extremely vulnerable to disturbance and habitat damage. In the past it has been assumed, however, that many deep-sea species are broadly distributed because there are few barriers to dispersal and little obvious habitat heterogeneity. If this assumption holds, then their vulnerability to extinction might be reduced. At present, our understanding of how quickly species turn over spatially is very limited, particularly for some of the groups like nematodes that have been least studied. With emerging molecular approaches, it is also becoming clear that species that have been treated as cosmopolitan may, in some instances, be species complexes.

Given that many deep-sea environments support species that are either of no commercial fishing interest or are not sustainable, is there any reason to exercise caution in how humans impact the deep sea? There are, in fact, several compelling reasons to be concerned. First, the deep sea represents one of the few remaining pristine habitats on Earth. We can say, with only a few exceptions, that deep-sea communities have not been compromised by human development. This attribute makes them one of the last natural laboratories on Earth where the 'chemicals' have not been tainted. Because it is so very diverse, the deep sea can provide a natural and uncompromised laboratory in which to test ideas on regulation of biodiversity. A second reason to exercise caution is that the deep sea may represent one of the largest species pools on Earth. From an ethical and esthetic perspective, it could be argued that this characteristic alone is sufficient motivation to limit human disturbance. But from an economic perspective, there is great interest among pharmaceutical companies in organisms with unusual physiologies; the thermophilic bacteria that live at hydrothermal vents, for example, have generated tremendous interest for their bioactive compounds. A third concern is with respect to remediation. Although material dumped in the deep sea may be out of sight and mind, any decision at a later time to remediate (e.g. leaking radioactive waste) would be prohibitively expensive, if it was possible at all.

In summary, the deep sea is a vast and relatively undisturbed habitat that may be very vulnerable to human disturbances. Our current understanding of the deep sea and its immense diversity is very limited, but is nonetheless advancing steadily. A precautionary approach will ensure that the unusual attributes of the deep sea, including its rich biodiversity, will not be inadvertently destroyed by ignorance.

See also

Benthic Boundary Layer Effects. Benthic Foraminifera. Benthic Organisms Overview. Demersal Fishes. Macrobenthos. Meiobenthos. Ocean Margin Sediments. Pelagic Biogeography.

Further Reading

Gage JD and Tyler PA (1991) *Deep-Sea Biology. A Natural History of Organisms at the Deep-Sea Floor*. Cambridge: Cambridge University Press.

Grassle JF and Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313–341.

Gray J, Poore G, Ugland K *et al.* (1997) Coastal and deep-sea benthic diversities compared. *Marine Ecology Progress Series* 159: 97–103.

Lambshead PJD (1993) Recent developments in marine benthic biodiversity research. *Oceanis* 19: 5–24.

May R (1992) Bottoms up for the oceans. *Nature* 357: 278–279.

Merrett NR and Haedrich RL (1997) *Deep-sea demersal fish and fisheries*. London: Chapman & Hall.

Poore GBC and Wilson GDF (1993) Marine species richness. *Nature* 361: 597–598.

Rex MA (1983) Geographic patterns of species diversity in the deep-sea benthos. In: Rowe GT (ed.) *The Sea*, vol. 8: *Deep-Sea Biology*, pp. 453–472. New York: John Wiley.

Rex MA, Stuart CT, Hessler RR *et al.* (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365: 636–639.

Sanders HL and Hessler RR (1969) Ecology of the deep-sea benthos. *Science* 163: 1419–1424.

DEEP-SEA FISHES

J. D. M. Gordon, Scottish Association for Marine Science, Argyll, UK

doi:10.1006/rwos.2001.0014

Introduction

For the purpose of this article a deep-sea fish is one that lives, at least for most of its life, at depths greater than 400 m. The fishes of the continental shelves are usually classified as either pelagic or demersal. These categories are often further subdivided in the deep sea. The pelagic component is comprised of the mesopelagic and bathypelagic fishes that live entirely in the water column and are generally of small adult size. Mesopelagic fishes, e.g. lantern fishes (family Myctophidae) and cyclothonids (family Gonostomatidae), live beneath the photic zone to a depth of approximately 1000 m. Bathypelagic fishes live below 1000 m and are usually highly adapted to life in a food-poor environment. Examples are the deep-water angler fishes (family Ceratidae) and the gulper eels (family Eurypharyngidae).

