

Most of these tropical coastal communities have long-standing fisheries based not only on fish like mullet, but also on the abundant populations of shrimp, crabs, bivalves, and snails. Fish nets and traps are often constructed, at least in part, from parts of the mangrove trees, and tannin extracted from the mangroves is used to increase the durability of fishing nets and sails.

Mangroves also have great importance in non-commercial aspects. They form protective barriers against wind damage and erosion in regions that are subject to severe tropical storms. In some areas, mangroves may facilitate the conversion of intertidal regions into semi-terrestrial habitats by trapping and accumulating sediment. For example, mangroves have spread seawards at rates of between 100 m and 200 m per year in Indonesia. The root system also serves as a protective nursery ground for many species of fish, shrimps, juvenile spiny lobsters, and crabs. The forest canopy not only supplies food for many of the arboreal and marine inhabitants, either directly or as detritus, but it is utilized for nesting sites for a variety of tropical birds.

8.8 DEEP-SEA ECOLOGY

The vast majority of the seafloor lies permanently submerged below tidal levels yet, relative to the intertidal regions, comparatively little is known about life in the bathyal, abyssal, and hadal zones (see Figure 1.1). This, of course, is due to their relative inaccessibility. Although it is possible to dive to several thousand metres in submersibles or to employ remote-controlled cameras, the number of hours of direct observations in the deep sea has so far been extremely low. Most information on deep-sea ecology comes from indirect inferences based on animals contained in benthic samples obtained from ships. Whatever the method, expense is a limiting factor in deep-sea research. Few countries or institutions have submersibles to use for basic research, and few have large research ships equipped to obtain deep-sea samples. Collecting a sample from 8000 m depth with towed gear, for example, requires a very large winch with at least 11 km of cable in order to allow for the towing angle. It may take up to 24 hours to let out that much wire, obtain a sample, and then retrieve it. With large ship costs easily exceeding tens of thousands of dollars per day, a single sample containing a few benthic animals can be beyond the budget of most oceanographic research facilities. Compounding this problem is the fact that animal life is just not very abundant in many deep-sea areas, so that it is desirable to have large numbers of samples. Nonetheless, new techniques for collection and observation, combined with accumulating numbers of analysed deep-sea samples, permit a general assessment of benthic life in deeper water.

The deep-sea environment has been generally regarded as stable and homogeneous in terms of many physical and chemical parameters. Water temperatures are generally low (from -1° to 4°C) and salinity remains at slightly less than 35. Oxygen content is also constant and is rarely limiting, with the exception of areas beneath upwelling zones or in some basins where water exchange is slight (e.g. the Cariaco Trench in the southern Caribbean Sea). Soft bottom sediments, originating from land and/or from the sinking of dead planktonic organisms, cover most of the deep seafloor. Hard substrates are largely limited to mid-ocean ridges and seamounts that jut up from the sea bottom. Relative to surface currents, bottom currents in the deep ocean basins are slow (generally <5 cm per second) but more variable than once believed. Some areas experience abyssal (or benthic) storms

small burrowing polychaetes commonly make up 50–75% of the macrofauna in many, widely scattered, soft-bottom deep-sea sites. Small crustaceans (amphipods, isopods, tanaids) are also common deep-sea macrobenthic species, followed by molluscs (especially clams), and a variety of worms (sipunculids, pogonophora, echiurids, and enteropneusts). Brittle stars (ophiuroids) can be abundant in some areas; for example, they make up over 60% by numbers of the macrobenthos in the Rockall Trough west of Ireland.

Certain groups of animals attain their greatest abundance and diversity in the deep sea. The soft-bodied or calcareous sponges that are common in shallow water are largely replaced by glass sponges with siliceous spicules in deep water. Cnidaria are principally represented in the deep sea by sea anemones that live in burrows, and by sea pens and gorgonian corals that may form densely populated beds under eutrophic waters where there is sufficient suspended material for feeding. Slender, branching colonies of black corals have been found in the greatest depths. The Pogonophora are mostly a deep-water group found down to 10 000 m, and echiurid worms become more common in depths exceeding 5000 m. Some echiurids reach body lengths of 1 m, and they can occur in dense aggregations in organically-rich sediments where they form a large proportion of the biomass. The more primitive crinoids, the stalked sea-lilies, are mostly restricted to deep-sea habitats.

Benthic foraminiferans and related protozoans, the giant xenophyophores (see Section 7.2.1), increase in importance in deep water, both in terms of abundance and biomass. Unlike the shallow-living species with calcareous tests, deep-water foraminiferans have proteinaceous tests or exoskeletons made of agglutinated sediment particles. In certain areas, 30–50% of the seafloor may be covered by foram pseudopodia and, in the Aleutian Trench, forams comprise 41% of the meiofauna. Xenophyophores are known to occur in nearly all areas of the deep-sea basins at depths below 1 km. They may occur in densities of up to 20 m^{-2} , and they constitute up to 97% of the total benthic biomass in some areas of the South Pacific.

Some animal groups show a tendency toward gigantism in the deep sea (see also Section 4.4); these include the benthic foraminifera and the xenophyophores, as well as certain amphipod species that attain lengths of about 28 cm. However, there is a reverse tendency in some groups toward miniaturization, and the deep-sea meiofauna is numerically dominant over the macrobenthos. Nematodes are ubiquitous in marine soft substrates and make up 85–96% of the deep-sea meiofauna. Harpacticoid copepods and ostracods are also common deep-sea members of this size category, the former group constituting 2–3% of the meiofauna in abyssal zones. Tanaids are extremely diverse in the deep sea, and many of the species are meiofaunal; in the north-west Atlantic, they occur in densities of about 500 m^{-2} .

Certain animal groups are poorly represented in deep water. Decapod crustaceans (e.g. crabs, shrimp, lobsters), sea anemones, and echinoid echinoderms are absent or uncommon below about 6000 m. Fish are also rare in very deep waters; one of the deepest captured fish came from 7230 m in the Kurile-Kamchatka Trench. These generalizations are largely based on collections made with dredges or trawls, both of which are difficult to use over rocky substrates or in relatively steep-walled trenches, and both of which can be avoided by swimming animals. It is well to keep in mind that Jacques Piccard and Lieutenant Don Walsh, who together made the deepest

dive in a bathyscaphe, observed flatfish and shrimp at over 10 000 m; neither of these groups of animals have been collected by conventional gear from such great depths.

