimpe 1916 is no longer considered valid (Collins & Henriques 2000), and the validity of *Froekenia* has also been questioned, Fig. A12; see Fig. 12.10. *Cirroteuthis* Eschricht 1836; *Cirrothauma* Chun 1911; *Stauroteuthis* Verrill 1897 [Octopodida, Cirrina]

Cranchiidae Prosch 1847: a large and widely distributed family of squid with 13 genera and 30 species. Most species are characteristically mesopelagic or mesobathypelagic, but the larvae and young of some species are present in the epipelagic. Characteristic of the family is the presence of a spacious coelomic cavity that contains a volume of ammonium chloride at concentrations above 300 millimolar. The retained NH_4Cl solution is less dense than the salt water it displaces, and consequently reduces the average density of the body to that of the surroundings. Cranchids are consequently 'neutrally buoyant' with rather globular flaccid bodies (see Fig. 12.3). This is one of the most intensively studied of the mid-water squid families (e.g. Dilly & Nixon 1976; Nixon 1983; Voss & Voss 1983; Voss, N.A. 1985, 1988a). Spawning is probably quite short and (in common with species from other deep-water families, e.g. Onychoteuthidae, Gonatidae and Histioteuthidae) mature animals undergo gelatinous

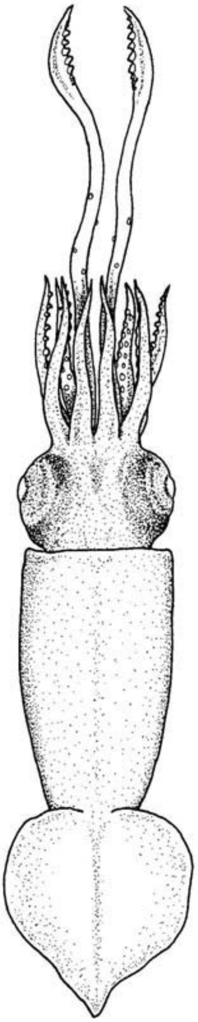


Fig. A13 Cranchiidae (*Mesonychoteuthis*).

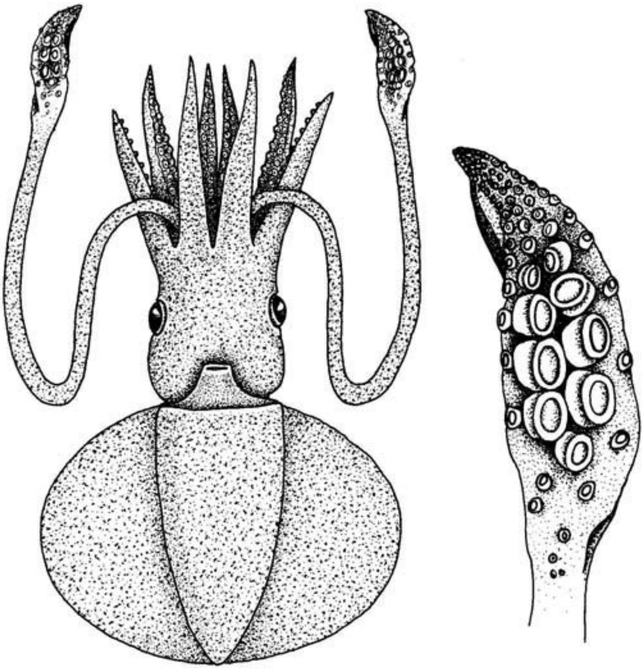


Fig. A14 Cycloteuthidae (*Discoteuthis*).

degeneration and may rise to the surface after spawning (Nesis *et al.* 1998). This feature of many deep-water squids may explain their common occurrence in the diets of shallow-diving marine birds, Fig. A13. *Cranchia* Leach 1817; *Liocranchia* Pfeffer 1884; *Leachia* Lesueur 1821; *Taonius* Steenstrup 1861; *Galiteuthis* Joubin 1898; *Mesonychoteuthis* Robson 1925; *Heliocranchia* Massy 1907; *Bathothauma* Chun 1906; *Sandalops* Chun 1906; *Liguriella* Issel 1908; *Egea* Joubin 1933; *Megalocranchia* Pfeffer 1884; *Teuthowenia* Chun 1910 [Teuthida, Oegopsina]

Cycloteuthidae Naef 1923: two genera and four species of medium-sized semi-gelatinous squids with tropical and sub-tropical distributions in the mesopelagic zone of all oceans, Fig. A14. *Cycloteuthis* Joubin 1999; *Discoteuthis* Young & Roper 1969 [Teuthida, Oegopsina]

Enoploteuthidae Pfeffer 1900: a large family of oceanic pelagic squids with species distributions ranging from epipelagic to bathypelagic, primarily in tropical and subtropical regions. Four genera and <40 species are recognised. The Japanese firefly squid (*Watasenia scintillans* (Berry 1911)) of the Sea of Japan, the Sea of Okhotsk, and Pacific coast of Japan is a small (<6 cm mantle length) squid with numerous photophores. The main distribution is mid-water, 225–1225 m deep, but in spring millions of animals migrate inshore into shallow water, where they are caught at night in fixed coastal nets and comprise one of the most important fished products in some bays (Hayashi 1993), and may be an important component of the diet of demersal fish (see Fig. 12.7). *Enoploteuthis* Rüpell 1844; *Abralia* Gray 1849; *Abraliopsis* Joubin 1896; *Watasenia* Ishikawa 1914 [Teuthida, Oegopsina]

Gonatidae Hoyle 1886: mid-water in temperate and cold waters of both hemispheres, mainly mesopelagic and bathypelagic in depth distribution. *Gonatus* are widely distributed and abundant in the North Atlantic, where they are important food sources for sperm whales and other cetaceans (Bjørke & Gjosaeter 1998; Santos *et al.* 1999). The pelagic eggs of *Gonatus onyx* Young 1972, an abundant species off the California coast where it has been the subject of intensive observations at depth from remotely operated underwater vehicles (ROVs) (Hunt & Seibel 2000) may be 'brooded' by the post-reproductive female at depths of 1250–1750 m. These females are apparently senescent and lacking tentacles (Seibel *et al.* 2000a). *Berryteuthis* is typically mesopelagic in distribution during the day (Bower *et al.* 2002), rising to near the surface at night, where it is the object of important fisheries, particularly around Japan (Natsukari *et al.* 1993; reviewed by Nesis 1987), Fig. A15. *Gonatus* Hoyle 1886; *Gonatopsis* Sasaki 1920; *Berryteuthis* Naef 1921 [Teuthida, Oegopsina]

Grimalditeuthidae Pfeffer 1900, see Chiroteuthidae

Grimpoteuthidae O'Shea 1999, see Cirroteuthidae

Histioteuthidae Verrill 1881: a single genus comprising 15 species of medium-to-large squids. Widely distributed in depth in the meso- and bathypelagic, but some extending down to bathybenthic and up to the lower sub-littoral. Globally distributed except in polar regions, important in the diet of whales and other predators. The mantle is usually small and conical, and the large head bears asymmetrically developed eyes with the left eye usually much larger than the right. Numerous complex photophores are distributed over the ventral surface of the mantle, head and arms. Review of the family by Voss 1969. Fig. A16, Fig. 12.4a, b. *Histioteuthis* Orbigny 1841 [Teuthida, Oegopsina]

Idioctopodidae Taki 1962: gelatinous, semi-transparent octopuses of the upper bathyal. One genus and one species, *I. gracilipes* Taki 1962. *Idioctopus* Taki 1962 [Octopodida, Incirrina]

Idiosepiidae Appellöf 1898: very small animals (6–17 mm mantle length males, 8–22 mm females). One genus with seven species living in the Indo-West Pacific. Coastal and living in beds of seaweed, often adhering to the plants by a dorsal attachment area, Fig. A17. *Idiosepius* Steenstrup 1881 [Order Sepioidea]