Although the term demersal, referring to fishes living on or close to the bottom, is equally appropriate to the deep sea it has become customary to divide these fish into benthic and benthopelagic species. There is also a trend to refer to these as 'deep-water' rather than 'deep-sea' fish, thus avoiding the nautical use of deep-sea meaning distance from land. Benthic fishes are those that spend most of their time on the bottom and include the rays (family Rajidae), the flatfishes (e.g. family Pleuronectidae) and the tripod fishes (family Chlorophthalmidae). The benthopelagic fishes are those that swim freely and habitually near the ocean floor and examples include the squalid sharks (family Squalidae), the macrourid fishes (family Macrouridae) and the smoothheads (family Alepocephalidae) (see **Figure 1**).

The long-held belief that deep-sea fish belonged to old (in evolutionary terms) and archaic groups is no longer tenable. The deep sea has been invaded many times and there is little doubt that the specialized pelagic fauna have undergone much of their evolution in the deep sea. On the other hand, the demersal fishes probably evolved mainly in the shallower waters and secondarily invaded the deep sea and therefore, although well-adapted for life at depth, their special morphological features are usually less well-developed than those found in the meso- and bathy-pelagic fishes. In some areas, such as the deep Norwegian Sea, the colonization by demersal fishes appears to be of fairly recent origin.

Although there are very marked regional differences in the deep-water demersal fish faunas there is also a degree of global similarity, and certain families such as the macrourids and smoothheads are dominant. Some species such as several deep-water sharks and the orange roughy (*Hoplostethus atlanticus*) are widely distributed on continental slopes. Many abyssal species, of which the armed grenadier (*Coryphaenoides armatus*), the blue hake (*Antimora rostrato*), and the lizardfishes (*Bathysaurus* spp.) are good examples, are cosmopolitan in their distribution.

Our knowledge of the deep-water demersal fishes ultimately depends on the sampling techniques. The bottom trawl, beam or otter, has been the most widely used sampling method. Each design of trawl is selective for a particular spectrum of fishes, and on the upper continental slope – especially in areas where there is commercial exploitation – a wide range of trawls have been used that has resulted in a better understanding of the fish assemblages. On the lower slope and at abyssal depths fewer, more specialized sampling gears have been utilized, and the assemblages may not be adequately described. Where the seabed is unsuitable for bottom trawling, sampling by longlines and traps has been successful. Advances in submersible technology continue to provide information on the distribution and behavior of deep-water fishes.

Depth-related Changes in Abundance and Biomass

The abundance, biomass, and usually the number of species, decreases with increasing depth. This in turn is related to the food supply which, with the exception of a very small contribution of probably $<1\%$ from chemosynthesis, is ultimately derived from photosynthesis at the surface, see **Figure 2**.

Surface production is not uniform throughout the world's oceans, as it depends on the factors necessary for photosynthesis such as light, temperature, and nutrients. In general, it tends to be greatest at higher latitudes where there is strong winter mixing and in areas of upwelling. On the basis of this production, the upper layer of the world's oceans can be divided into a series of fairly well-defined faunal provinces, which extend into the mesopelagic. These provinces have been well-defined for some groups such as the myctophid fishes. Since the demersal fishes ultimately depend on the same energy supply it is not unreasonable to suppose that such faunal provinces exist also for the demersal fishes, but with a few exceptions the level of sampling has been insufficient to identify their presence. An indication that such faunal provinces may exist and that they might be directly related to surface production comes from some work on the deep-water, abyssal fishes of the north-eastern Atlantic. The investigations were carried out in three main areas, the Porcupine Abyssal Plain (*c.* 48°N; 16°W), the Madeiran Abyssal Plain (*c.* 31°N; 25°W) and off the west African coast (20°N). All the stations were at depths between about 4000 and 5550 m. Striking differences in species composition, morphology,