QUESTION 8.10 What explanations can you give for why large sponges are so successful in shallower areas, and why sea cucumbers often dominate the macrobenthos of deep water?

Some deep-sea residents have a cosmopolitan distribution and are found in all the major oceans; other species are restricted to relatively small areas. In general, species become more limited in geographic range as water depth increases. Only about 20% of the species present below 2000 m in the Atlantic Ocean are also found in the Pacific or Indian oceans.

Table 8.1 Percentages of species living below 6000 m depth that are endemic to the hadal region.

Taxonomic group	Number of hadal species	% endemic
Foraminiferans	128	43
Sponges	26	88
Cnidaria	17	76
Polychaetes	42	52
Echiurid worms	8	62
Sipunculid worms	4	0
Crustaceans		
barnacles	3	33
cumaceans	9	100
tanaids	19	79
isopods	68	74
amphipods	18	83
Molluscs		
aplacophorans	3	0
snails	16	87
bivalves	39	85
Echinoderms		
crinoids	11	91
holothurians	28	68
starfish	14	57
brittlestars	6	67
Pogonophorans	26	85
Fish	4	75

Many species found in areas deeper than 6000 m are endemic to the hadal region, and many are restricted to a particular trench. Table 8.1 lists the number of hadal species known in particular invertebrate groups, and the percentages of these that are endemic to this deep-sea region. Endemic species constitute up to 75% of the benthos in certain Pacific trenches. The high degree of endemism suggests that trenches are fundamentally isolated habitats which are centres for the generation of new species.

Trenches often have relatively high abundances of aplacophorans (wormlike, shell-less molluscs), enteropneust worms, and echiurid worms, all of which are poorly represented elsewhere. In the Aleutian Trench at depths of 7000–7500 m, the macrofauna is dominated by polychaetes (49%), bivalves (12%), aplacophorans (11%), enteropneusts (8%), and echiurid worms (3%).

The meiofauna is dominated by benthic foraminifera (41%), followed by nematodes (36%) and harpacticoid copepods (15%). Some of the zoobenthos of trenches exhibit pale coloration and are blind, characteristics that are shared with cave fauna. Very large size is also a characteristic of some hadal isopods, tanaids, and mysids.

Deposit-feeding infaunal animals are dominant in the soft, organically-rich sediments of the deep sea, usually comprising 80% or more of the fauna by numbers. At one site in the Atlantic, at a depth of 2900 m, 60% of the polychaetes, >90% of the tanaids, 90% of the isopods, >50% of the amphipods, and 45% of the bivalves are deposit feeders. Other groups, like sea cucumbers and sipunculids, also ingest the detritus and small organisms contained in surface or subsurface sediments. Because bottom currents are usually slow and do not disturb compacted sediments, the topographic features produced by these animals persist for long periods. Faecal mounds, burrows, trails, and tubes are some of the biological features that are commonly recorded in the deep sea by remote cameras.

Animals that feed on suspended particles are also found in the deep sea, but they are much less abundant and are usually restricted to particular localities. This is because most of these epifaunal animals require relatively firm substrates for attachment as well as high concentrations of suspended food particles. As a result, many types of epifaunal suspension feeders (e.g. common sponges, sea anemones, barnacles, mussels) show a marked decrease in abundance with increasing depth and distance from shore. They do flourish, however, on the rock substrates found on mid-ocean ridges and seamounts, and some may dominate in deep-sea sulphide communities (see Section 8.9). Relative proportions of deposit feeders and suspension feeders vary throughout the deep sea according to the degree of organic enrichment of the sediments and the supply of suspended food.

It is useful, in discussing deep-sea distribution of epifauna, to distinguish between two types of suspension feeding. **Active suspension feeders** (e.g. shallow species of sponges and tunicates) use their own energy to pump water through a filtering structure. These animals are successful in environments where suspended particle concentrations are high enough to repay the energetic costs of pumping. **Passive suspension feeders** (e.g. crinoids, some polychaetes, and most benthic Cnidaria like sea anemones and sea-fans) rely on external water currents to convey food to feeding appendages that are held into the flow. The passive feeders succeed only in environments where flow conditions are predictable and fast enough to supply them with sufficient particulate food. Suspended particle concentrations decrease with depth, but flow conditions become more predictable. Active suspension feeders disappear as suspended loads diminish, and the large filter feeders in the deep sea are passive feeders. Depending on the current speed, the friction of water moving over the seafloor may create physical mixing of the bottom water; this **benthic boundary layer** extends from 10 to several 100 metres above the bottom. Turbulence in this layer can result in resuspension of bottom sediments; heavy inorganic particles remain close to the seafloor, but suspended light organic particles will reach maximum concentrations some distance above the bottom. Typical deep-sea passive suspension feeders, such as sea-lilies (stalked crinoids) and bryozoan colonies, are found in highest densities where there is moderate current flow and resuspension of sediments. In contrast to their shallow-dwelling relatives, these animals are often supported

by long stalks which hold them well above the seafloor where concentrations of suspended organic material may be optimal.

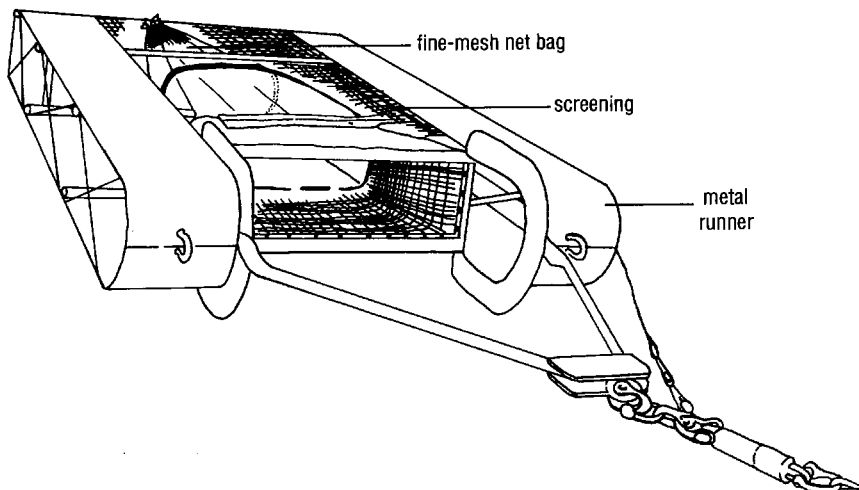
Some deep-sea groups have very different feeding mechanisms from those used by shallow-water related species. Glass sponges, for example, have an extremely porous body wall and water currents can enter passively as well as by active pumping. Members of one family (Cladorhizidae) of small-sized sponges occur in deep water to about 9000 m depth; at least some of them are highly modified carnivores that passively capture small swimming prey by means of filaments provided with hook-shaped spicules. Whereas shallow-water tunicates are active suspension feeders and many are colonial species, deep-sea representatives tend to be solitary forms that may supplement active pumping with mucous nets held into currents to capture food. Some deep-sea tunicates are even more highly modified and have become carnivorous.

