tunicates. The meiofauna fall prey to macrofaunal deposit feeders, shrimp, and young fish.

Fecundity of the meiofauna is low owing to their small sizes and the consequent physical constraints on producing large numbers of gametes. Many of the species produce only one to ten eggs at a time, and about 98% of the species lack pelagic larvae. The young are often brooded by the parent until they are able to live freely or, alternatively, eggs are attached to the sand and the young hatch as benthic juveniles. Dispersal is by passive transport of those eggs or adults that are caught in water currents when the sand is washed away, or by organisms attached to sand particles that adhere to the feet of wading birds.

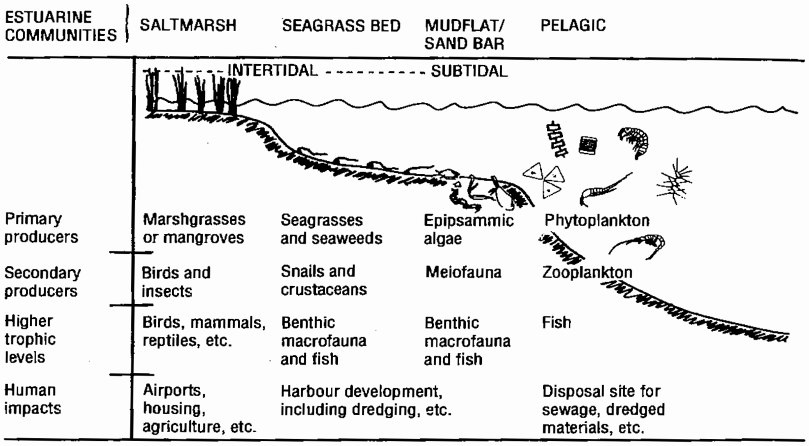
QUESTION 8.2 About 98% of the meiofauna in sand do not produce planktonic larvae. What factors favour direct development and suppression of a pelagic phase in these species and in this environment?

8.5 ESTUARIES

Estuaries are partially enclosed regions where large rivers enter the sea. They rank among the most productive of marine ecosystems as they typically contain a high biomass of benthic algae, seagrasses, and phytoplankton, and support large numbers of fish and birds. Estuaries are enriched by nutrients from land drainage, but their high productivity is also the result of nutrient retention within the estuary. This is due to the water circulation pattern that is set up when less dense freshwater overlies heavier salt water. Figure 3.15 illustrates how estuaries tend to entrain nutrients from deep, saline water into the freshwater flowing seaward from the river, with the nutrient enrichment usually leading to a phytoplankton bloom seaward of the river mouth. Some of the bloom will sink out into the lower, more saline layers, and the decomposing phytodetritus will then be carried back toward the land. Thus the special circulation pattern of estuaries, combined with tidal flow, results in the sinking of particles and nutrients from seaward-flowing river water, and in these nutrients being carried back at depth in the saline water that flows inward and upwells to replace that carried away by the surface flow.

Each estuary has unique physical features that influence its ecology. These include the amount of river discharge, depth and general topography, specific circulation patterns, climatic regime, and vertical tidal range. Nevertheless, certain generalities emerge from the many comparative studies of life in estuaries. In several respects, the estuarine ecosystem is much more complex than open ocean ecosystems, and the plankton community at the seaward edge of the estuary is only one of several communities governed by different groups of primary producers. The major components that typically make up estuaries are illustrated in Figures 8.6 and Colour Plate 33; the relative area occupied by each of these communities depends on local tidal action and the topography of the estuary.

Starting from the upper reaches of temperate-latitude estuaries, there is firstly a sheltered, upper intertidal **saltmarsh community** dominated by a variety of marshgrasses (e.g. *Spartina, Salicornia*); this community is largely replaced by mangroves in tropical and subtropical latitudes (see Section 8.7). The marshgrasses, which are rooted flowering plants, may be as much as 2 m high, and they function as a trap for nutrient-rich sediment. Above-ground



ESTUARINE COMMUNITIES	SALTMARSH	SEAGRASS BED	MUDFLAT/ SAND BAR	PELAGIC
Primary producers	Marshgrasses or mangroves	Seagrasses and seaweeds	Epipsammic algae	Phytoplankton
Secondary producers	Birds and insects	Snails and crustaceans	Meiofauna	Zooplankton
Higher trophic levels	Birds, mammals, reptiles, etc.	Benthic macrofauna and fish	Benthic macrofauna and fish	Fish
Human impacts	Airports, housing, agriculture, etc.	Harbour development, including dredging, etc.		Disposal site for sewage, dredged materials, etc.

Figure 8.6 A schematic depiction of the communities composing the estuarine ecosystem, showing their dominant flora and fauna and potential human impacts.

primary production of marshgrasses ranges from 200 to 3000 g C m^{-2} yr^{-1}, and production by benthic mud algae contributes another 100 to 600 g C m^{-2} yr^{-1}. Thus saltmarshes rank among the most productive ecosystems on Earth. Most of the living plant material is not grazed directly, but enters detritus food webs either on the marsh or in adjacent waters. This plant debris decays slowly and, over long periods, the accumulation of debris and trapped sediment may create peat deposits that are several metres deep. This upward growth of saltmarshes results in changes in relative tidal level and drainage, and thus in changes in the species composition of plants; this process of marsh evolution eventually contributes to the infilling of estuaries.