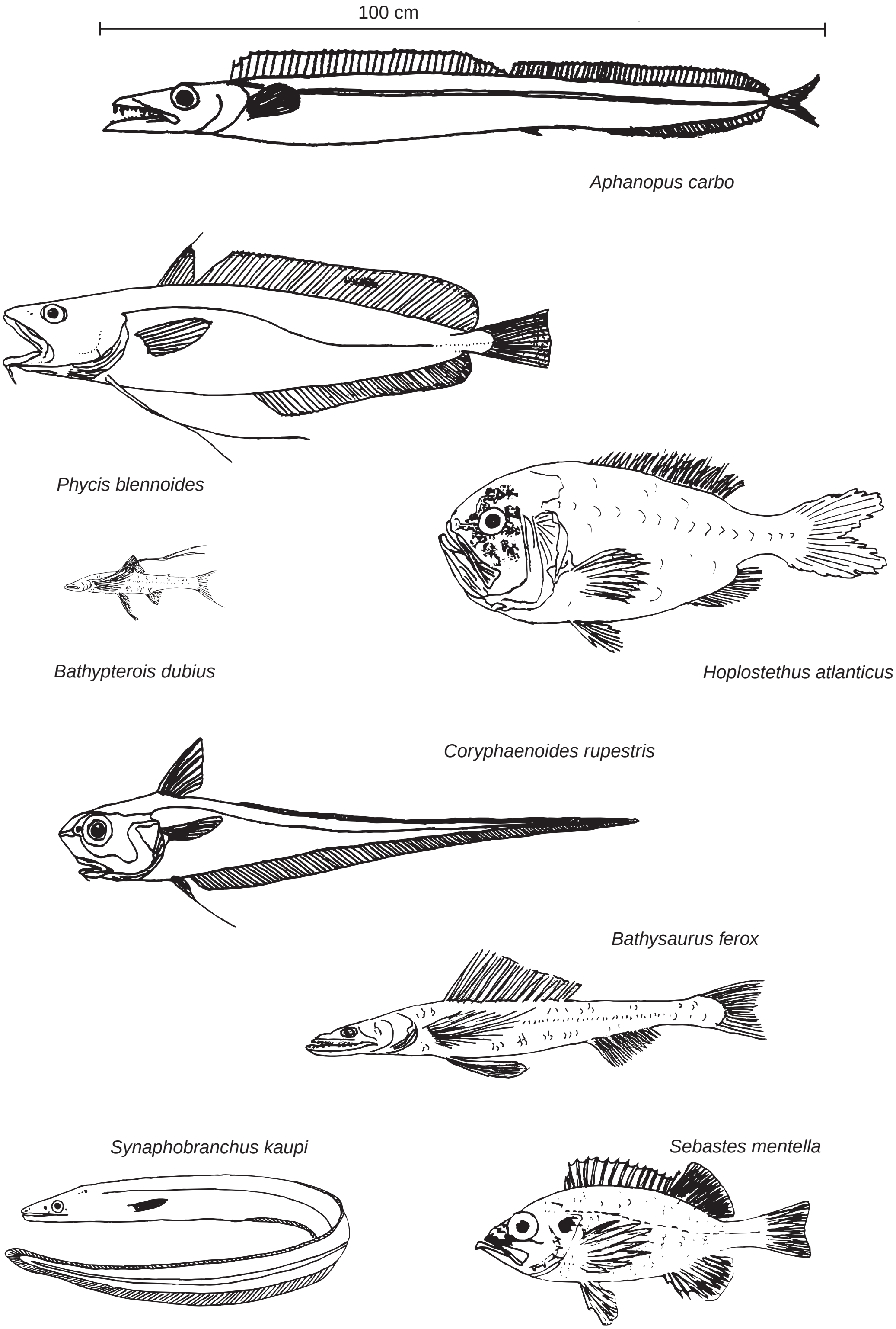

Figure 1 Some deep-water species to show different morphologies.

maximum fish size, feeding pattern, and reproductive strategies were demonstrated between the fish catches of these areas. In the area of the Madeiran Abyssal Plain, where there is a well-established seasonal thermocline and surface productivity is relatively low, the abyssal fish fauna is most diverse. The individual fish tend to be of small body size and adapted to life where the food supply is dispersed