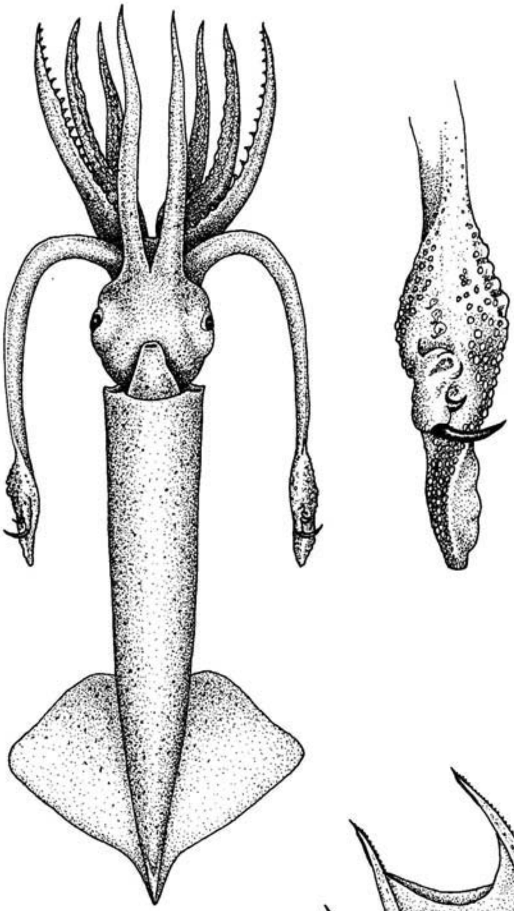


Fig. A15 Gonatidae (*Gonatus*).

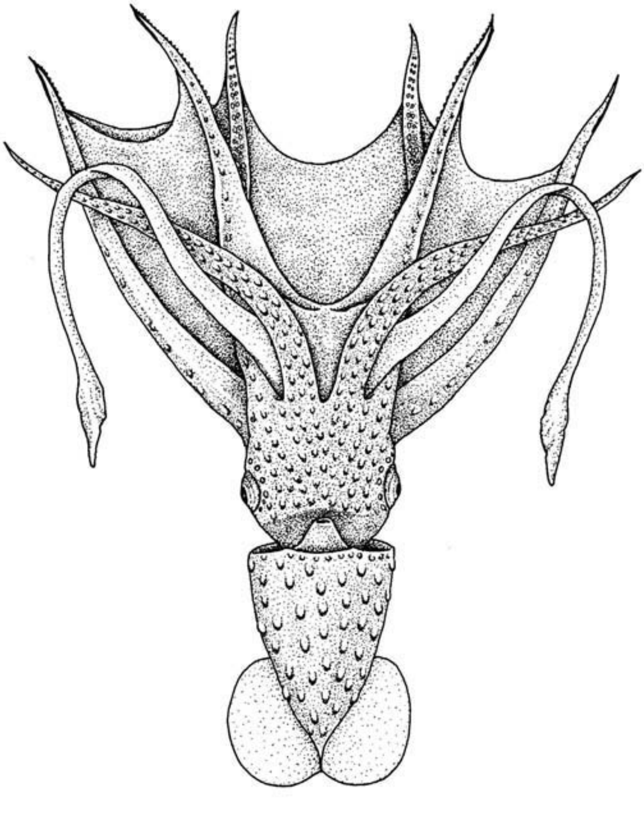


Fig. A16 Histioteuthidae (*Histioteuthis*).

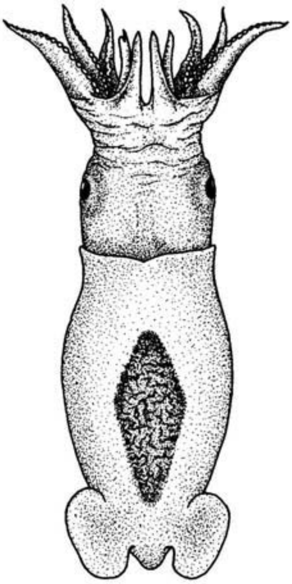


Fig. A17 Idiosepiidae (*Idiosepius*).

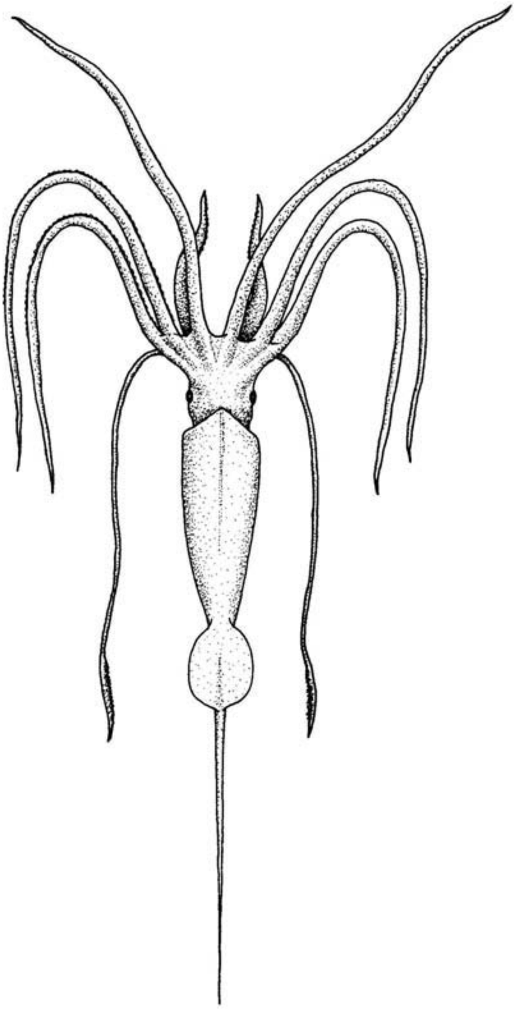


Fig. A18 Joubiniteuthidae (*Joubiniteuthis*).

Joubiniteuthidae Naef 1922: a monospecific genus (*J. portieri* Joubin 1916) of meso- and bathypelagic zones of the tropical and sub-tropical Atlantic, and including the Caribbean Sea and the north Pacific, Fig. A18. *Joubiniteuthis* Berry 1920 [Teuthida, Oegopsina]

Lepidoteuthidae Pfeffer 1908: large squids (<80 cm mantle length) with a narrow cylindrical mantle with the surface (except the sector between the fins) covered on the dorsal and ventral sides with flat plates of connective tissue (often described as 'papillae', Clarke 1963) resembling the scales of early fish. Photophores are not described. 'Scaled squids', fairly active deep-water predators, with mesobathypelagic and bathyal–benthic distributions down to 2000 m, Fig. A19. *Lepidoteuthis* Joubin 1895; *Pholidoteuthis* Adam 1950; *Tetronychoteuthis* Pfeffer 1900 [Teuthida, Oegopsina]

Fig. A19 Lepidoteuthidae (*Lepidoteuthis*).

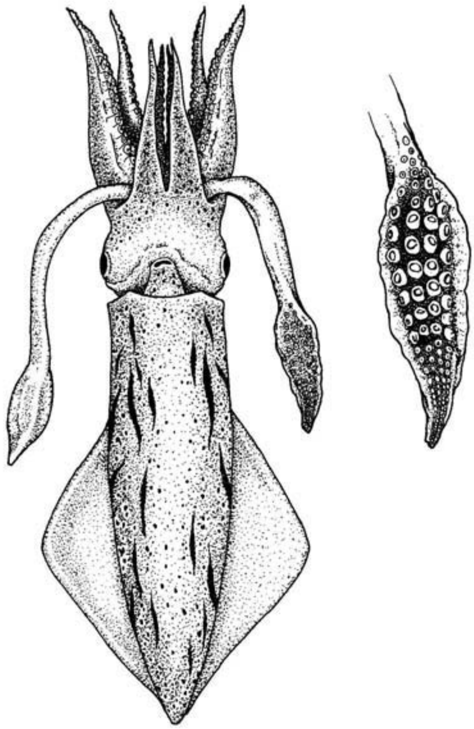


Fig. A20 Loliginidae (*Loligo*).