The upper reaches of a saltmarsh mark the transition between the sea and land. This habitat has great variations in salinity and temperature, and relatively few species of plants and animals live here permanently. Terrestrial animals such as raccoons, rats, and snakes invade this area, and there are large insect and bird populations. Faunal diversity is greater in the lower intertidal areas of the marsh, and the saltmarsh macrobenthos may include deposit-feeding fiddler crabs (*Uca*) that build burrows in the mud, snails (e.g. *Nassarius, Hydrobia, Littorina*) that feed on the rich deposits of benthic diatoms, and mussels of the genus *Modiolus* that are specially adapted to live in or on mud and that can respire in both air and water. The leaves and stems of the marshgrasses serve as attachment sites for many small organisms, and significant numbers of micro- and meiobenthos live on or in the bottom sediments. Bacteria attain densities as high as 10^9 cm^{-3} in the sediments, and they are an important food for protozoans and meiofauna. Saltmarshes fulfil the important function of providing shelter and food for shrimp, juvenile lobsters, and the young stages of many species of marine and estuarine fish.

A seagrass community is located seaward of the saltmarsh, in the intertidal and subtidal zones. It may contain significant stands of seaweeds in addition to the seagrasses, but in general, seaweeds do not grow as well in muddy estuarine waters as they do in clear waters. The dominant plant of this estuarine community in temperate latitudes is *Zostera*, commonly called eelgrass; in tropical climates, it is replaced by *Thalassia*, or turtlegrass. The brown seaweed *Fucus* and green seaweeds, *Enteromorpha* and *Ulva*, may grow on patches of rock among the seagrass beds. Measurements of the productivity of seagrasses are complicated by the fact that many epiphytic diatoms may grow on the blades of the seagrass, and these may add to the total primary productivity. For example, on the eastern coast of the United States, *Zostera* may produce about 350 g C m^{-2} yr^{-1}, and associated plants contribute a further 300 g C m^{-2} yr^{-1}. Generally, the annual production of temperate seagrasses is about 120–600 g C m^{-2}, while tropical seagrass communities have higher net primary productivities of up to about 1000 g C m^{-2} yr^{-1}.

Numerous meiofauna, including protozoans and nematodes, are associated with the seagrass epiphytes which are grazed by snails, isopods, amphipods, and harpacticoid copepods. Sessile filter-feeding invertebrates (e.g. hydroids, bryozoans, and tunicates) attach to the seagrass leaves. Snails, bivalves, polychaetes, and various types of crustaceans dominate the mobile invertebrate fauna of seagrass communities. This estuarine zone, like the saltmarsh, serves as a nursery area for the young of many species of fish, including commercial species such as menhaden and salmon.

In both the saltmarsh and seagrass communities, little of the primary production is consumed by herbivores. Both communities are dominated by detritus-based food chains because marshgrasses and seagrasses contain large amounts of refractory material, such as cellulose, that is difficult for herbivores to digest. Less than 10% of the marshgrass is grazed by terrestrial herbivores, and usually only a small fraction of the seagrass production is eaten by such animals as sea urchins and migrant birds (e.g. geese). However, in some tropical regions, turtlegrass may be consumed in large quantities by dugongs or manatees, and by sea turtles. In general, though, by far the largest fraction of the net primary production in both communities dies and is colonized by fungi and bacteria, to be converted eventually into microbial biomass. The numbers of bacteria in estuarine water are much higher than in seawater, and bacterial densities in sediments may reach 200–500 × 10^6 per gramme of estuarine mud. Thus a large amount of plant detritus is produced, some of which is exported out of the estuary, and much organic carbon is recycled to re-enter the food chain through the microbial loop (see Section 5.2.1). Within the sediments, much of the organic matter is decomposed under anoxic conditions, with anaerobic bacteria using primarily inorganic sulphate as a source of oxygen.

QUESTION 8.3 Is the occurrence of hydrogen sulphide in sediments an indication of pollution?

On the seaward side of the seagrasses, either a subtidal **mudflat** or **sand-bar community** will be present depending on the current and tidal regime. In fact, this community is continuous underneath both the intertidal seagrass and saltmarsh communities. The dominant primary producers of mudflats or sand bars are the **epipsammic** algae, which are generally species of benthic diatoms or dinoflagellates that are specially adapted to grow on sediment particles. The surface of mud is sometimes colonized by thick mats of filamentous blue-green algae of several types. The productivity of this region tends to be inversely correlated with the grain size of the sediment particles, so that mudflats are generally more productive than sand bars in the same location. The primary productivity of these communities (in the absence of a cover of marshgrasses or seagrasses) tends to be low. Sand bars have a primary productivity of about 10 g C m^{-2} yr^{-1} but mudflat production by benthic microphytes may be as high as 230 g C m^{-2} yr^{-1}.

QUESTION 8.4 Why should the particle size of sand vs. mud affect the productivity of the epipsammic algae?

The mudflat community supports a wide range of animals, with crabs and flatfish being common epifauna, and bivalves, polychaetes, and mud shrimp dominating the infauna. There is a rich meiofauna of small copepods, nematodes, and polychaetes, and an equally rich microfauna of protozoans, especially ciliates. Detritivores are usually predominant in the community. In the shallower reaches of this community, large numbers of birds eat the detritivorous invertebrates. Food consumption by birds may represent a significant impact on the mudflat species. For example, each of several thousands of knots (*Calidris canutus*) on a large mudflat may eat as many as 730 small clams (*Macoma*) per day; a single redshank (*Tringa totanus*) may consume up to 40 000 burrowing amphipods (*Corophium*); and one oyster-catcher (*Haematopus ostralegus*) can eat 315 cockles (*Cardium*) daily. Overall, birds may take between 4% and 10% of the accessible invertebrate fauna.

The **pelagic community** located on the seaward edge of the estuary is controlled largely by the primary productivity of the phytoplankton, and this ranges from about 100 to 500 g C m^{-2} yr^{-1}, depending on water clarity. Although nutrients may be plentiful, turbidity of the water often restricts light penetration and limits phytoplankton production. In shallow estuaries, as much as half of the phytoplankton may be consumed by filter-feeding benthos, with the rest being eaten by zooplankton. Zooplankton also may feed on benthic diatoms and bacteria-covered sediment particles that are resuspended by intense mixing in shallow estuaries. In deep fjordlike estuaries, benthic plants are light-limited and most of the estuarine primary production is carried out by phytoplankton.