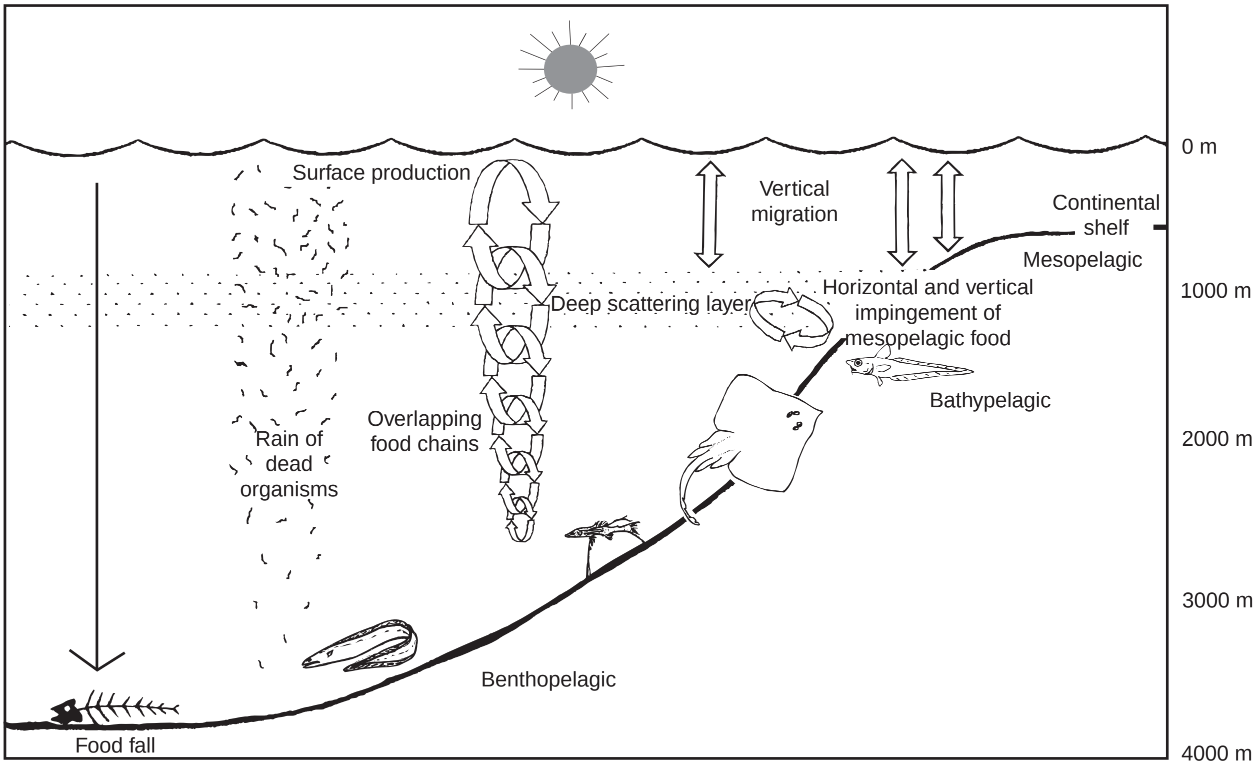

Figure 2 A diagram showing some of the pathways by which food reaches the deep-sea fish. Vertical migration is probably an important food source for bottom fish at around 1000 m and could account for the increased biomass at this depth.

and limited. The stations off the African coast have a distinct fauna, which is probably attributable to higher productivity caused by upwelling along the continental margin. Further north, where there is a marked seasonal cycle of productivity, the fauna is less diverse and the individual fish have larger body sizes and are adapted to exploiting food sources that tend to be patchily distributed. There appears to be a general trend for decreasing diversity and increasing body size from low to high latitudes. Overall, the biomass at abyssal depths is low compared with the continental slope and shelf. Another trend that has been reported in the Pacific is for a decrease in fish biomass with increasing distance from the continental land mass. This probably results from increased surface productivity attributable to terrestrial inputs.

The abyssal fishes are dependent on the 'rain' of detritus and associated bacteria and occasional large food falls for their food supply and as these decrease exponentially from the surface to the seabed, the low biomass is easy to explain. However, at depths of around 1000 m on the continental slopes or around seamounts there is often an increase in demersal fish abundance and biomass. It is this increase in biomass that forms the basis of the developing deep-water fisheries. Most of the fishes at this depth are benthopelagic and studies of their diets (see below) have shown that pelagic and benthopelagic organisms dominate their diet. Many of the prey organisms are vertical migrators, ascending towards the surface at night to feed and descending to a depth of about 1000 m during the day, where they form a deep-scattering layer. Where this scattering layer impinges either vertically or horizontally onto the slope, it provides a rich source of food for the benthopelagic fishes.