Loliginidae Lesueur 1821: the dominant family of coastal and neritic squid comprising seven genera and 41–50 species (see Chapters 11, 17 and 18). With their dependence on the bottom for egg deposition, and association with feeding on demersal prey species, they are normally limited in distribution to the shelf, where they are major and valuable fisheries (mostly trawling) in temperate and tropical regions throughout the world. In the course of dispersal and migratory movements, however, they are often over deep oceanic water and occupy significant depth ranges: *Loligo gahi* Orbigny 1835, <800 m; *L. forbesi* Steenstrup 1856, <400 m; *L. pealei* Lesueur 1821, <400 m; *L. vulgaris* Lamarck 1798, <500 m; *Alloteuthis media* Linnaeus 1758, <350 m. The North Atlantic *Loligo forbesi* is unusual in appearing to occupy a significant 'offshore' distribution (Pierce *et al.* 1994e) in addition to the coastal range, and to be present in truly oceanic water around the seamounts and islands of the Azores (Martins & Porteiro 1988). No evidence is available to support migrations to and from the mainland of Europe or Africa (1500 km), but from evidence of genetic distance, a single introduction event some 750 000 years ago is postulated (Brierley *et al.* 1995), Fig. A20. *Loligo* Lamarck 1798; *Loliolus* Steenstrup 1856; *Lolliguncula* Steenstrup 1881; *Sepioteuthis* Blainville 1824;*Uroteuthis* Rehder 1945 [Teuthida, Myopsina]

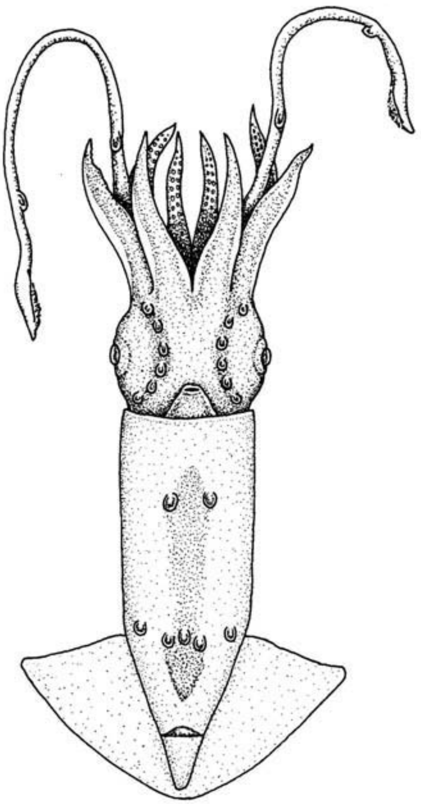


Fig. A21 Lycoteuthidae (*Lycoteuthis*).

Lycoteuthidae Pfeffer 1908: small mesopelagic and benthic–bathyal squids of the tropics and sub-tropics, commonly with numerous luminous organs of a variety of structures and functions (see Fig. A21). *Lycoteuthis* Pfeffer 1900; *Selenoteuthis* Voss 1959; *Nematolampas* Berry 1913 [Teuthida, Oegopsina]

Magnapinnidae Vecchione & Young 1998: a family established to accommodate an unusual paralarva from Hawaii and two juvenile specimens described by Young (1991). Although related to the chiroteuthid group of families (Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Batoteuthidae, Promachoteuthidae), *M. pacifica* Vecchione & Young 1998 was named after its most distinguishing 'bigfin' characteristic. Subsequently, it has been suggested that some of the remarkable animals seen from submersibles but not captured belong to this family of oceanic squids (Vecchione *et al.* 2001a). *Magnapinna* Vecchione & Young 1998 [Teuthida, Oegopsina]

Mastigoteuthidae Verrill 1881: a squid genus with 16 species of medium size (15–30 cm mantle length) and of bathypelagic and mesopelagic depth distribution. The vacuolated body and arms provide buoyancy, probably leading to a vertical attitude of the body in life, with the elongated whip-like tentacles (covered in minute, sticky pedunculated suckers) hanging passively down where they might entangle passing prey (Dilly 1977), Fig. A22. *Mastigoteuthis* Verrill 1881 [Teuthida, Oegopsina]

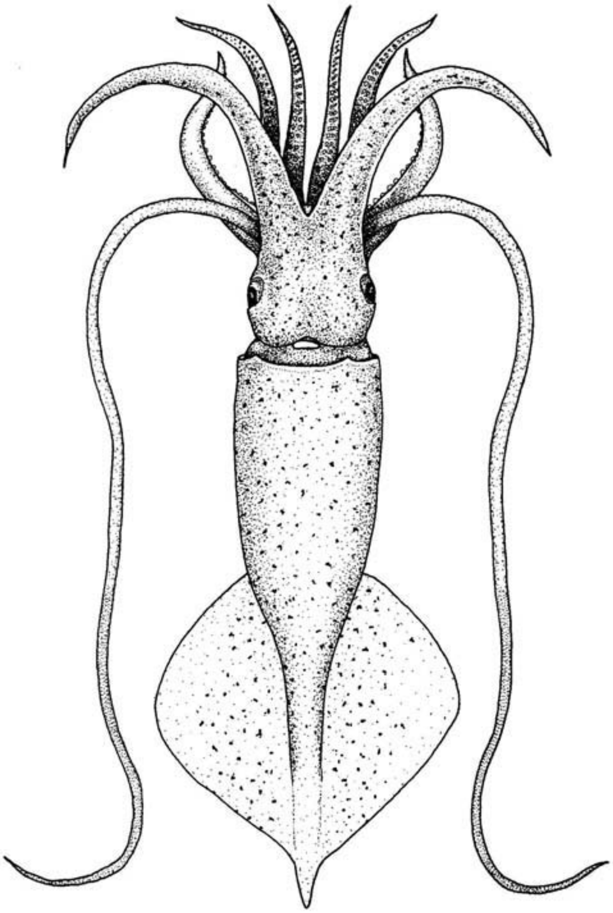


Fig. A22 Mastigoteuthidae (*Mastigoteuthis*).

Nautilidae Blainville 1825: living relatives of the extinct forms found in the fossil record since the early Palaeozoic. Occupying a strong, chambered, calcareous shell enclosing a gas space adjustable in volume to result in neutral buoyancy, these animals range at least from the surface to 1000 m. Common close to the bottom at 600–700 m off islands in the tropical Indo-Pacific, they are the subject of baited trap fisheries for their flesh and the valuable shells. Many aspects of their biology and life cycle differ from those of the 'modern' order Coleoidea (see Chapter 4), and they are particularly well adapted metabolically to the low-oxygen conditions of the oxygen minimum layer (Boutilier *et al.* 1996). Seven nominal species in two genera, Fig. A23, Fig. 4.5. *Nautilus* Linnaeus 1758; *Allonautilus* Ward & Saunders 1997 [Subclass Nautiloidea, Order Nautilida]

Neoteuthidae Naef 1921: small to medium (<27 cm mantle length) mesobathypelagic species from two genera. *Alluroteuthis antarctica* Odhner 1923 (750–2800 m), Fig. A24. *Neoteuthis* Naef 1921; *Alluroteuthis* Odhner 1923; *Nototeuthis* Nesis & Nikitina 1986 [Teuthida, Oegopsina]

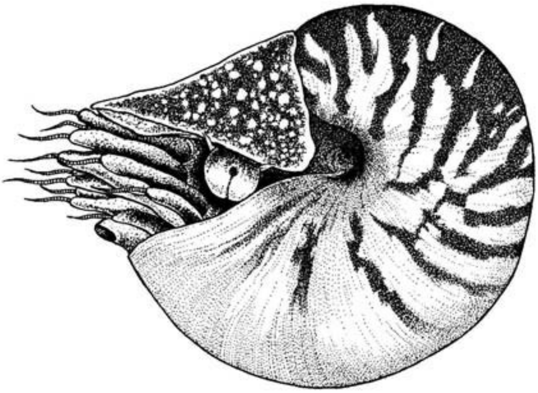


Fig. A23 Nautilidae (*Nautilus*).