Although estuaries are highly productive and host many juvenile fish, as well as large numbers of crustaceans, molluscs, shorebirds and waterbirds, the number of species found in these areas is relatively small compared with other marine habitats. Few species are adapted to cope with the salinity, temperature, and turbidity variations present in this habitat. Salinity tolerance plays a major role in the distribution of any particular species in an estuary, although distribution is also determined by such factors as substrate type and degree of tidal exposure.

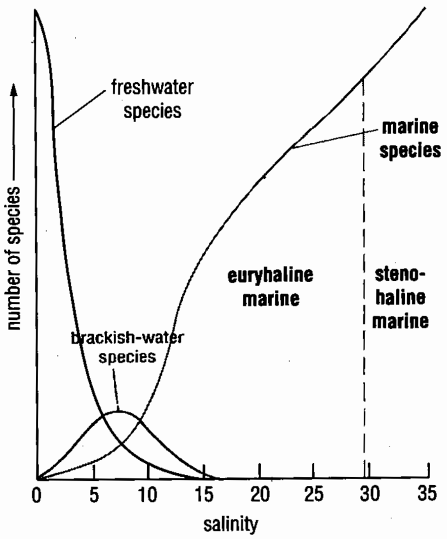


Figure 8.7 An idealized diagram of the distribution of freshwater, brackish-water, and marine animals relative to salinity. (Numbers of species given in relative units.)

Figure 8.7 illustrates the typical distribution and relative diversity of freshwater, brackish, and marine animals in relation to estuaries. Estuaries support an essentially marine fauna, but the number of marine species declines as the water becomes less saline, and the species change from those that are stenohaline to those that are euryhaline (see Section 2.3.2). The majority of animals living in rivers do not tolerate salinities greater than about 0.5, and they do not penetrate further seaward than the uppermost reaches of the estuary. Only a few freshwater organisms (**oligohaline** species) can survive in water having a salinity of 0.5 to about 5; these include principally various insect larvae, oligochaete worms, snails, and some fish such as sticklebacks. There are relatively few brackish-water species that are restricted to estuarine conditions with salinities of about 5–20, and most are animals with marine affinities. Euryhaline marine organisms constitute the majority of species living in estuaries, and their distributions extend from the sea into the central regions of estuaries.

Stenohaline marine species are unable to tolerate salinities lower than about 25–30, and they are largely excluded from estuaries. Some fish (e.g. salmon, eels) are transient residents of estuaries, and move freely from the sea to rivers and lakes, or vice versa (see Section 6.6.1). Overall, estuaries have fewer species than adjacent aquatic environments, but abundance within individual species as well as biomass are often markedly increased.

In general, the extent of penetration into estuaries by marine and, conversely, freshwater species is determined by the rate and magnitude of tidal change, rather than by the salinity gradient. That is, marine species penetrate farther upstream, and freshwater organisms reach much closer to the sea, in estuaries where tides are small and the salinity gradient is relatively stable. The minimum number of species occurs in that part of the estuary where the salinity variation is greatest. Finally, the distributions of benthic species within estuaries are also controlled by sediment type.

QUESTION 8.5 Can you offer any explanation(s) as to why species diversity declines in estuaries relative to adjacent environments, but numbers of individuals and biomass increase?

8.6 CORAL REEFS

Coral reefs are well known for their spectacular beauty (Colour Plates 34 and 35), and they are perhaps the most diverse and ecologically complex of marine benthic communities. They are unique in being formed entirely by the biological activity of certain corals belonging to the Phylum Cnidaria (see Table 7.1). These tropical reefs result from massive deposits of calcium carbonate laid down by the corals over aeons of geologic time. These are among the oldest of marine communities, with a geological history stretching back for more than 500 million years.

8.6.1 DISTRIBUTION AND LIMITING FACTORS

Living coral reefs cover about 600 thousand km^2, or somewhat less than 0.2% of the global ocean area and about 15% of the shallow sea areas within 0–30 m depth. The largest reef is the Great Barrier Reef that extends along the east coast of Australia for a distance of more than 2000 km and is as much as 145 km wide. Reefs are located exclusively within water bounded by the 20°C isotherms and so are virtually confined to the tropics (Figure 3.10). Reef-building corals cannot tolerate water temperatures of less than 18°C, and optimal growth usually occurs between 23° and 29°C, although some corals tolerate temperatures of up to 40°C. A number of other physiological demands further limit the distribution of reef-building corals. They require high salinity water ranging from 32 up to 42. High light levels are also necessary for reef-building (for reasons that will be explained below), and this restricts corals to the euphotic zone. Even in the clear oligotrophic water of the tropics, most reef-building species live in water that is shallower than 25 m. The upward growth of a reef is restricted to the level of lowest tides, as exposure to air for more than several hours kills corals. Corals are also absent in turbid waters, as they are very sensitive to high levels of suspended and settling sediment which can smother them and clog their feeding mechanisms. High turbidity also affects reef-building by decreasing the depth of light penetration. New reefs are initially formed by the attachment of meroplanktonic coral larvae to a hard substrate, and for this reason reefs always develop in association with the edges of continents or islands.

QUESTION 8.6 Refer to Figure 3.10. (a) Can you explain why coral reefs are generally absent on the west coasts of the Americas and Africa between 30° S and 30° N? (b) What might prevent reef formation off north-eastern South America, northward from the mouths of the Amazon and Orinoco rivers?