The Diet of Deep-water Demersal Fishes

In situ investigations in the deep sea are difficult and inevitably this means that much of our knowledge on feeding is derived from stomach content analysis. This has many inherent difficulties, such as the very high percentage of empty or everted stomachs due to the expansion of the gas during recovery from depth in those species that have gas-filled swim bladders. Very often all that remains are hard parts such as vertebrae, squid beaks, and crustacean appendages that become trapped in the lining of the stomach and which can lead to an overestimation of these prey types. The problem of identifying food items, often from fragments, can lead to bias especially when some prey taxa are poorly known, as is often the case in the deep sea. Indeed in some studies, the contents of the fish stomachs have been considered as yet another method of sampling the deep-sea fauna. For example, a significant part of the mesopelagic fauna of Madeira was described from the stomachs of deep-water species such as the black scabbardfish (*Aphanopus carbo*) landed by the commercial fishery. Net feeding is also considered to be a problem because of the long time the fish spend in the net after initial capture. In some fishes, such as the Alepocephalidae, there is often a high percentage of unidentified soft tissue that may result from feeding on gelatinous plankton. The gelatinous plankton is poorly sampled by nets but the deployment of cameras has shown that it can be abundant and therefore it should not be neglected as a potentially significant food source. Indirect evidence of feeding modes can be obtained from parasite loadings, presence of sediment in the gut, the morphology of the fish, and its associated sensory systems. Stable isotope ratios are beginning to be used to determine the level of the different fishes in the food chain. Direct observation from manned submersibles, remotely operated vehicles, and baited camera systems is a useful tool for understanding feeding behavior.

The feeding strategies of the deep-sea fishes cover as wide a range as their shelf counterparts and, as one might expect, reflect the habitat differences (e.g. depth, bottom topography). The piscivorous fishes can broadly be divided into those that adopt a sit-and-wait strategy, such as the lizardfish (*Bathysaurus*) and those that are active predators such as some deep-water sharks and the black scabbardfish. Many deep-water species, including the macrourids, feed on a mixed diet of the larger pelagic and benthopelagic crustaceans, cephalopods, and small fishes. Others feed on a mixed diet of the smaller benthopelagic organisms and epifauna including amphipods, mysids, and copepods. Again this group can be divided into those that actively forage, such as some of the smaller macrourid fishes, and those that sit and wait, such as the tripod fish (*Bathypterois* spp.). Feeding directly on the benthos, whether it is browsing at the surface, sifting the sediment for infauna, cropping or even scavenging is relatively unimportant and reflects the relatively low amount of energy that reaches the deep-sea floor.

Sensory Systems

Olfaction is well developed in some groups such as the Gadiformes (families Macrouridae and Moridae), some of the sharks, and the synaphobranchid eels. It is probably mostly used for the detection of food, but because it can be sexually dimorphic in some species it may also be used for mate recognition. For example, many male macrourids have larger nostrils than the female.

In general the eyes of the benthopelagic fishes do not have the wide range of adaptations to life in the deep sea that are found in the meso- and bathypelagic fishes. The eyes tend to remain large and functional and are probably used mainly to detect bioluminescence. Relatively few of the benthopelagic fishes have photophores. Some families have adaptations to maximize the incoming light. In the Alepocephalidae there is a large aphakic space which allows more light to reach the retina from around the edge of the lens, even if it is less focussed. In the squalid sharks and in some teleosts there is a reflective tapetum behind the retina which maximizes the stimulation resulting from the light entering the eye. Some species such as the tripod fish and the forkbeards (*Phycis* spp.) have developed long fin rays that are sensitive to touch and are used for detecting prey. As may be expected in a dark environment, the lateral line system for detecting movements is particularly well developed in deep-water species and in some species it is particularly elaborate and extends onto the head as a series of canals. The elongate body form of many species is probably an adaptation to increase the sensitivity of the lateral line.

In some deep-water species, including many macrourids and gadids of the slope, the males have drumming muscles on their swim bladders for producing sound. This adaptation is absent in the abyssal species.

Buoyancy

Fishes in general have evolved many different methods of reducing the energy required to maintain them in the water column and deep-water fishes are no exception. Gas-filled swim bladders are widely used by the benthopelagic fishes of the continental slopes and also in some abyssal fishes, such as the macrourid fishes, where it has been shown that there is a direct relationship between the length of the retia mirabila (the blood supply to the gas gland) and the depth of occurrence. In some species the swim bladder has become filled with low-density lipid, such as wax esters as in the orange roughy. Some gas-filled swim bladders also have considerable amounts of phospholipid and/or cholesterol, although their role in buoyancy control is uncertain. Reduction in body density can be achieved by having lipids distributed throughout the body. The orange roughy has wax esters in a layer beneath the skin and in vacuoles on the head. Density can also be decreased by reducing the ossification of the skeleton and by having a high water content in the tissues, such as in the alepocephalid fishes. The deep-water sharks have very large livers and also generate hydrodynamic lift by their pectoral fins during swimming, as in their shallow-water counterparts.