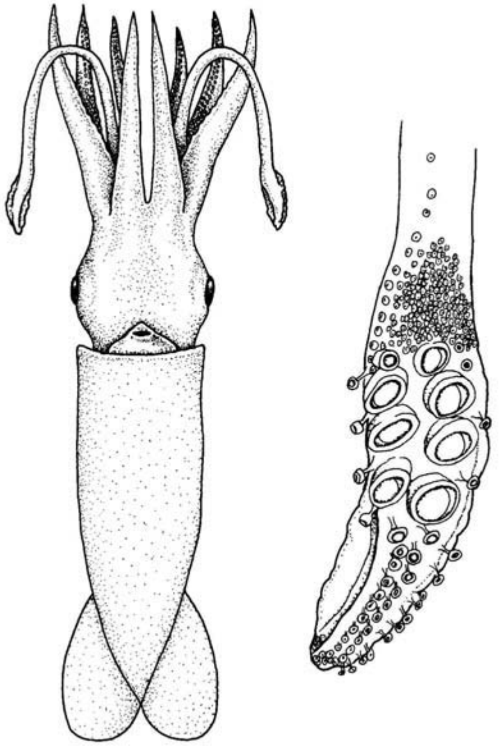


Fig. A24 Neoteuthidae (*Alluroteuthis*).

Octopodidae Orbigny 1840: the abundant common octopuses of the neritic (shelf) zone. The genus *Octopus* alone has over 100 described species, has provided the model for much of the general knowledge of cephalopods and is the basis for valuable inshore fisheries (see Chapters 2 and 11). Some species of typical shelf genera extend downwards on the continental slope, e.g. *Eledone cirrhosa* (Lamarck 1798) (<850 m), *E. moschata* (Lamarck 1798) (<300 m), *Octopus longospadiceus* (Sasaki 1917) (<800 m), *Pareledone* spp. (<750 m), *Pteroctopus tetracirrhus* (Chiaie 1830) (<750 m), *Scaeurgus unicirrhus* (Chiaie 1839–1841, in Férrusac and Orbigny 1834–1848) (<800 m). Other genera are characteristic of the upper shelf, e.g.

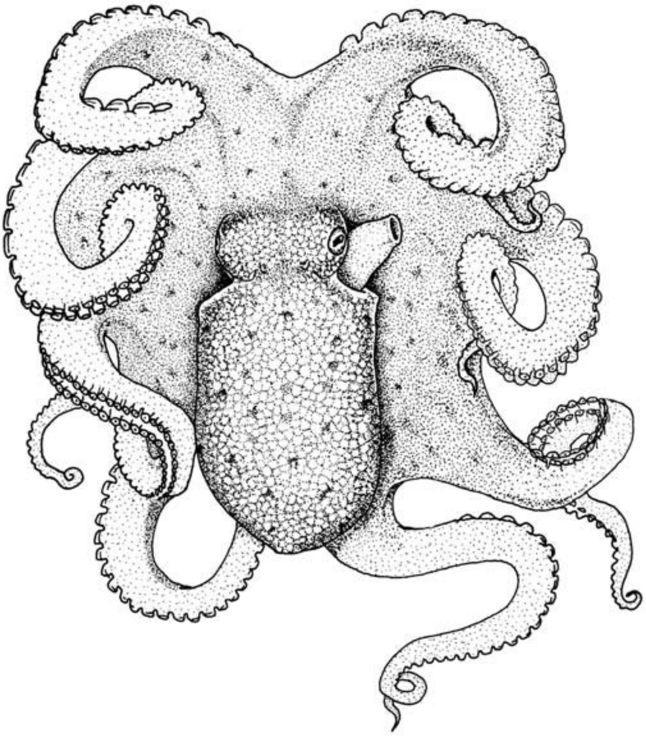


Fig. A25 Octopodidae (*Octopus*).

Pteroctopus hoylei (Berry 1909) (50–850 m), *P. schmidti* (Joubin 1933) (300–1200 m), *Benthoctopus ergasticus* (Fischer & Fischer 1892) (450–1400 m), *B. hokkaiddensis* (Berry 1921) (130–1000 m), *Graneledone*. A succession of octopus genera and species with on the upper limits of distribution extend down the slope into bathyal regions, where some are quite characteristic faunal components, such as *Bathypolypus*, *Bentheledone*, *Thaumeledone*, *Benthoctopus piscatorum* (Verrill 1879) (80–2500 m), *B. profundorum* Robson 1932 (150–3400 m), *Graneledone verrucosa* (Verrill 1881) (850–2300 m), *G. boreopacifica* Nesis 1982 (1000–2000 m), Fig. A25. *Octopus* Cuvier 1797; *Ameloctopus* Norman 1992; *Aphrodoctopus* Roper & Mangold 1992; *Cistoctopus* Gray 1849; *Enteroctopus* Rochebrune & Mabille 1889; *Euaxoctopus* Voss 1971; *Hapalochlaena* Robson 1929; *Pteroctopus* Fischer 1882; *Robsonella* Adam 1938; *Scaeurgus* Troschel 1857; *Eledone* Leach 1817; *Pareledone* Robson 1932; *Tetracheledone* Voss 1955; *Vosseledone* Palaccio 1978; *Velodona* Chun 1915; *Graneledone* Voss 1988; *Bentheledone* Robson 1932; *Thaumeledone* Robson 1930; *Megaledone* Taki 1961; *Bathypolypus* Grimpe 1921; *Benthoctopus* Grimpe 1921; *Teretoctopus* Robson 1929; *Grimpella* Robson 1928 [Octopodida, Incirrina]

Octopoteuthidae Berry 1912: gelatinous, medium- and large-size squids of the mesopelagic and benthic–bathyal of tropical and temperate seas. Two genera with 7–10 species. *Taningia danae* Joubin 1931 is a large (<1.6 m mantle length) cosmopolitan species, mainly in tropical and sub-tropical waters (Clarke 1967), that

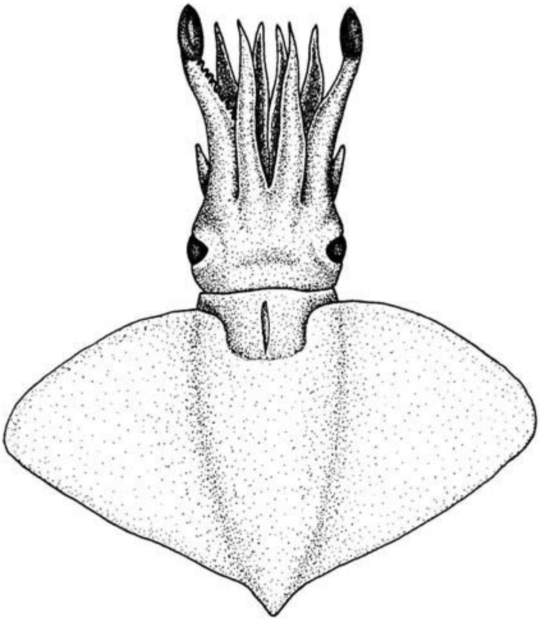


Fig. A26 Octopoteuthidae (*Taningia*).

is occasionally caught in deep-water trawls at high latitudes (Santos *et al.* 2001), Fig. A26. *Octopoteuthis* Rüppell 1844; *Taningia* Joubin 1931 [Teuthida, Oegopsina]

Ocythoidae Gray 1849: females (mantle length <30 cm) much larger than males (mantle length <3 cm). Males often found in empty tests of doliolids and salps (Tunicata). One genus and one species, cosmopolitan, sub-tropical. Retention of a small gas bubble is described by Packard & Wurtz (1994), Fig. A27. *Ocythoe* Rafinesque 1814 [Octopodida, Incirrina]