8.6.2 CORAL STRUCTURE

Corals are closely related to benthic sea anemones (both are in the Class Anthozoa) and are more distantly related to planktonic jellyfish, benthic marine hydroids, and the freshwater *Hydra*. Not all corals are reef-builders; some are solitary or colonial animals that are capable of living in deeper and/or colder water and are found throughout the world's oceans. Reef-building stony corals are colonial animals, and each reef is formed of billions of tiny individuals called polyps (Figure 8.8; Colour Plate 36). Each polyp secretes a calcium carbonate exoskeleton around itself that generally measures about 1–3 mm in diameter. Each polyp is equipped with tentacles containing batteries of nematocysts (see Section 4.2), and these stinging cells can be used to capture prey and for defence. The polyps can produce a large colony by asexual division, or budding, and all the polyps in a colony remain connected to each other by extensions of their tissues. Corals also reproduce sexually, producing planktonic larvae that disperse, settle, and establish new colonies.

Individual coral colonies vary in size, but some are very large, weighing up to several hundred tonnes. The form of a colony, whether it is branching, massive, lobed, or folded, depends on the species and also on the physical

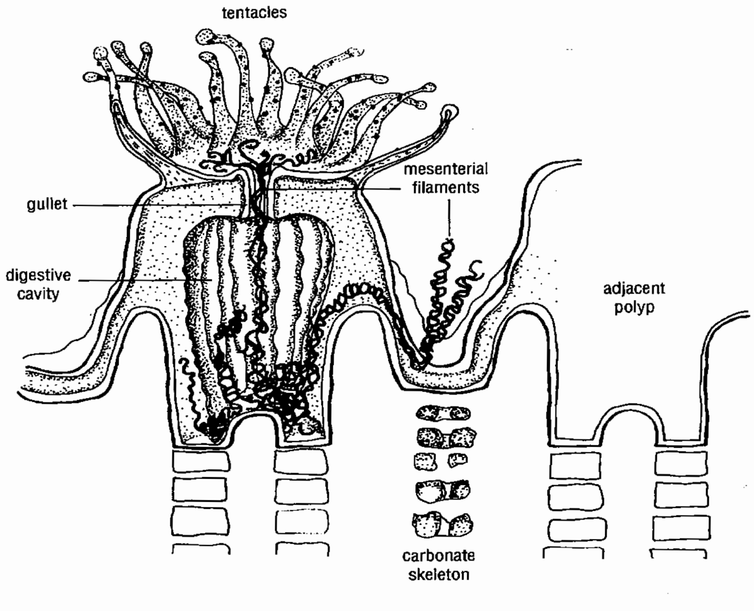


Figure 8.8 Anatomy of a coral polyp. The animal is basically a contractile sac housed in a carbonate skeleton. The central mouth is surrounded by six, or a multiple of six, tentacles equipped with batteries of nematocysts. The tiny zooxanthellae live in cells in the lining of the central digestive cavity. Each polyp secretes a protective carbonate exoskeleton consisting of a radial arrangement of vertical plates; as it grows upward, the polyp deposits new layers under itself.

environment in which the coral is located. The same species may have a very different form when it grows in areas exposed to wave action as opposed to calm conditions, or when it grows in shallow versus deeper waters.

8.6.3 DIVERSITY

The diversity of life on a coral reef is extraordinarily rich. Figure 8.9 illustrates only a very few dominant types of the coral-reef fauna. The Great Barrier Reef is composed of about 350 species of hard corals, and is home to more than 4000 species of molluscs, 1500 species of fish, and 240 species of seabirds. In addition, there are many more species of macrobenthos, and the numbers of micro- and meiofauna remain unknown. Representative species of almost all phyla and classes can be found in the reef ecosystem.