Longevity

The otoliths (earbones) of most deep-water fishes have well defined opaque and transparent zones typical of those found in shallow water where, at least in temperate latitudes, they correspond to seasonal changes in growth and hence can be used to age the fish (**Figure 3**). In shallow water the broader opaque zones are associated with faster summer growth, but it is not so obvious why fish living in the aseasonal deep sea should have changes in growth rate, unless they are linked to seasonal changes in food availability and/or quality. Although otoliths, and sometimes scales, have been used to estimate age of deep-water species on the assumption that the rings are laid down annually it has seldom been possible to directly validate these age estimates except in juvenile specimens. Radiometric aging, although controversial, has tended to confirm the generally held view that many deep-water species are long-lived. The commercially exploited grenadiers (Macrouridae) can live to about 50 years and the orange roughy in New Zealand waters lives to more than 100 years.

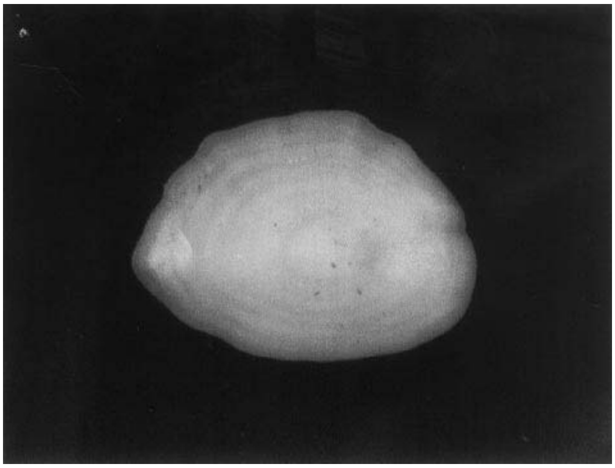

Figure 3 An otolith (ear bone) of an abyssal macrourid (*Coryphaenoides rupestris*) showing growth zones similar to the annual rings in shallow-water fish. If these rings are annual then this fish will be 6 years old.

Reproduction

The benthopelagic fishes have relatively few of the more extreme reproductive adaptations, such as parasitic males and hermaphroditism that are more frequently found in the meso- and bathy-pelagic fishes. However, hermaphroditism does occur in some groups such as the tripod fishes and live-bearing occurs in the Scorpaenidae (e.g., *Sebastes* spp.) and in the deep-water squalid sharks. It was a long held belief that the lack of seasonality in the deep sea would result in year-round reproduction. However, it has become increasingly apparent that many of the deep-water species of the continental slopes, especially in areas of the oceans where there are marked seasonal cycles of production at the surface, have well-defined spawning seasons. At greater depths year-round spawning or asynchronous spawning is more common. It is also possible that some abyssal species, such as the armed grenadier, are semelparous (spawn once in a lifetime). Many shallow-water fishes begin spawning before they reach full adult size, however there is some evidence that some deep-water fishes may not mature until they reach adult size, thus partitioning the energy supply first for somatic growth and then for reproduction.

There is a lack of information on the egg and larval stages of many of the benthopelagic fish species. For example, the eggs and larvae of the commercially important black scabbardfish are unknown and the eggs of the roundnose grenadier (*Coryphaenoides rupestris*) another widespread and exploited species in the Atlantic, have only been described from the Skagerrak. On the other hand, the abundance of eggs of the orange roughy in the South Pacific has been used for stock assessments. It is probable that the eggs of most species are pelagic, but although there has been speculation about the eggs rising and hatching in the food-rich waters associated with the thermocline, there is little evidence to substantiate this. Indeed, recent investigations suggest that the ornamentation of the surface of the eggs of some macrourid species might be an adaptation to restrict the ascent of the eggs through the water column and avoid too wide a dispersal.