Ommastrephidae Steenstrup 1859: the major family of pelagic squid exploiting high-energy and productive regions of the open ocean and shelf-break regions (see Chapters 11, 17 and 18) and the subject of the most important commercial fisheries world-wide. They are active, muscular species, voracious, shoaling and abundant predators, often making extensive feeding migrations over the shelf. Eggs are laid in diffuse gelatinous masses, apparently neutrally buoyant at density discontinuities (pycnoclines) at depth. Hatchlings rise to the surface, growing and feeding in upwelling and convergence zones before returning to breed at depth. Species from this family comprise about 70% of the global landings from commercial cephalopod fisheries, most of the catch arising from jig-fishing for squid of the genera *Illex*, *Todarodes*, *Nototodarus*, *Todaropsis*, *Dosidicus* and *Ommastrephes*. Although these major catches arise in the productive epipelagic zone at night, ommastrephid species undergo diurnal migration throughout the upper 1000 m and many may be distributed to significantly greater depths: *Illex argentinus* (Castellanos 1960) (<800 m); *Illex coindetii* (Verany 1839) (<1000 m); *I. illecebrosus* (Lesueur 1821) (<1000 m); *I. oxygonius* (Roper Lu & Mangold 1969) (<550 m); *Todaropsis eblanae* (Ball 1841)

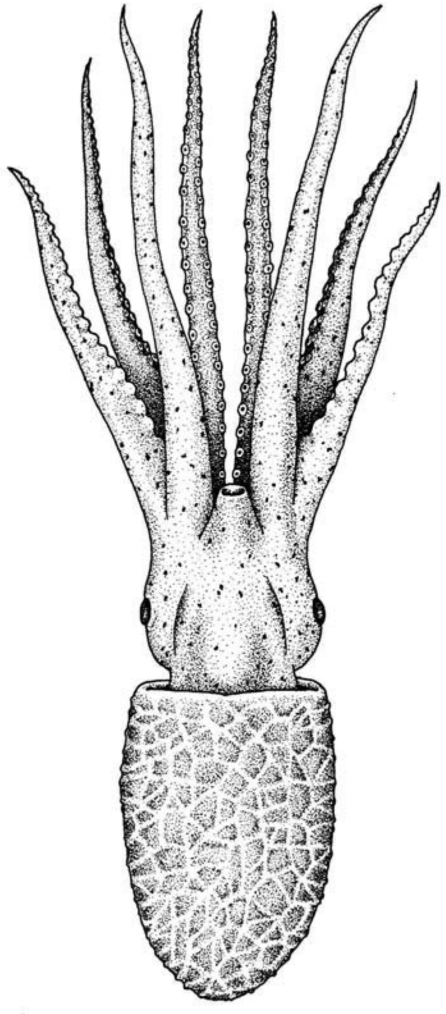


Fig. A27 Ocythoidae (*Ocythoe*).

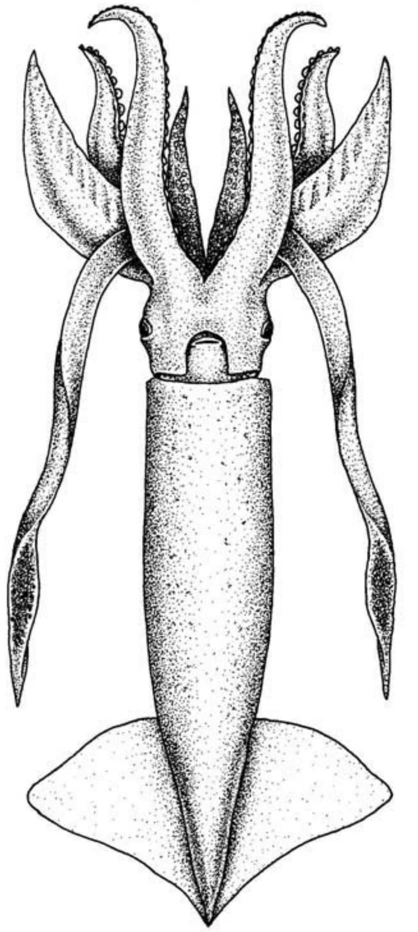


Fig. A28 Ommastrephidae (*Ommastrephes*).

(<700 m); *Todarodes filippovae* (Adam 1975) (<500 m); *T. sagittatus* (Lamarck 1798) (1000 m); *T. pacificus* (Steenstrup 1880) (<500 m); *Nototodarus* sloanii (Gray 1849) (<500 m); *N. gouldi* (McCoy 1888) (1130 m); *N. hawaiiensis* (Berry 1912) (570 m); *Martialia hyadesi* Rochbrune & Mabille 1889; *Ornithoteuthis antillarum* (Adam 1957) (<1100 m); *Dosidicus gigas* (Orbigny 1835) (<500 m); *Ommatrephes bartrami* (LeSueur 1821) (<1500 m); *Sthenoteuthis pteropus* (Steenstrup 1855) (<3160 m); *S. oualaniensis* (Lesson 1830) (<1000 m); *Hyaloteuthis pelagica* (Bosc 1802) (<200 m); *Eucleoteuthis luminosa* (Sasaki 1915) (<1300 m); Fig. A28. *Illex* Steenstrup 1880; *Todarodes* Steenstrup 1880; *Todaropsis* Girard 1890; *Nototodarus* Pfeffer 1912; *Martialia* Rochebrune & Mabille 1889; *Ommastrephes* Orbigny 1834; *Sthenoteuthis* Verrill 1880; *Dosidicus* Steenstrup 1857; *Eucleoteuthis* Berry 1916; *Ornithoteuthis* Okada 1927; *Hyaloteuthis* Gray 1849 [Teuthida, Oegopsina]

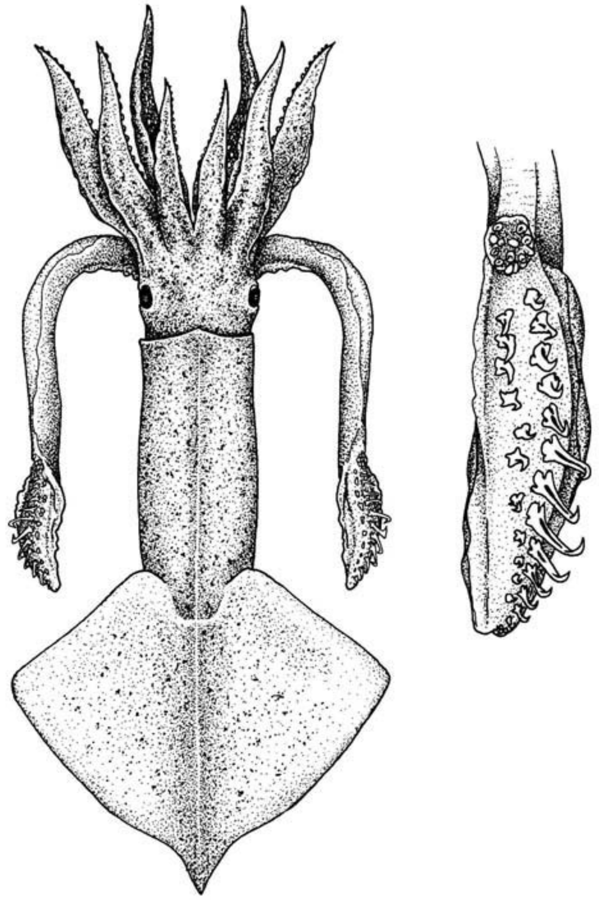


Fig. A29 Onychoteuthidae (*Onychoteuthis*).