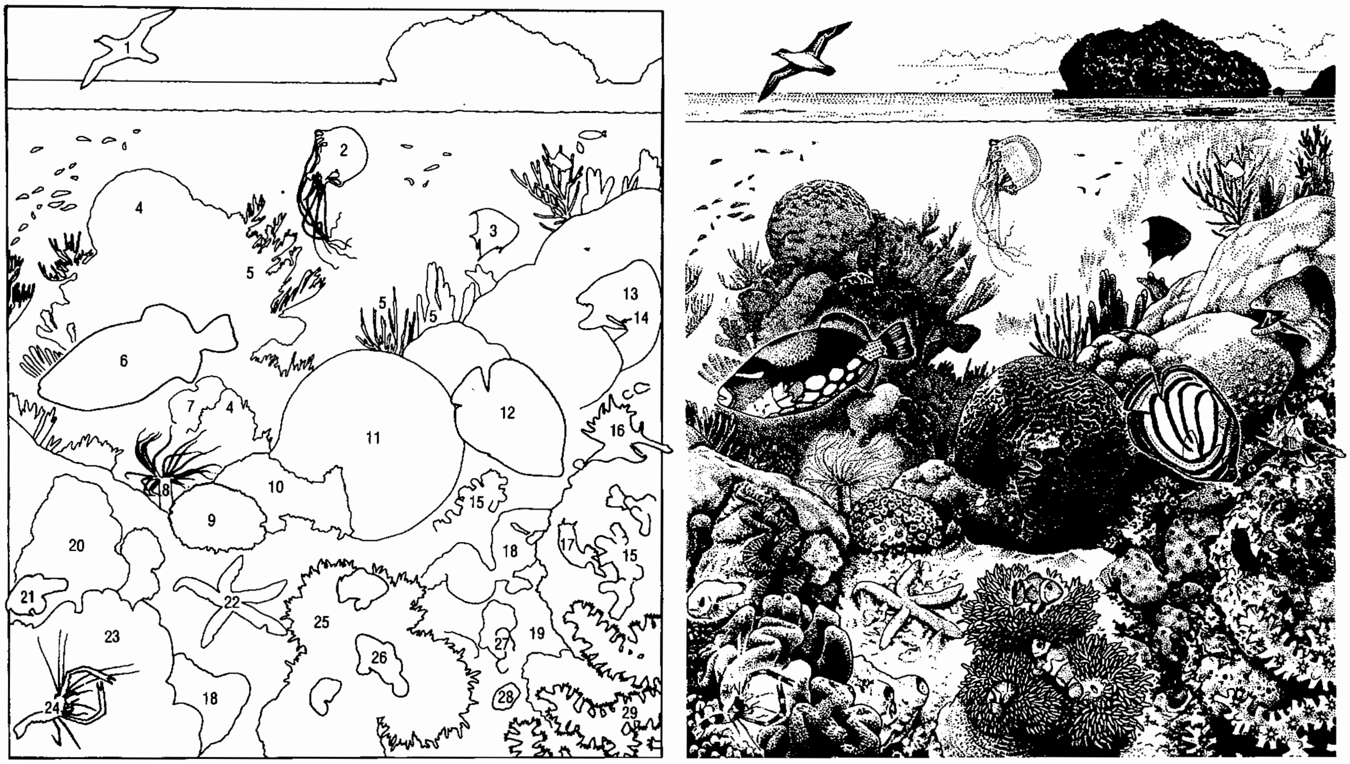


Figure 8.9 A coral reef habitat illustrating some of the many inhabitants of this diverse ecosystem.

1	petrel
2	jellyfish
3	angelfish
4	lobed corals
5	sea whips (gorgonian corals)
6	triggerfish
7	sea fans (gorgonian corals)
8	tube anemone
9	stone coral
10	bryozoans
11	brain coral
12	butterfly fish
13	moray eel
14	cleaner fish
15	tube corals
16	snail
17	nudibranch (sea slug)
18	sponges
19	colonial tunicate
20	giant clam (*Tridacna*)
21	pseudochromid fish
22	starfish
23	soft corals
24	cleaner shrimp
25	sea anemones
26	clownfish
27	worm tubes
28	snail (cowry)
29	sea fan (gorgonian)

Reefs in the Indo-Pacific have a high diversity of coral species, with at least 500 reef-building species throughout the entire region. Atlantic reefs are impoverished in comparison, with only about 75 species of reef-building corals. The number of species in other animal groups associated with reefs is also generally lower in the Atlantic sector than in the Indo-Pacific. The number of mollusc species is estimated at about 5000 in the Pacific versus 1200 in the Atlantic, and there are about 2000 versus 600 fish species in these respective reef areas. The differences in species diversity may result from differences in the age of the oceans, and the respective geologic times over which reefs have evolved. Geologically, the Atlantic is a more recent ocean, and its reefs were also more severely influenced by decreased temperatures and lowering sea levels during ice ages. Most Atlantic reefs are only 10 000–15 000 years old, these dates corresponding to the last glacial age. In contrast, the Great Barrier Reef is about 2 million years old, and some Pacific atolls date back about 60 million years.

The reef itself provides food and shelter for many plants, invertebrates, and fish. For sessile species, the reef offers a site of attachment. Surface irregularities in the reef limestone create a variety of microhabitats like crevices and tunnels, and these contribute to the faunal diversity of the system. Areas of rubble and sand also accumulate between coral heads, and these sediment types require different sets of adaptations and develop different communities from that associated with the hard-substrate reef. A reef is also differentiated into regions distinguished by physical differences in wave action, depth, and degree of tidal exposure. This wealth of different habitats is a major factor in supporting the many species of a reef.

Coral polyps usually dominate the living biomass of a reef, but other reef organisms also contribute to the carbonate reef structure. These include the hard, coralline red algae that grow in thin layers over the surface of the reef. These encrusting algae precipitate $CaCO_3$ and play a role in cementing the reef fragments together. Some green algae also secrete calcium carbonate, other green algae do not. In addition to encrusting algae, there are benthic algae that are erect species, and some that live within the spaces of the coral framework. Seagrasses often grow in the sandy areas within or surrounding the reef. All of these plants provide food for herbivorous species of invertebrates and fish. However, the algae are generally inconspicuous inhabitants of the reef, and animal life is visually dominant.

In addition to the reef-building stony corals, other types of cnidarians are prominent reef members (see Figure 8.9 and Colour Plate 37). These include several types of non-reef-building corals, including fire corals, pipe corals, and soft corals. Sea whips and sea fans are also common reef inhabitants; they are close relatives of stony corals and have internal skeletons composed of calcareous spicules. Other major invertebrate groups in a reef community include echinoderms (starfish, sea urchins, and sea cucumbers), molluscs (limpets, snails, and clams), polychaete worms, sponges, and crustaceans (including spiny lobsters and small shrimp). Some of the invertebrates are encrusting species, like bryozoans; some build calcareous tubes, like certain polychaete worms; and some snails attach tube-like shells to the reef. All of these activities serve to cement the limestone reef framework together. In the Pacific, giant clams belonging to the genus *Tridacna* are also important structural components of reefs (Figure 8.9). These molluscs contribute an astonishing biomass to the reefs, as they grow to over 1 m in length and may exceed 300 kg in weight.

Fish comprise the dominant vertebrates on a reef. Many of the reef fish are brightly coloured and visually conspicuous. About 25% of the world's species of marine fish are found only in reef areas. These diverse species of fish show a high degree of feeding specialization and food selection. Some are herbivores, feeding on algae or seagrasses; some specialize in being plankton-feeders; and some are piscivorous, or are predators of benthic reef invertebrates. Fish not only play important ecological roles in grazing or predation, but the faeces of these abundant animals contribute an important source of nutrients to the reef ecosystem.