Life Histories

The relatively low level of sampling in the deep sea, its restriction to a small number of areas and/or depths, and a general lack of seasonal sampling have all resulted in incomplete life history information. Except where there are special physical features, such as extreme temperature changes with depth (e.g. Norwegian Sea), there is little evidence of zonation in the deep-sea fishes. Instead each species has a depth range which can extend over several thousand meters, as in the cut-throat eel (*Synaphobranchus kaupi*) or over a few hundred meters, as in the tripod fish (*Bathypterois dubius*) (both examples from the north-east Atlantic). The ‘bigger-deeper’ phenomenon is a common feature among the deep-water demersal fishes, although it might be more correctly referred to as ‘smaller-shallower’. The juveniles of many of the demersal fishes of the continental slopes live at shallower depths than the adults. While in some regions the horizontal distribution of a species can be well documented there is little information on stock discrimination. With present technology it is difficult to tag, release, and recapture deep-water fishes and therefore there is very little information on the movements of deep-water fishes. Some of the commercial deep-water fisheries exist because they often target spawning aggregations, such as orange roughy in the South Pacific and blue ling (*Molva dypterygia*) in the North Atlantic. Some of the shark species are often found in single sex shoals, and in the exploited leafscale gulper shark (*Centrophorus squamosus*) of the North Atlantic the gravid females have never been found. The juveniles of many demersal species have never been found in trawl surveys, which suggests that there are separate nursery grounds or that they occur higher in the water column and are not sampled by bottom trawls.

See also

Bioluminescence. Deep-sea Fishes. Demersal Species Fisheries. Fish Migration, Vertical. Fish Reproduction. Fish Schooling. Mesopelagic Fishes. Open Ocean Fisheries for Deep-water Species. Upwelling Ecosystems.

Further Reading

Garter JV Jr, Crabtree RE and Sulak KJ (1997) Feeding at depth. In: Randall DJ and Farrell AP (eds), *Deep-sea Fishes*, 115–193. San Diego: Academic Press.

Gordon JDM and Duncan JAR (1985) The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. *Progress in Oceanography* 15: 37–69.

Gordon JDM, Merrett NR and Haedrich RL (1995) Environmental and biological aspects of slope-dwelling fishes of the North Atlantic Slope. In: Hopper AG (ed.) *Deep-water Fisheries of the North Atlantic Oceanic Slope*, pp. 1–26. Dordrecht: Kluwer Academic Publishers.

Haedrich RL (1997) Distribution and population ecology. In: Randall DJ and Farrell AP (eds) *Deep-sea Fishes*, pp. 79–114. San Diego: Academic Press.

Marshall NB (1979) *Developments in deep-sea biology*. Poole: Blandford Press.

Mauchline J and Gordon JDM (1991) Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* 74: 109–115.

Merrett NR (1987) A zone of faunal change in assemblages of abyssal demersal fish in the eastern North Atlantic; a response to seasonality in production? *Biological Oceanography* 5: 137–151.

Merrett NR and Haedrich RL (1997) *Deep-sea Demersal Fish and Fisheries*. London: Chapman and Hall.

Montgomery J and Pankhurst N (1997) Sensory physiology. In: Randall DJ and Farrell AP (eds) *Deep-sea Fishes*, pp. 325–349. San Diego: Academic Press.

Pelster B (1997) Buoyancy at depth. In: Randall DJ and Farrell AP (eds) *Deep-sea Fishes*, pp. 195–237. San Diego: Academic Press.

Randall DJ and Farrell AP (eds) (1997) *Deep-sea Fishes*. San Diego: Academic Press.

DEEP-SEA RIDGES, MICROBIOLOGY

A.-L. Reysenbach, Portland State University, Portland, OR, USA

doi:10.1006/rwos.2001.0103

Introduction

Microbes are central to deep-sea ridge ecosystems. Here, in the absence of light energy, the geochemical energy is the primary energy source for microbial growth. These microbes gain energy from oxidation of inorganic compounds such as sulfide and are referred to as chemolithotrophs. Chemolithotrophy or chemosynthesis is the basis of the primary productivity at deep-sea hydrothermal vents, and its discovery challenged our traditional view that all ecosystems were driven by light energy and photosynthesis. The chemolithotrophic microbes are found free-living as well as associated as symbionts with the invertebrates. Additionally, heterotrophic microbes are present that utilize the abundant organic carbon available as a result of the high productivity of these ecosystems.