Onychoteuthidae Gray 1849: active nektonic and mostly muscular squids, ranging in size from small (*Onychia* <12 cm mantle length) to very large (*Moroteuthis*, <2.3 m mantle length in *M. robusta* (Verrill 1876)) species, and in depth throughout the epipelagic to the mesopelagic and bathybenthic. Terminal spawning is described in *Moroteuthis ingens* Smith 1881, with degeneration of muscular tissues associated with the onset of maturity, leading to post-spawning gonad regression, breakdown and disorganisation of musculature, and death possibly from asphyxia (Jackson & Mladenov 1994). Luminescent organs only in *Onychoteuthis* (*O. banksii* (Leach 1817) is epipelagic and commercially fished in the northwestern Pacific), *Ancistroteuthis* and *Kondakovia* (Antarctic) (Arkhipkin & Nigmatullin 1997), Fig. A29. *Onychoteuthis* Lichtenstein 1818; *Onykia* Lesueur 1821; *Ancistroteuthis* Gray 1849; *Moroteuthis* Verrill 1881; *Kondakovia* Filippova 1972 [Teuthida, Oegopsina]

Opisthoteuthidae Verrill 1896: small to large semi-gelatinous octopuses, lacking secondary web and with cirri of small to moderate length. The ‘flapjack devilfish’ of Berry (1955, 1952). Bathyal to abyssal. Four genera: *Opisthoteuthis*; *Grimpoteuthis*; *Luteuthis*; *Cirroctopus*. This group of genera may be divided into separate families,

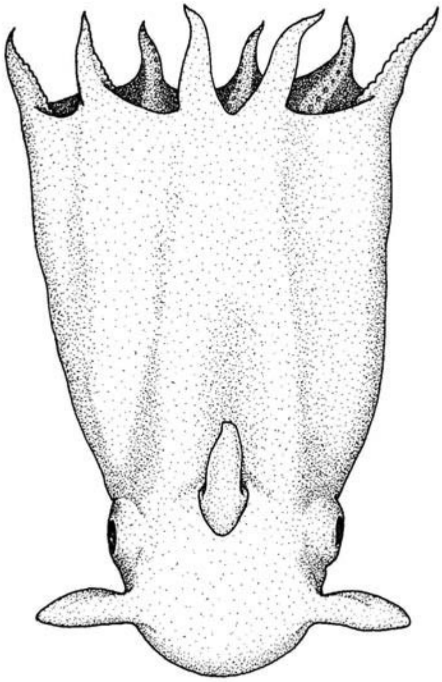


Fig. A30 Opisthoteuthidae (*Opisthoteuthis*).

Opisthoteuthidae (*Opisthoteuthis*) and Grimpoteuthidae (*Grimpteuthis*, *Luteuthis*), with molecular evidence suggesting a new family for *Cirroctopus* (formerly considered a junior synonym of *Grimpoteuthis*) (Piertney *et al.* 2003). *O. agassizii* Verrill 1883 (500–2250 m), *O. californiana* Berry 1949 (125–1100 m), *O. depressa* Ijima & Ikeda 1895 (130–1100 m), *O. pluto* Berry 1918 (275–1100 m). *Grimpoteuthis umbellata* (Fischer 1883) (2235 m), *G. albatrossi* (Sasaki 1920) (136–3400 m), Fig. A30, Fig. 12.10. *Opisthoteuthis* Verrill 1896; *Grimpoteuthis* Robson 1932; *Luteuthis* O'Shea 1999; *Cirroctopus* Naef [Octopodida, Cirrina]

Pickfordiateuthidae Voss 1953: very small squid (15–20 mm mantle length) of shallow waters over sand and seagrass meadows of the tropical western Atlantic, Fig. A31. A single species, *Pickfordiateuthis pulchella* Voss 1953, in one genus. *Pickfordiateuthis* Voss 1953 and later placed within the family Loliginidae by Brachionecki 1996. Another species, *Pickfordiateuthis bayeri*, has been caught by submersible operation (Roper & Vecchione 2001) [Teuthida, Myopsina]

Promachoteuthidae Naef 1912: a single genus with two species of squid in which the thick semi-gelatinous mantle is partially fused with the head. Taken only from bathypelagic and abyssopelagic zones, Fig. A32. *Promachoteuthis* Hoyle 1885 [Teuthida, Oegopsina]

Psychroteuthidae Thiele 1920: a monospecific genus (*Psychroteuthis glacialis* Thiele 1920) of squid (<44 cm mantle length) with two undescribed species from the Antarctic (Nesis 1987). An unusually large composite photophore on the tips of the

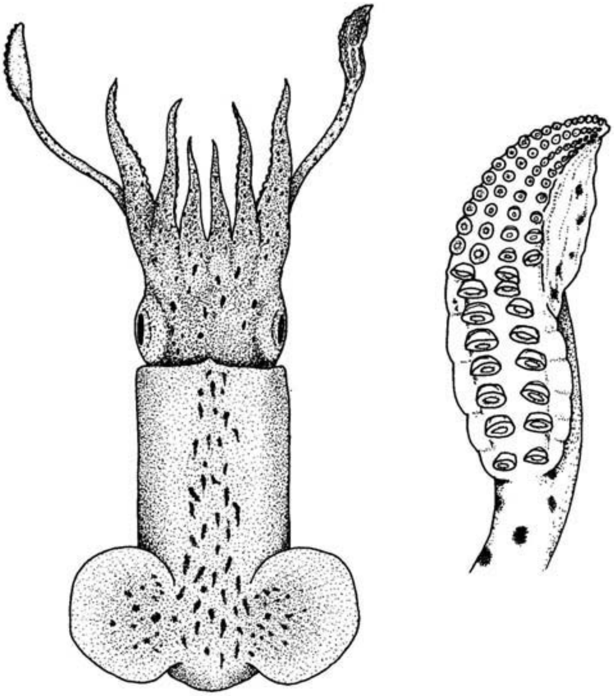
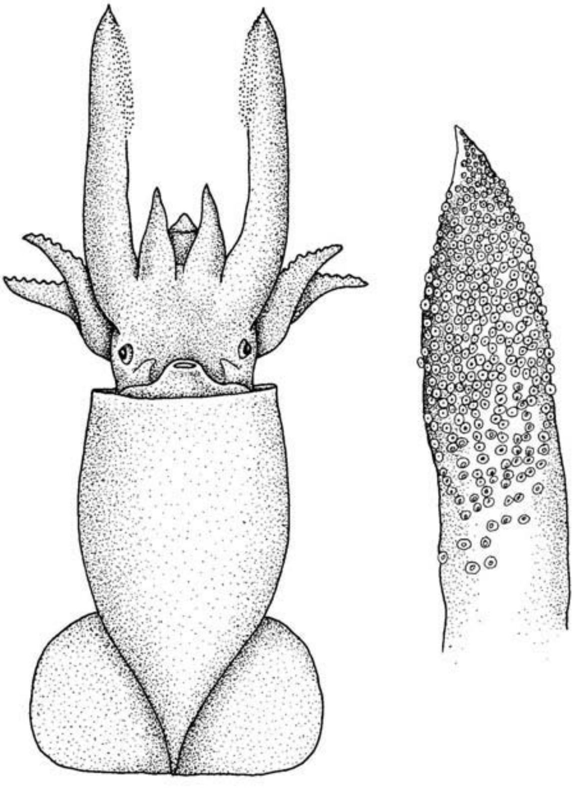


Fig. A31 Pickfordiateuthidae (*Pickfordiateuthis*).

Fig. A32 Promachoteuthidae (*Promachoteuthis*).



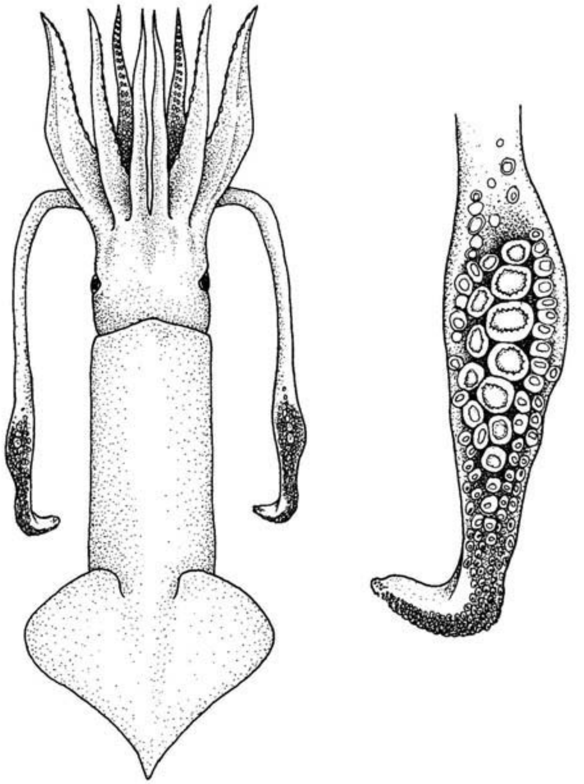


Fig. A33 Psychroteuthidae (*Psychroteuthis*).