In addition to deposit feeders and suspension feeders, the deep-sea food chain includes many scavengers. Cameras have recorded the speed with which a variety of swimming animals approach bait placed on the seafloor in deep water. These include giant amphipods, isopods, fish, and shrimp. Brittle stars and some polychaetes are among the slower-moving scavengers. Strict predators appear to be rare in very deep waters. However, diets of deep-sea benthic animals are not well known; feeding type is usually inferred from anatomical structure and gut contents.

8.8.2 SPECIES DIVERSITY

The number of species of many types of macrobenthos (e.g. snails, clams, polychaete worms) and fish tends to increase with depth from about 200 m to 2000 or 2500 m, then declines rapidly with further depth. Based on these observations, it was believed for many years that deep-sea species diversity was low compared with that of shallow-water communities. However, the development and use of a new collection device, called an **epibenthic sled**, changed this perception. The epibenthic sled (Figure 8.14) was designed to

Figure 8.14 An epibenthic sled designed to collect animals living on or just above the seafloor. The mesh-size is small enough to retain meiofauna, and the sampler can be closed during retrieval so that the entire sample is retained.



collect and retain smaller animals, in a size category that was previously not well sampled. When this gear was first employed in the 1960s, a single collection sometimes contained more animals than were collected by all the combined expeditions of the previous 100 years. To further demonstrate the effectiveness of this apparatus, one paper reported that over 120 new species of cumaceans (small crustaceans) had been collected. It soon became evident that the diversity of many smaller organisms increases with depth. For example, the number of species of meiobenthic copepods increases to at least 3000 m, and maximum diversity of benthic foraminiferans is found in depths exceeding 4000 m.

It is now established that there is high species diversity in the deep sea, especially among the small infaunal deposit feeders. As additional samples are obtained from the deep sea and more new species are described, the more diversity in this area seems to approach that of highly diverse terrestrial environments, such as the tropical rain forest. Some researchers estimate that there may be more than one million species of marine benthic animals, most of them living in deep-sea sediments. Species diversity does, however, vary in different oceanic areas. For example, in the North Atlantic, species diversity declines from the tropics toward north polar regions; but in the Southern Hemisphere, zoobenthos species diversity in the Weddell Sea (Atlantic sector of the Antarctic) is of the level normally associated with tropical regions. Deep-sea diversity also may vary according to different levels of surface primary production. In some areas, zoobenthos diversity is depressed under areas of upwelling and high surface productivity, probably as the result of reduced oxygen concentrations from decomposition of large amounts of organic material.

As more areas of the deep sea are surveyed with increasingly sophisticated gear, it is becoming apparent that the environment itself, in terms of substrate features and/or current regime, is more diverse than was once thought. Environmental diversity in the form of microhabitats (small areas having slightly different environmental characteristics) can itself lead to higher diversity in animals. Indeed, the deep-sea benthos is patchily distributed, with significant aggregations of animals having been detected in different taxonomic groups on scales ranging from centimetres to metres to kilometres. This patchy distribution underscores the importance of obtaining representative samples when assessing biomass and species diversity of deep-sea animals.

8.8.3 BIOMASS

Although the number of species is high in the deep sea, communities occupying the typical soft-sediment seafloor are characterized by low population densities and low biomass. Numbers of benthic individuals (both macrofauna and meiofauna) per unit area tend to decrease roughly exponentially with increasing depth and, to a lesser degree, with distance from shore. Under the central oceanic gyres, the total density of macrofauna ranges from 30 to 200 individuals per m². With a few exceptions, the dominant infaunal species tend to be small as well as sparse. In the central North Pacific, meiofauna and microfauna dominate the benthos in numbers (0.3% and 99.7%, respectively), and in biomass (63.8% and 34.9%, respectively). Deep-sea biomass values do not include the larger demersal species, which are more difficult to capture and to quantify on an areal basis; their inclusion would undoubtedly increase the biomass values given here.

Table 8.2 Average biomass values of benthic animals at different depths.

Depth range (m)	Mean biomass (g wet weight m ⁻²)
Intertidal to 200	3×10^3 200
500–1000	<40
1000–1500	<25
1500–2500	<20
2500–4000	<5
4000–5000	<2
5000–7000	<0.3
7000–9000	<0.03
>9000	<0.01

Average biomass values for different depth zones are given in Table 8.2. Benthic biomass is highest in shallow coastal areas within the euphotic zone, and it is lowest under oligotrophic, central, oceanic regions. Keeping in mind that the average depth of the world ocean is 3800 m, most of the seafloor supports less than 5.0 g wet weight m⁻² of living organisms.

However, benthic biomass at any particular depth varies according to the amount of organic material delivered to the seabed. This is reflected, for example, in the different levels of biomass found in various trenches, all of which are deeper than 6000 m. Trenches are located in regions of frequent seismic activity, and thus are subject to brief episodes of high sedimentation caused by slumping of sediments down the trench walls. This results in the deposition of organically rich sediments from shallower depths, but also in the burial of benthic communities. The biomass of hadal fauna may be very high in trenches that lie near large land masses as they receive land-derived sediments and organic matter, as well as organic material sinking from the overlying nutrient-enriched and highly productive surface water. Under these conditions, benthic biomass may range from 2 to 9 g wet weight m⁻² at depths of 6000–7000 m in the Kurile-Kamchatka Trench (North Pacific) and in the South Sandwich Trench (South Pacific). Trenches far from land masses and under oligotrophic water (e.g. Mariana Trench) have very low biomass values of about 0.008 g m⁻².