The very large number of reef species, and the abundance of life on the reef, lead to intense competition between species and between individuals for limited resources. The high degree of food specialization observed in many reef species is a reflection of the high species diversity of the reef, and every available food resource is efficiently utilized. There is also intense competition for space on the reef, and every microhabitat is occupied by organisms adapted to their particular site. Experimental work has revealed that the mesenterial filaments (Figure 8.8) of some corals contain substances that kill polyps of adjacent colonies. Aggressive, slow-growing corals can thus avoid being overgrown by less aggressive, but faster-growing species.

8.6.4 NUTRITION AND PRODUCTION IN REEFS

Reef-building corals are also called **hermatypic** corals. They are distinguished from non-reef-building (**ahermatypic**) species by having a special symbiotic association with certain algae. Each hermatypic coral polyp contains masses of photosynthetic dinoflagellates, called **zooxanthellae**. These are a vegetative form of free-living dinoflagellates; when cultured under laboratory conditions, they develop into motile flagellate forms identical with planktonic dinoflagellates (see Section 3.1.2). The zooxanthellae in all corals belong to a single genus, *Symbiodinium*, with different species or strains being specific to particular coral species. The zooxanthellae live within cells in the lining of the gut of corals, reaching concentrations of up to 30 000 cells per mm^3 of coral tissue. Under stressful environmental conditions, the symbiotic algae can be expelled from the coral. Because much of the colour of corals is due to the pigmentation of the zooxanthellae, this expulsion is referred to as 'bleaching'.

The algal-coral relationship is beneficial to both species. The coral provides the algae with a protected environment, but it also provides certain chemical compounds that are necessary for photosynthesis. Carbon dioxide is produced by coral respiration, and inorganic nutrients (ammonia, nitrates, and phosphates) are present in waste products of the coral. In return, the algae produce oxygen and remove wastes; but most importantly, they supply the coral with organic products of photosynthesis that are transferred from the algae to the host. These chemical products include glucose, glycerol, and amino acids, all compounds that are utilized by the coral polyps for metabolism or as building blocks in the manufacture of proteins, fats, and carbohydrates. The symbiotic algae also enhance the ability of the coral to synthesize $CaCO_3$. Rates of calcification are significantly slowed when zooxanthellae are experimentally removed from corals, or when corals are kept in shade or darkness. The relationship between the two independent processes of CO_2 fixation by photosynthesis and CO_2 fixation as $CaCO_3$ is complex and not fully understood. However, the symbiotic association with photosynthetic dinoflagellates explains why hermatypic corals require clear, lighted water. This association also leads to intense competition for space within areas of sufficient light to support the zooxanthellae.

QUESTION 8.7 Can any corals grow below the euphotic zone?

The coral–zooxanthellae symbiosis is maintained over time and distance because the algae are already contained in coral larvae before they are released from the parent polyp. This relationship is not unique on the reef, however. Zooxanthellae are also present in other reef inhabitants, including the majority of other cnidarians, some tunicates, some shell-less snails, and in the giant clam *Tridacna*.

The symbiotic arrangement between algae and corals or other invertebrates results in nutrients being tightly recycled within coral reefs. This internal nutrient cycling is of primary importance in maintaining the productivity of the reef in oligotrophic tropical water.

Symbiotic algae do not supply all the nutritional requirements of their hosts. All the animals harbouring zooxanthellae are mixotrophic and capable of meeting their additional nutritional needs in other ways. Corals are true carnivores that capture zooplankton, employing their nematocysts to paralyse the prey. Many coral species can also feed on suspended particles by producing mucous nets or mucous filaments to entangle food that is then drawn to the mouth by rows of cilia. Ciliary-mucus feeding extends the size range of potential food items to include even bacteria. Corals may also directly absorb dissolved organic matter.

The relative importance of zooxanthellae versus captured particulate food to the nutrition of any particular coral probably depends on the particular species, and it will be influenced by the specific chemical that is produced and translocated from the symbiotic algae to the host. It should also be influenced by various environmental parameters such as depth, light intensity, abundance of zooplankton, etc.

8.6.5 PRODUCTION ESTIMATES

Primary production in the coral reef system is carried out by the benthic algae attached to or associated with the reef, by the suspended phytoplankton, and by the zooxanthellae living within the animals of the reef. This ecological fractionation of primary producers makes accurate measurements of primary productivity extremely difficult because different techniques must be employed for each. With the exception of the phytoplankton, it is also difficult to assess the standing stock of primary producers. To do so requires determining the plant/animal proportions of coral polyps and the relative contributions of various types of benthic algae to total reef biomass. Until these have been determined, the size of the primary producer trophic level remains uncertain.

Production studies of coral reefs suggest that gross primary productivity ranges from about 1500 to 5000 g C m^{-2} yr^{-1}, values that are much higher than those of open tropical oceans (see Section 3.5 and 3.6). In fact, they represent some of the highest rates of primary production of any natural ecosystem. However, many of the nutrients contributing to this production are recycled (i.e. the f-ratio <0.1, see Section 5.5.1). Symbiosis between primary producers and dominant animal species of the community, with nutrients prevented from being washed away, is a dominant controlling feature of the biological production, just as it is in the deep-water, sulphide-communities which will be described in Section 8.9.

Net primary production on reefs is lower than might be expected because respiration of the primary producers is high, with gross production to respiration ratios (P/R) usually ranging from 1.0 to 2.5. In comparison, healthy phytoplankton have a P/R ratio of about 10. In addition, the coral-reef food chain is much longer than in upwelling zones (see equation 5.2), so that respiration losses throughout the entire ecosystem are high. This results in lowering the production of top-level predators relative to the high gross primary productivity.