third arms of females consists of alternating light plates with covering black vanes (screens), Fig. A33. *Psychroteuthis* Theile 1920 [Teuthida, Oegopsina]

Pyroteuthidae Pfeffer 1912: small mesopelagic and epipelagic squids of tropical and sub-tropical waters. Two genera each with three species, formerly included within the Enoploteuthidae. *Pyroteuthis* Hoyle 1904; *Pterygioteuthis* Fischer 1896 [Teuthida, Oegopsina]

Sepiadariidae Fischer 1882: small animals (20–40 mm mantle length), benthic on the shelf of tropical and sub-tropical seas. Two genera, *Sepiadarium* with five species in the Indo-West Pacific and *Sepioloidea* with two species off Australia and New Zealand, Fig. A34. *Sepiadarium* Steenstrup 1991; *Sepioloidea* Orbigny 1845 [Order Sepioidea]

Sepiidae Keferstein 1866: the abundant 'true' cuttlefishes of the neritic (shelf) zone with a calcareous chambered 'cuttlebone' acting as a buoyancy organ. The genus *Sepia* alone has >100 described species and comprises valuable fisheries (see Chapters 11, 16 and 17), but no cuttlefish occur on the coasts of the North or South Americas. *Sepia officinalis* Linnaeus 1758, the common cuttlefish of the eastern Atlantic and Mediterranean, occurs on sandy to muddy bottoms from the coastline to 200 m, and is most abundant in the upper 100 m. Cuttlefish are typically active at

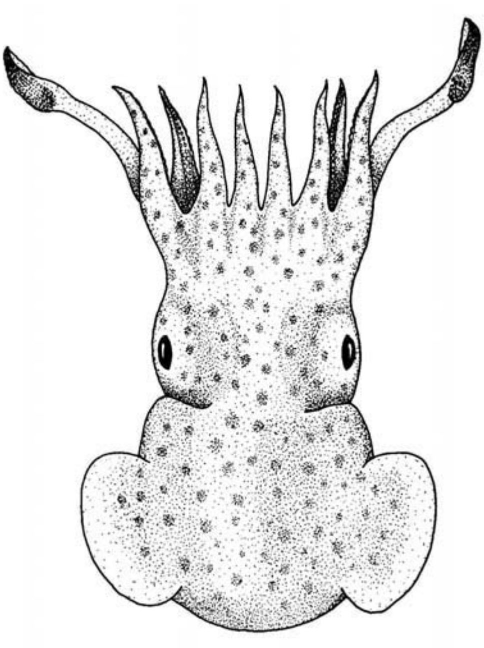


Fig. A34 Sepiadariidae (*Sepiadarium*).

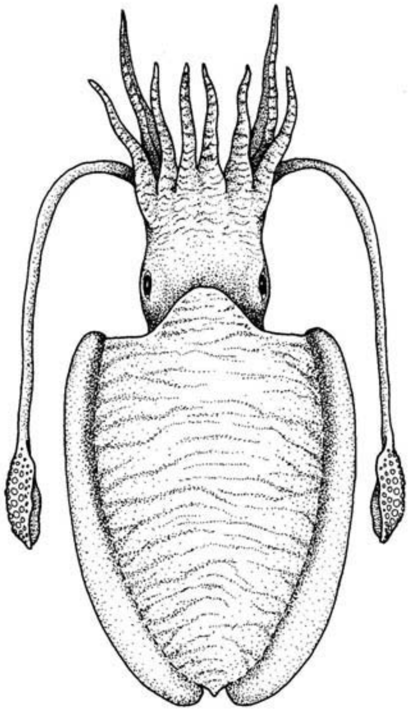


Fig. A35 Sepiidae (*Sepia*).

night, but they sit on the bottom during daylight, often covering themselves with sediment. Distributions of some typical shelf species extend downwards on the upper continental slope. These include *Sepia cultrata* Hoyle 1885 (150–820 m), *Sepia elegans* Blainville 1827 (<439 m), *Sepia orbignyana* Férrusac in Orbigny 1826 (<150 m), Fig. A35. *Sepia* Linnaeus 1758; *Metasepia* Hoyle 1885; *Sepiella* Gray 1849 [Order Sepioidea]

Sepiolidae Fioroni 1981: small (usually <10 cm mantle length) animals, mostly benthic animals of the shelf, with some mid-water pelagic species. Three sub-families, 14 genera with 51–56 species, a few having depth distributions extending down the continental slope. *Sepiola rondoleti* Leach 1834 (<450 m), *Sepietta oweniana* (Orbigny 1839–1841 in Férrusac and Orbigny 1834–1848) (50–600 m), *Rondletiola minor* (Naef 1912) (80–400 m), *Austrorossia antillensis* (Voss 1955) (540–700 m), *Rossia bullisi* Voss 1956 (<400 m), *R. macrosoma* (Chiaie 1830) (30–600 m), *R. tortugaensis* (Voss 1956) (540–480 m), *Neorossia caroli* (Joubin 1902) (300–1000 m), *Semirossia equalis* (Voss 1950) (130–260 m), Fig. A36. *Sepiola* Leach 1817; *Euprymna* Steenstrup 1887; *Rondeletiola* Nael 1921; *Sepietta* Naef 1921; *Inioteuthis* Verrill 1881; *Rossia* 1834; *Austrorossia* Berry 1918; *Semirossia* Steenstrup 1887; *Neorossia* Boletzky 1971; *Heteroteuthis* Gray 1849; *Nectoteuthis* Verrill 1883; *Iridoteuthis* Naef 1912; *Stoloteuthis* Verrill 1881; *Sepiolina* Naef 1912 [Order Sepioidea]

Spirulidae Owen 1836: one mesopelagic species, *Spirula spirula* (Lamarck 1758), with a nerito-oceanic distribution above the continental slopes of the tropical Atlantic and

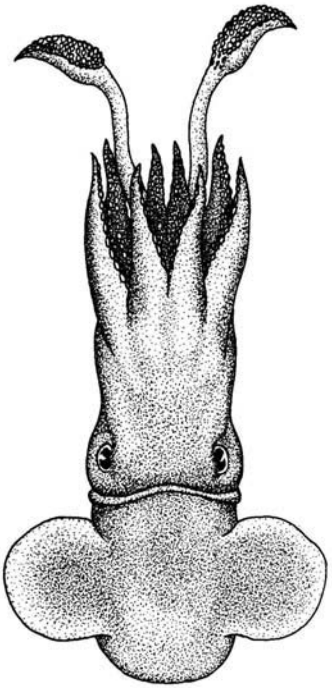


Fig. A36 Sepiolidae (*Rossia*).

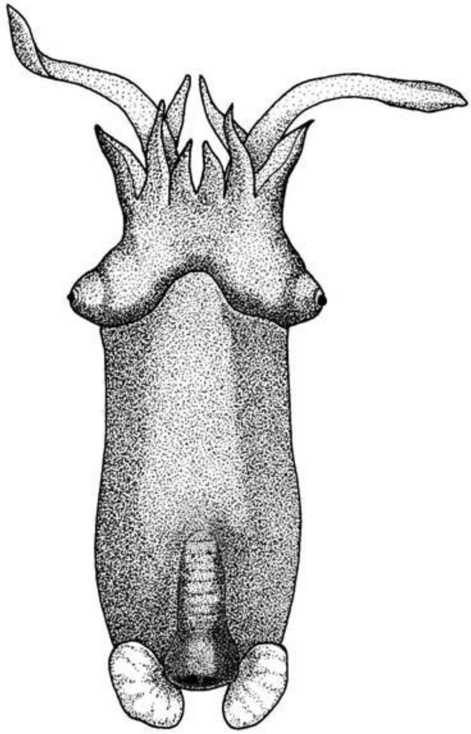


Fig. A37 Spirulidae (*Spirula*).