Benthic productivity cannot be assessed directly from biomass values, but many deep-sea species grow relatively slowly and their small biomass must indicate low productivity. Various estimates suggest that annual secondary production over most of the deep ocean floor is between 0.005 and 0.05 g C m⁻².

QUESTION 8.11 How does the decline in benthic biomass with depth compare with the vertical distribution of zooplankton biomass? Refer to Section 4.4 and Figure 4.14.

8.8.4 FOOD SOURCES

Except for localized chemosynthetic production around deep-sea hot springs (see Section 8.9), there is no primary production in the dark, deep areas of the sea. Food availability, not low temperature nor high pressure, limits benthic biomass in the deep sea. The deep-sea food chain is dependent on surface production, and only a small percentage (1–5%) of the food produced in the euphotic zone is transferred to the abyssal seafloor. The

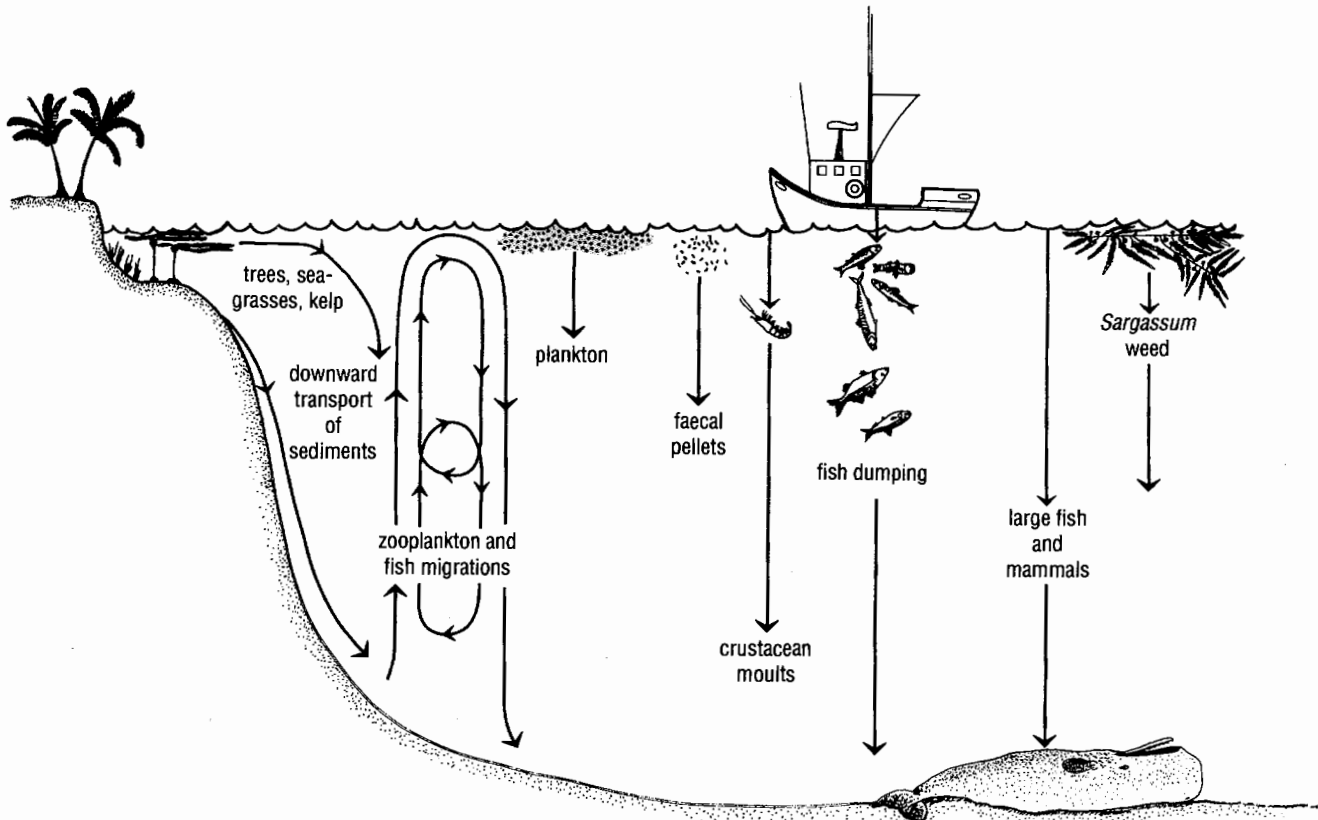


Figure 8.15 Potential food sources for deep-sea organisms.

percentage diminishes with increasing depth because of the increasing probability that organic particles sinking from the euphotic zone will be consumed or will decay before reaching the bottom.

A variety of potential food sources sink from the productive surface zone and thus may become available to deep-sea benthos (Figure 8.15). The relative contribution of each of these sources depends on their sinking rates and attrition in intermediate depths.

1. Dead phytoplankton, zooplankton, fish, and mammals. In many areas of the ocean, much of the phytoplankton is consumed by herbivorous zooplankton in the euphotic zone. That fraction which is not eaten sinks very slowly because of its small size and, in very deep areas, it is lost through predation, disintegration, or decomposition at intermediate water depths. In some regions like the North Atlantic, however, the phasing between seasonal phytoplankton blooms and zooplankton growth is such that much of the phytoplankton dies without being consumed (see Section 3.6), and the sinking phytodetritus may reach the seabed at depths down to 4000 m. The fate of most uneaten epipelagic zooplankton is similar, although sinking rates are somewhat faster because of their larger size. The corpses of large fish, squid, or marine mammals sink rapidly enough so that they may reach the seafloor in deep waters, where they become available to benthic scavengers; however, some are no doubt consumed by large animals at intermediate depths. In any event, the arrival of large animal carcasses on the sea bottom is generally an unpredictable and rare event, except perhaps under the

seasonal migration routes of some fish and mammals. This is not the case, however, in heavily fished regions where tonnes of unwanted, incidentally captured fish ('trash' fish) are dumped back into the sea. The dumping of unmarketable by-catch may amount to a very significant fraction of the total reported fish catch, but it will only locally increase benthic food supplies.