8.6.6 FORMATION AND GROWTH OF REEFS

During the voyage of the *Beagle* in the 1830s, Charles Darwin observed that there were three basic types of coral reefs, and he formulated an hypothesis of reef formation that linked these types. His ideas are summarized below and illustrated in Figure 8.10.

Reef formation is initiated with the attachment of free-swimming coral larvae to the submerged edges of islands or continents. As the coral grows and expands, a **fringing reef** is formed as a band along the coast or around an island. This type of reef is predominant in the West Indies (Caribbean Sea). It is also the first stage in the process of forming atolls.

If the fringing reef is attached to the edges of a volcanic island or other land mass that is slowly sinking, while the coral continues to grow upward, a **barrier reef** will eventually form. Barrier reefs are separated from the land mass by a **lagoon** of open deep water. The Great Barrier Reef of Australia is the best known of this type, but it is in fact an aggregation of many reefs.

Atolls mark the last stage in this geological process. When a volcanic island subsides below sea level, the coral reef is left as a ring around a central lagoon. Continued coral growth maintains the circular reef, but calm conditions and hence increased sedimentation in the central lagoon prevent development of a reef in this area. Hundreds of coral atolls are found throughout the South Pacific Ocean, all of them located far from land but attached to underwater **seamounts** (volcanic elevations rising from the seafloor) which have subsided with age.

Darwin's ideas on atoll formation were not substantiated until the 1950s, when drilling programmes on coral atolls encountered volcanic rock hundreds of metres below the surface. His hypothesis has been further supported by the discovery of seamounts, submerged far below the sea surface, that still have attached remnants of shallow-water corals.

QUESTION 8.8 Excluding pollution influences, would you expect to find a difference in total biological production between a barrier reef located offshore of a continent and a mid-oceanic atoll? Explain your answer.

The rate at which a reef develops depends on a balance between the growth rates (budding) and calcification of the coral polyps and the rates of destruction of the limestone framework. Corals always grow upward, toward light, as each polyp deposits new carbonate layers under itself (Figure 8.8). Growth of the coral skeleton is much faster in sunlight than in darkness (and

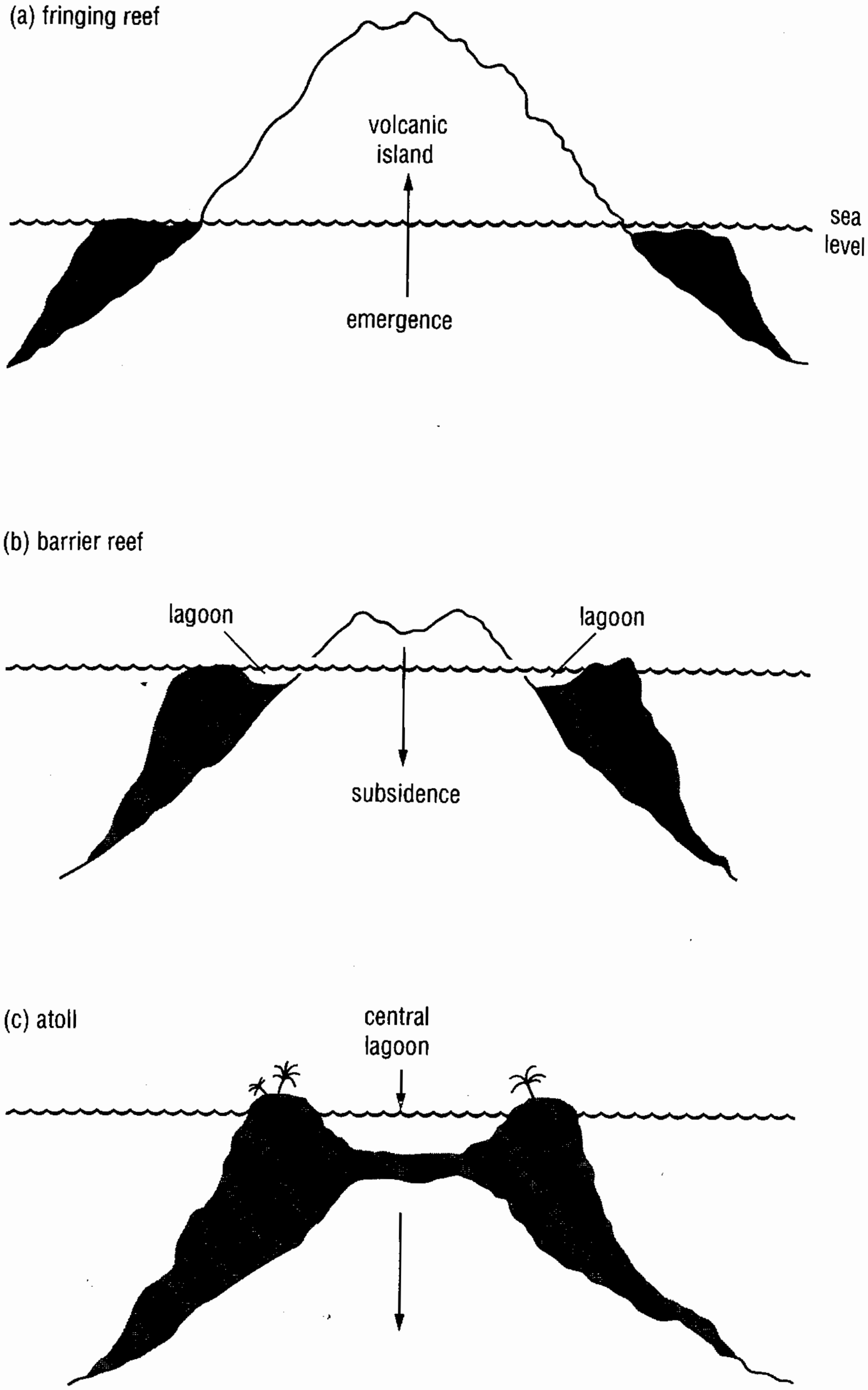


Figure 8.10 The formation of coral atolls according to Darwin's theroy of subsidence.

therefore also faster in shallower water) and, not surprisingly, the rate of growth can be decreased if photosynthesis of the zooxanthellae is reduced by sediment-laden water or chemicals (see Section 8.6.4). Growth rates may also decline with age and increasing size of a colony. In general, corals are regarded as slow-growing, with measured rates of growth usually varying from <1 to 10 cm yr^{-1}.