Indo-West Pacific. The plano-spiral chambered shells have a buoyancy control function, and after death they float and drift over oceanic distances to be cast up in millions on beaches, Fig. A37. *Spirula* Lamarck 1799 [Order Sepioidea]

Stauroteuthidae Grimpe 1916: see Cirroteuthidae

Thysanoteuthidae Keferstein 1866: family with a single genus and species, *Thysanoteuthis rhombus* Troschel 1857, probably cosmopolitan in warmer waters (Clarke 1966; Guerra *et al.* 2002c). Large (<1 m mantle length, 20 kg weight) nektonic squids of the open ocean, rarely approaching coasts. They are not particularly active animals, but maintain a high growth rate (<800 mm mantle length in 300 days) with lowered energy consumption (Nigmatullin & Arkhipkin 1996). They occur worldwide in oceanic tropical waters (see Fig. 12.9) and are reported to be macroplanktonic or micronektonic feeders, concentrating on mesopelagic fish at 400–600 m deep during daytime. A large pelagic egg mass (1–2 m long) is described, in which the small pink–violet eggs are distributed around the surface of a gelatinous mucous cylinder. Found close to the surface, up to 180 000 eggs have been counted in the egg mass (Nigmatullin *et al.* 1991; Billings *et al.* 2000), Fig. A38. *Thysanoteuthis* Troschel 1857 [Teuthida, Oegopsina]

Tremoctopodidae Tryon 1879: tropical and sub-tropical seas. Eggs small and carried by the female on the basal part of the 1st arms. Dwarf males but females large (<2 m overall), 1st arms very long and bear specialised suckers at their ends. In response to predator attack, a piece of this arm with a sucker, ocellar spots and part of a

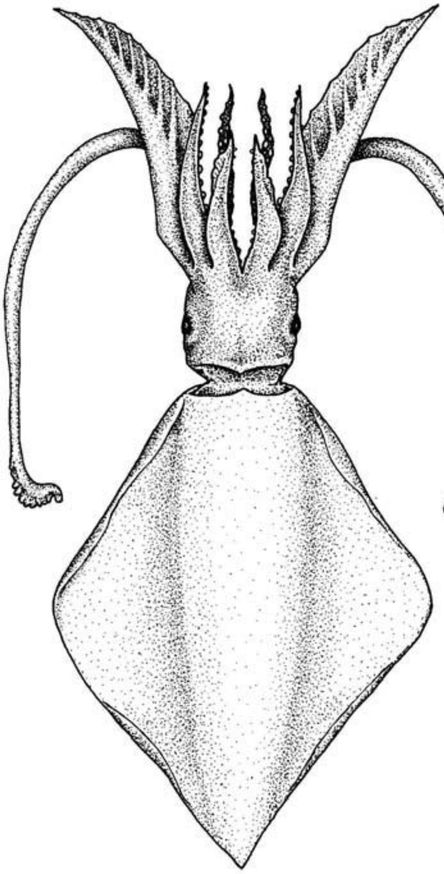


Fig. A38 Thysanoteuthidae (*Thysanoteuthis*).

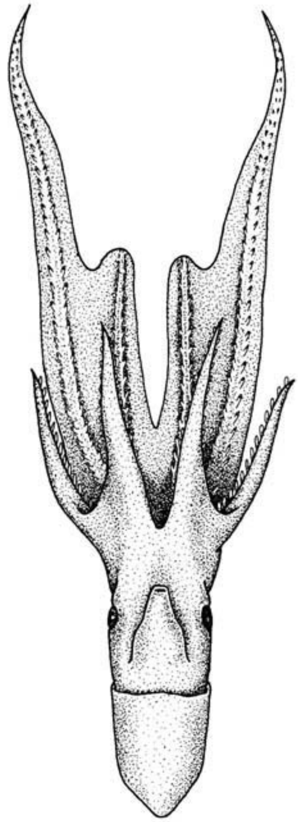


Fig. A39 Tremoctopodidae (*Tremoctopus*).

luminous gland may break off suddenly, disorientating and frightening the attacker. Males and young females frequently carry small pieces of stinging tentacles of *Physalia* (Portuguese Man-of-War), a pelagic siphonophore, as additional defence (Voss & Williamson 1971; Thomas 1977), Fig. A39. *Tremoctopus* Chiaie 1830 [Octopodida, Incirrina]

Vampyroteuthidae Theile in Chun 1915: medium-sized (<13 cm mantle length) gelatinous squids of one species, *Vampyroteuthis infernalis* Chun 1903, having a mantle partially fused to the head and with a deep web joining the arms. Large eggs (3–4 mm diameter) are shed singly into the water. Chromatophores are present, but apparently are not able to change diameter actively. Tropical and sub-tropical bathypelagic animals, probably positioned head-down in the water, Fig. A40. *Vampyroteuthis* Chun 1903 [Order Vampyromorphida]

Vitreledonellidae Robson 1932: a single species, *Vitreledonella richardi* Joubin 1918, of transparent, almost colourless gelatinous pelagic octopuses. Supposedly viviparous, brooding the eggs until hatching. Cosmopolitan tropical–subtropical bathypelagic animals with juveniles present in the meso- and epipelagic zones, Fig. A41. *Vitreledonella* Joubin 1918 [Octopodida, Incirrina]

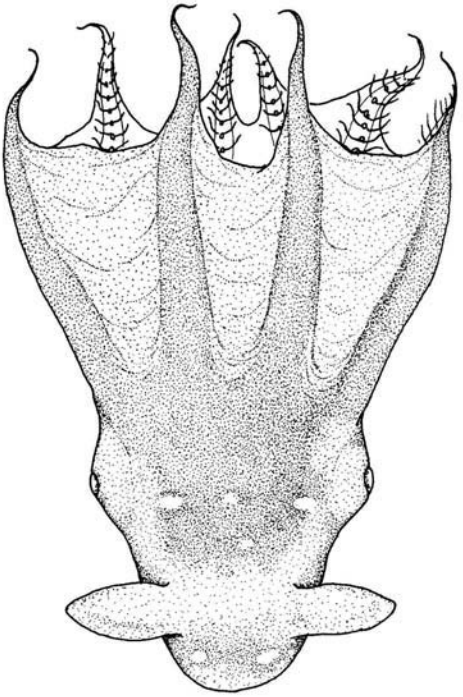


Fig. A40 Vampyroteuthidae (*Vampyroteuthis*).

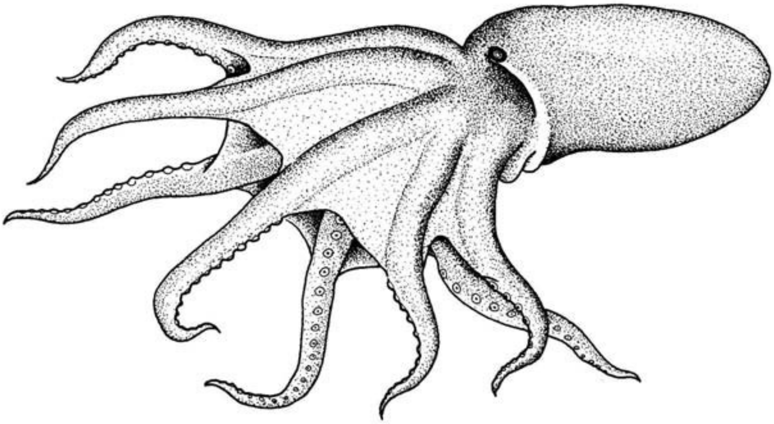


Fig. A41 Vitreledonellidae (*Vitreledonella*).

Walvisteuthidae Nesis & Nikitina 1986: proposed to accommodate a single species of deep-sea squid, *Walvisteuthis virilis* Nesis & Nikitina 1986, collected from depths of 960–1080 m. With similarities to squid from the families Onychoteuthidae and Batoteuthidae, the species is presumed to have a bathypelagic, south-subtropical distribution. *Walvisteuthis* Nesis & Nikitina 1986 [Teuthida, Oegopsina]

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