2. Faecal pellets and crustacean moults. Compact faecal pellets of some zooplankton (about 100–300 μm in size) are collected in mid-water traps designed to capture sedimenting particles, and their settling rates are such that they may reach the seafloor relatively intact. Faecal material of fish may also reach the seabed almost undegraded. Although some animals ingest faecal pellets, these wastes generally contain large fractions of indigestible materials. Moulded exoskeletons of planktonic crustaceans occur in the benthic boundary layer, but they may result from deep-water species. Moults are also low in nutritional value as they are composed primarily of chitin which cannot be digested directly by most animals, but it is broken down by **chitinoclastic** bacteria living in the guts of many species. Faecal pellets and moults are colonized by bacteria during their descent in the water column, and they are eventually converted to bacterial biomass. Bacteria are important nutritional intermediates in the food cycle of the deep sea, and they comprise a major food source for benthic deposit feeders. There is, in fact, an increase in bacteria in the bottom sediments of the deep sea, with numbers exceeding one million per gramme of sediment between depths of 4000 and 10 000 m.

3. Macrophyte detritus. A certain amount of organic material enters the sea near coastal zones in the form of wood from terrestrial plants, or from dislodged seagrasses and kelp. Some of this is carried well offshore in currents before becoming waterlogged and sinking. *Sargassum* is also a potential source of organic material in areas where it occurs (see Section 4.4). Larger plant particles sink rapidly enough to reach the seafloor more or less intact. Panels of wood placed at a depth of 1830 m and recovered 104 days later were riddled with burrows made by wood-boring clams, some of the very few animals that can utilize wood for food. These bivalves convert woody plant material to foods that are available to other animals. They produce faecal pellets that can be consumed by detritivores; those larval or adult clams that become exposed by the disintegration of the wood can be eaten by predators; and their dead remains become available for scavengers. Bacteria decompose and convert other types of macrophyte detritus into biomass available to benthic animals.

4. Animal migrations. The vertical migrations of zooplankton and fish result in a downward transfer of organic materials. Food that is captured in shallower depths is converted to animal biomass that may be consumed by predators at deeper levels, and faecal pellets may be released by migrators when they return to deeper water (see Section 4.5). Some deep-sea fish (e.g. angler-fish) spend their larval stages near the surface and then migrate into the depths as juveniles or adults, where they become potential food for deep-sea predators. All of these events accelerate the pace at which food enters the deep sea.

There is seasonal variability in the amount of organic material reaching the seafloor in temperate and high latitudes due to seasonal differences in surface production. The sinking of large amounts of macrophyte detritus also may be linked to seasonal storms that dislodge seagrasses or trees. The

dumping of trash fish also is largely restricted to seasons of relatively calm weather and availability of fish schools. Some fish die after spawning (e.g. mesopelagic blue whiting), and their carcasses deliver a seasonal signal to the underlying deep-sea fauna.

Although some deep-sea species have seasonal reproduction, and growth bands in mollusc shells and echinoderm skeletal plates reveal seasonal growth in certain species, many deep-sea animals have continuous reproduction and their production does not appear to be linked to seasonal surface events. Secondary production may be linked, however, to the sporadic nonseasonal occurrence of an adequate food supply.

Although life in most of the deep sea is dependent on surface production, the deep-sea environment is spatially and temporally separated from the euphotic zone. In general, it is estimated that 75–95% of the organic matter in particles sinking from the euphotic zone is decomposed and recycled in the upper 500–1000 m of the water column, above the permanent thermocline. In the Sargasso Sea, surface production is $>100 \text{ mg C m}^{-2} \text{ day}^{-1}$ and the flux to the bottom at over 3000 m varies from 18 to $60 \text{ mg m}^{-2} \text{ day}^{-1}$ depending on season. However, organic matter constitutes only about 5% of the total sedimenting material, the remainder being mostly inorganic carbonate and silicate. In the north-east Atlantic, seasonally deposited phytodetritus has an even lower organic carbon content of less than 1.5%; however, deep-sea animals have been observed to feed on this material despite its low nutritive value. In general, only about 5–10% of organic matter produced in the euphotic zone will reach depths of 2000 to 3000 m, and progressively less in abyssal and hadal zones. Thus food is very scarce in the deep sea compared with other ocean regions. Food limitation is one of the most important factors governing biological processes and community structure of the deep-sea benthos.

QUESTION 8.12 Using the maximum sinking rates for diatoms (from Section 3.1.1), how long would it take a single dead *Chaetoceros* cell to sink to 5700 m depth?

8.8.5 RATES OF BIOLOGICAL PROCESSES

Accumulating evidence suggests that various biological processes in deep-sea animals, such as metabolism, growth, maturation and population increase, are slow in comparison to such processes in shallow-water environments. One of the first pieces of evidence resulted from an accident at sea. In 1968, the research submersible *Alvin* slipped from its launching cradle after the pilot and scientists were on board, but before the ports were secured. All three men managed to exit safely, but the *Alvin* sank in 1540 m of water and carried their packed lunches with it. The submersible was not recovered until over 10 months later, at which time it was discovered that the scientists' lunches, although waterlogged, were still in good condition and edible. Placed for three weeks in a refrigerator at 3°C (the same temperature as at 1540 m), the food spoiled. This unexpected observation stimulated experiments in which organic substrates were exposed *in situ* at depths down to 5300 m; when these were recovered, they confirmed very low rates of bacterial metabolism in the abyss. The metabolic rate of abyssal bacteria living in sediments is from 10 to over 100 times slower than that of equivalent bacterial densities maintained in the dark, at the same low temperature, but at atmospheric pressure. Bacterial productivity is thought to

range from about $0.2 \text{ g C m}^{-3} \text{ day}^{-1}$ (at 1000 m) to $0.002 \text{ g C m}^{-3} \text{ day}^{-1}$ (at 5500 m).

Low metabolic rates have also been reported for some benthopelagic animals, including teleost fishes. However, studies of large deep-sea epibenthic decapods and echinoderms indicate respiration rates comparable to those of related forms in shallow water when measured at the same temperature. When oxygen uptake by benthic communities is compared, that in the deep sea is two to three orders of magnitude lower than that of shallow-water communities. This reduction in oxygen uptake is partly due to a lower density of organisms per unit area, but it also reflects the lower metabolic activity of deep-sea organisms.

Another indication of slower biological processes came from studies of *Tindaria callistiformis*, a small (<9 mm long) clam inhabiting soft sediments of the North Atlantic at 3800 m depth. Radioactive dating of the shells of this little deposit feeder suggested that it grows extremely slowly, with the shell increasing in length at about 0.084 mm yr^{-1} (see Figure 8.16 for a comparison with other molluscs). This would mean that *Tindaria* requires 50 years to reach sexual maturity, and that its life span would be about 100 years. However, the technique used to obtain these results has since been criticized, and faster growth rates have been estimated for other deep-sea benthos.

The wood-boring clams (see Section 8.8.4) that rely on ephemeral falls of wood in the deep sea are notable exceptions to slow growth rates. In order to search out and colonize new sources of wood, they have evolved opportunistic life strategies that involve rapid growth, early maturity, and production of many young.

QUESTION 8.13 Would you consider *Tindaria callistiformis* and wood-boring clams to be primarily examples of *r*- or *K*-selected species? (Refer to Section 1.3.1 and Table 1.1.)

Many deep-sea species have low fecundity. The number of eggs produced per individual is generally much lower in many deep-sea residents when compared with their shallow-water relatives; this can be related to the miniaturization that occurs in many groups. One small (< 1 mm long) deep-sea clam, *Microgloma*, produces only two eggs at a time, and even larger deep-sea clams may produce only a few hundred eggs at any one time. In contrast, shallow-water clams typically spawn tens or hundreds of thousands of eggs. Although type of development is not known for many deep-water species, the dominant mode appears to be production of lecithotrophic larvae.

Low fecundity and therefore low dispersal suggest slow rates of recolonization in the deep sea, and this has been confirmed by experimental studies. Boxes of sterilized azoic sediment were placed at depths of 10 m and 1760 m, and examined after 2 months and after 26 months. The shallow boxes were colonized rapidly by invertebrates; after only 2 months, the boxes contained 47 species and 704 individuals ($35\,714 \text{ individuals m}^{-2}$). In comparison, the deep-sea boxes yielded only 14 species and 43 individuals ($160 \text{ individuals m}^{-2}$) in the same period of time. Even after 26 months, recolonization of the deep-sea boxes was such that they contained 10 times fewer individuals and species than samples taken from the surrounding sediment at the same depth.

The low rates of metabolism and production shown by many deep-sea animals can be correlated with low food supply in their environment, but it is also likely that the food requirements of deep-sea species are much lower than those of surface-dwelling animals. Only a limited number of biochemical studies have been done on deep-sea animals, but these suggest that body protein concentrations and caloric content decrease with depth in fish and crustaceans. On a weight for weight basis, the food requirements of a slow-moving rat-tail fish living in the deep sea are likely to be about 20 times less than those of an active epipelagic salmon. Low rates of metabolism may also result from the physical-chemical constraints on enzyme kinetics that are known to occur at high pressures and low temperature.

8.8.6 FUTURE PROSPECTS

Much remains to be explored in the deep sea. Only a very small percentage of the seafloor has been examined using dredges, cores, submersibles, or remote cameras. By 1995, less than 100 m² of the deep seafloor had been *quantitatively* sampled. Certainly we can expect that many more new species will eventually be discovered. More detailed physical studies, particularly of water flow over the seafloor, may further alter our perception of homogeneity in this environment. For example, the effect of abyssal storms on benthos is not known.

We need to learn more about the biology of individual species in terms of their food and feeding patterns and energy requirements; their patterns of reproduction, development, and growth; and their interactions with other species. Only then can we approach an understanding of the factors that establish community structure, that determine production, and that maintain high species diversity in the deep sea.

8.9 HYDROTHERMAL VENTS AND COLD SEEPS

In 1977, scientists working off the Galapagos Islands discovered unusually high seawater temperatures at about 2500 m depth in an area where new seafloor is being formed. The hydrothermal activity accompanying this process manifests itself in the release of mineral-laden fluid either emitted as a warm (5–100°C) diffuse flow from cracks and crevices in the seafloor, or emerging as plumes of superheated (250–400°C) water from chimneylike vents. As the hydrothermal fluid mixes with the surrounding seawater, temperatures are moderated to between 8° and 23°C. Chemical analyses of the water in the vent areas revealed low concentrations of oxygen but very high concentrations of hydrogen sulphide (H₂S), a compound that is usually highly toxic to animals even in much lower concentrations.

QUESTION 8.14 What is the normal ambient seawater temperature at a depth of 2500 m? Refer to Section 2.2.2.

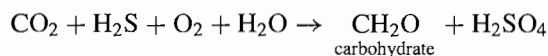
One of the most exciting events in benthic marine ecology occurred when scientists, diving in a submersible, discovered extremely dense concentrations of benthic animals living in this hydrothermal vent area. Since that time, similar deep-sea communities of animals have been found in other localities around the world, all of them in areas of tectonic activity. Sites at which

biological investigations have been conducted include the Mid-Atlantic Ridge and spreading centres along the rim of the Pacific Ocean basin.

8.9.1 CHEMOSYNTHETIC PRODUCTION

Many of the animals in the densely populated vent communities are of extraordinarily large size. The occurrence of very high benthic biomass in deep waters, far removed from surface photosynthetic production, immediately raised the question of how these animals obtained sufficient food.

Further studies revealed the existence of a food chain driven entirely by geothermal (terrestrial) energy, and not dependent on solar energy. Vent communities are dependent on the presence of hydrogen sulphide, a reduced sulphur compound that is released in hydrothermal fluid. This compound is utilized by sulphur-oxidizing bacteria (e.g. *Thiomicrospira* and *Beggiatoa*), and the energy released by the oxidation is used to form organic matter from carbon dioxide by the same biochemical pathway that is employed by photosynthetic organisms. The reaction requires molecular oxygen which is provided by the surrounding seawater. The biochemistry of the chemosynthetic production can be generally summarized as:



In vent communities, chemosynthetic bacteria are the primary producers of the food chain, and the bacterial biomass becomes available for consumption by higher animals. Mats of filamentous bacteria (up to 3 cm thick at some sites) can be grazed by animals like limpets, and bacteria suspended in water can be filtered by suspension feeders. In some cases, the bacterial production proceeds within tissues of host animals in special symbiotic relationships.

At present, the sulphur-oxidizing bacteria have received the most attention and are believed to comprise most of the bacterial biomass in vent areas. However, it is probable that other types of bacteria, utilizing different reduced materials (e.g. methane, ammonia) as sources of energy, also contribute to chemosynthetic production in these regions. In any event, bacterial production at hydrothermal vents is estimated to be two to three times that of photosynthetic production in the overlying water.

8.9.2 VENT FAUNA

Approximately 95% of the animals discovered at hydrothermal vents have been previously unknown species. To date, about 375 new species have been described, many requiring the establishment of new taxonomic families because they are so different from related species.

Spectacular giant, red, tube-dwelling worms found initially at the Galapagos vents proved to be a new genus and species, *Riftia pachyptila* (Colour Plate 39). These **vestmentiferans** (see Section 7.2.1 and Table 7.1) are encased in leathery tubes, with only a plume of many tentacle-like respiratory filaments protruding from the open end. They are highly unusual in lacking a mouth or digestive tract, but they are free-living and not parasitic. The largest vestimentiferans from the Galapagos site measure 1.5 m long and 37 mm in diameter, and have tubes of up to 3 m in length. These animals have extraordinarily high growth rates of up to 85 cm year⁻¹.

Densities of *Riftia* can be as high as 176 individuals m^{-2} , and biomass of *Riftia* alone ranges from 6800 to 9100 g wet weight m^{-2} . When combined with the wet weight of large bivalves living in the same site, biomass of this particular vent community can exceed 20–30 kg m^{-2} .

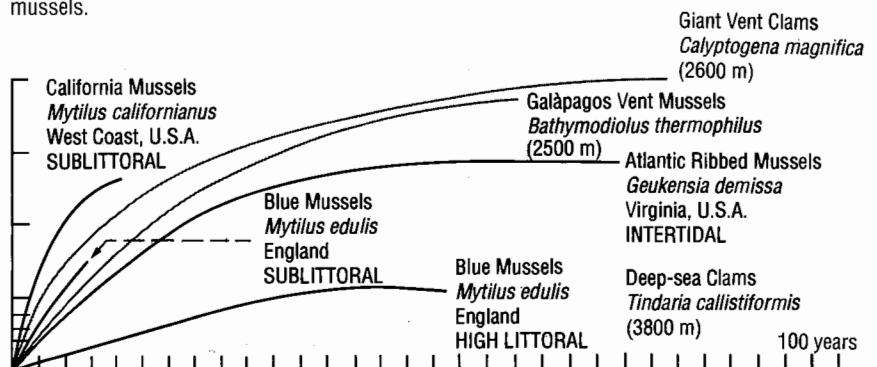
QUESTION 8.15 How does the biomass of the Galapagos vent community compare with typical biomass values at 2500 m depth? Refer to Table 8.2.

Riftia has a special internal organ known as a trophosome (meaning ‘feeding body’), which contains masses of symbiotic bacteria. These bacteria make up to 60% of the dry weight of a *Riftia* individual, and it becomes a semantic question as to whether this organism is more a bacterial colony than a worm. The haemoglobin of *Riftia* is unique in being able to carry both oxygen and hydrogen sulphide simultaneously. The bacteria obtain energy from hydrogen sulphide brought to them in the blood system of the worm; the bacteria utilize CO_2 and the energy derived from the oxidation of the sulphide to form organic carbon. Some of this organic carbon is, in some way, passed into the tissues of the worm. Whether this is the sole source of nutrition for these large worms, or whether they are also able to absorb dissolved organic matter (e.g. amino acids) from the surrounding seawater, remains unanswered.

Another conspicuous and dominant animal at the Galapagos hydrothermal vents is a clam, *Calyptogena magnifica*, that reaches lengths of 30–40 cm (Colour Plate 40). The soft body parts of this bivalve are red, as they are in *Riftia*. In both animals, the colour is derived from haemoglobin in the blood. Most molluscs contain the blood pigment haemocyanin; its replacement in *Calyptogena* by haemoglobin, a more efficient oxygen-carrier, may be an adaptation to the low and variable oxygen concentrations in the surrounding water. The gills of *Calyptogena* contain masses of attached sulphur bacteria and the clams, like *Riftia*, benefit nutritionally from this symbiotic relationship.

Growth rates of *Calyptogena* have been calculated to be from 10 mm yr^{-1} to as high as 60 mm yr^{-1} ; these rates are compared with growth rates of various other species of molluscs from different localities in Figure 8.16. Note that clams and mussels from vent areas have rates of growth that are comparable to those of shallow-water relatives, but they are approximately three orders of magnitude greater than those estimated for another deep-sea clam, *Tindaria* (see Section 8.8.5). Metabolic rates of *Calyptogena* and other

Figure 8.16 Growth curves for different species of shallow- and deep-water clams and mussels.



large vent animals are also similar to those of shallow-water relatives, and are orders of magnitude higher than those of related animals in other parts of the deep sea.

Related species of vestimentiferans and large clams similar to *Calymene magnifica* occur at other hydrothermal vent sites. Other vent molluscs include *Bathymodiolus thermophilus*, a giant mussel that has symbiotic bacteria on its gills but also is capable of suspension feeding, and limpets (>30 species) and snails which graze directly on mats of free-living bacteria covering hard surfaces. Several types of suspension-feeding polychaete worms are associated with vents, including tube worms (Family Alvinellidae) that attach in large numbers to vents emitting superheated water.

Deposit-feeding polychaetes are found in sediments around the vents. Long, thin enteropneusts, commonly known as spaghetti worms because of their appearance, can be abundant. Various types of crabs are found at most vents; some are scavengers, at least part of the time, and some prey on *Riftia*, small mussels, or polychaetes. Shrimp in densities of up to 1500 m⁻² surround smoking vents on the Mid-Atlantic Ridge, and they apparently feed on bacterial mats. Sea anemones are abundant at certain sites, but other types of cnidarians are absent in these communities. A primitive type of barnacle dominates some Pacific hydrothermal localities. Fish are not usually important members of these communities; only five species have so far been recorded from vents.

Zooplankton are found in higher densities around vents than in surrounding waters. Copepods, amphipods and other planktonic crustaceans have been described, but few have been studied in detail. A new copepod genus (*Stygiopontius*), with seventeen species, occurs at every vent site. Vent meiofauna is dominated by nematodes and benthic copepods, as it is in other deep-sea regions. As more hydrothermal vents are discovered and sampled, the list of new species of animals grows rapidly.

8.9.3 SHALLOW VENTS AND COLD SEEPS

All of the explored hydrothermal vent sites are in waters deeper than 1500 m, but geothermally-driven chemosynthetic production is not restricted to the deep sea. There are, for example, hydrothermal vents that release high concentrations of sulphides in intertidal areas off southern California. There, benthic mats of sulphide-oxidizing bacteria contribute to the total primary production of the area along with photosynthetic production by benthic plants and phytoplankton. Limpets living near these vents are reported to graze on the bacterial mats, whereas limpets living in non-vent areas typically graze on photosynthetic algae encrusting rocks.

In 1984 a community of exotic organisms was discovered in the Gulf of Mexico, at the base of the Florida Escarpment. This massive limestone cliff rises some 2000 m above the sea bottom; at a depth of 3270 m, hypersaline waters containing high concentrations of sulphides and methane seep out onto the seafloor. Although the water temperature is low, the organisms in this cold sulphide seep area are remarkably like those found in hydrothermal vents. White bacterial mats cover exposed substrates. There are dense concentrations of 1-m-long tube worms (a new genus and species of vestimentiferan) as well as thick patches of large mussels and clams (the latter a new species of *Calymene*). Snails, limpets, and crabs are also conspicuous inhabitants of this particular seep.

Cold-water seeps result from a variety of causes, and they have been found along continental margins and in subduction zones where oceanic crust is carried back down into the Earth's mantle. Those that have been explored support similar assemblages of animals. Seep communities are also dependent upon chemosynthetic production by sulphide bacteria, and not on photosynthesis. The discovery of cold seeps demonstrates that the most important component necessary for high biological production in the deep sea is a source of reduced inorganic compounds, not heat. The existence of hydrothermal vents and cold seeps in deep waters indicates that low temperature and high pressure do not limit activities of deep-sea organisms. In deep areas where benthic ecology is dependent on photosynthetic production at the surface, biological processes and benthic production are limited by low food. In areas where sulphide-based food chains are possible, biological production in the deep sea may exceed that in the euphotic zone.

Although each hot vent or cold seep site has distinctive physical features and distinctive fauna, the communities of animals associated with high sulphide concentrations are similar in some respects. The dominant species are often ecologically similar, if not taxonomically related. Large vestimentiferans commonly occur at many sites, as well as similar species of limpets, clams, mussels, and crabs. All of the communities are characterized by having high population densities, high biomass, and rapid growth rates. These are unique concentrations of life in depths that usually are characterized by low density and low productivity; as such, these sulphide communities are appropriately referred to as 'oases'. Bacterial chemosynthesis is the major source of food in all of these communities. No sunlight is necessary and no photosynthetic production is needed from the surface; the populations of organisms are sustained entirely by inorganic materials that are converted into bacterial biomass, which then becomes available for consumption by higher animals.

8.9.4 UNIQUE ENVIRONMENTAL FEATURES OF SULPHIDE COMMUNITIES

Although hydrothermal vents and cold seeps support communities with high biomass, species diversity is low compared to that at other deep-sea localities. Endemic species predominate; over 90% of the animals found at vents and seeps do not occur outside their special habitats. The environments of vents and seeps possess certain attributes that place physiological constraints on animals and require special adaptations. Many animal groups are not represented at these sites, presumably because they have not evolved the ability to cope with the special conditions. With a few exceptions, cnidarians other than sea anemones, echinoderms of all types, sponges, xenophyophores, brachiopods, bryozoans, and fish are uncommon or absent. Molluscs, polychaetes, and crustaceans account for more than 90% of all vent species.

Hydrothermal vents, in particular, are transient environments that undergo large and rapid changes. The geological processes that create vents are dynamic events, and new vents are being formed as others close. Vent communities probably persist only for several years to several decades. Old, inactive vents are surrounded by the shell remains of clams and mussels that died when their energy source disappeared.

Animals living around vents are subjected to high temperature variance and to an oxygen concentration that can switch rapidly from anoxic to oxic conditions. There are also short-term fluctuations in H₂S concentrations. Salinity in vent plumes varies from about one-third to twice that of normal

seawater. Hydrothermal fluid contains many inorganic substances which precipitate upon contact with seawater. The chimneys that emit superheated water are formed from the precipitation of sulphide deposits containing copper and zinc. This also means that animals are subjected to a rain of inorganic precipitates that coat their surfaces, and that they are exposed to potentially toxic concentrations of dissolved and precipitated heavy metals.

Both vents and seeps contain very high concentrations of H_2S (to 19.5 mM in hydrothermal fluid), and this raises the question of how the animals escape being poisoned by the high levels of H_2S . Hydrogen sulphide, even at concentrations less than one-thousandth of those found in some vent animals, poisons aerobic respiration. Only certain bacteria have the appropriate enzyme systems to oxidize this molecule in order to obtain chemical energy. Preliminary studies on *Riftia* indicate that it has special biochemical adaptations that protect the worm from H_2S toxicity. These include a special sulphide-binding protein in its blood, and enzyme systems in its body wall that oxidize any free sulphide entering the cells. Other vent species may be similarly equipped with sulphide-detoxifying systems.

Hydrothermal vent communities are quite small, usually only about 25–60 m in diameter, and they (as well as cold seeps) may be separated from other similar communities by as much as hundreds to thousands of kilometres. Vents are also ephemeral, lasting only on scales of years.

Given these features, how can animals maintain populations in widespread localities and how are new vents populated?

In order to succeed in short-lived, scattered habitats, animals of these communities could be expected to grow rapidly to sexual maturity, produce many young, and have efficient means of dispersal (see Section 1.3.1). Such *r*-selected traits would allow them to reproduce within the time span of their habitat and to continually colonize new vent areas. Although reproductive studies of vent fauna are few, zoogeographic studies suggest that vent species do rely on larval dispersal. On-going research into types of larval development and dispersal mechanisms is seeking information on these aspects.

8.10 SUMMARY OF CHAPTER 8

1 Relative to most other marine habitats, intertidal areas are characterized by great fluctuations in environmental conditions. Littoral plants and animals are specially adapted to cope with variable temperatures and salinity, and to withstand periodic exposure to air.

2 Rocky intertidal regions support dense communities with a high proportion of epiflora and epifauna that may compete for limited space. Many of the sessile species are arranged in distinct vertical zones. The upper boundary of any particular zone is often set by physiological limits of the species, such as tolerance to desiccation and temperature change. The lower limits of zones are generally established by biological factors such as predation and competition.

3 Intertidal areas of sand beaches support communities in which the primary producers are benthic species of diatoms, dinoflagellates, and blue-green bacteria, and the resident animals are predominantly infauna and