However, growth rates of individual coral species do not necessarily describe the rate of growth of an entire reef system. This is partly because different species of corals have different growth rates, but also because growth and expansion of the reef is regulated by many other factors such as predation, competition for space with other organisms, and light intensity, to name only a few. Further, the limestone framework is continually being destroyed by biological activities and physical events (see below). Estimates of total reef growth can be made from measured changes in reef topography over several years, or from geological information on the thickness of reef limestone deposits. These estimates of net vertical upward growth of reefs vary greatly, from only a few millimetres per year, to 30 cm per 11 years under favourable conditions.

In order to obtain better estimates of the rate at which entire reef systems grow, it is also necessary to know something about the factors that destroy the reef and the rate at which the limestone is broken down. Reefs are subject to physical erosion by wave action and currents, and tropical storms can cause extensive damage. Reefs are also subject to continual **bioerosion**, or breakdown of the calcium carbonate skeleton by reef inhabitants. Some organisms associated with the reef remove part of the coral skeleton by boring into the reef, using chemical dissolution or mechanical abrasion; these include certain species of algae, clams, sponges, sea urchins, and polychaete worms. Some animals (e.g. herbivorous limpets and snails, parrotfish) remove pieces of the reef skeleton inadvertently during grazing. Small coral fragments are consumed by deposit-feeders such as sea cucumbers, and thus become further reduced in size. These destructive activities eventually break down reef material to fine-grained carbonate sand. Much of the fine-grained detritus is flushed away from the reef by waves and currents, but some accumulates in pockets between coral heads.

8.6.7 ZONATION PATTERNS ON REEFS

All reefs exhibit zonation patterns resulting from a combination of bottom topography and depth, and different degrees of wave action and exposure. The patterns differ according to locality and type of reef, with atolls having the most complex zonation. The major divisions are illustrated in Figure 8.11 and discussed below, but depending on locality, the zones may be subdivided into as many as a dozen.

The **reef flat** (or back-reef) is located on the sheltered side of the reef, extending outward from the shore or coastline to the reef crest. This area is only a few centimetres to a few metres deep, and large parts may be exposed at low tide. The width of the reef flat varies from a few tens to a few thousands of metres. The substrate is formed of coral rock and loose sand. Beds of seagrasses often develop in the sandy regions, and both encrusting and filamentous benthic algae are common. Because it is so shallow, this area experiences the widest variations in temperature and salinity, but it is protected from the full force of breaking waves. The reduced water circulation, accumulation of sediments, and periods of tidal emersion combine to limit coral growth. Although living corals may be scarce except near the seaward section, this area of many microhabitats supports a great number of species in the reef ecosystem, with molluscs, worms, and decapod crustaceans often dominating the visible macrofauna.

The **reef crest** (or algal ridge) lies on the outer side of the reef, with its exposed seaward margin marked by the line of breaking waves. As the name implies, the reef crest is the highest point of the reef, and it is exposed at

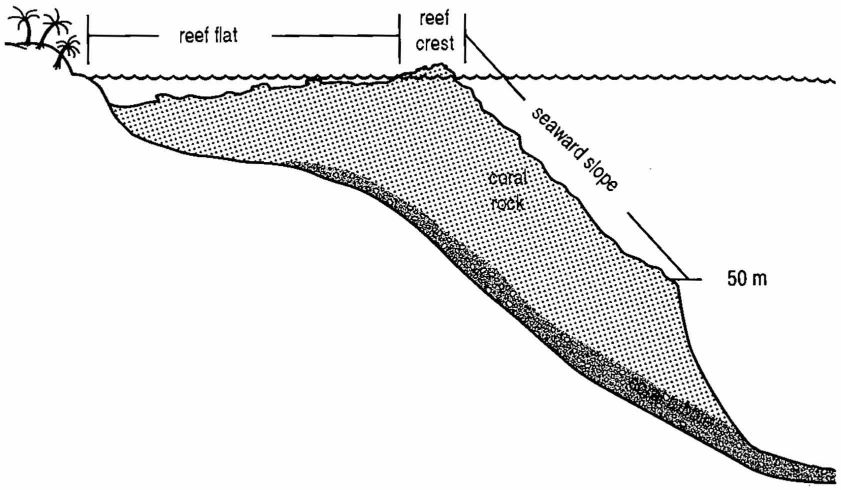


Figure 8.11 A generalized cross section of a typical Caribbean fringing reef, illustrating the major ecological zones.

low tide. The width of this zone varies from a few to a few tens of metres. In some localities, encrusting red coralline algae are dominant; in other reefs, brown algae predominate in this zone. Living corals are very scarce where wave action is severe; usually only one or two robust coral species dominate in this region.

The outermost **seaward slope** (also called fore-reef) extends from the low tide mark into deep water. The upper part of this zone is broken by deep channels in the reef face, through which water surges and debris from the coral reef leaves. Large corals dominate here, and there are many large fish. The maximum number of coral species tends to occur at 15–25 m, then declines fairly rapidly with increasing depth. At 20–30 m depth, there is little wave action and the light intensity is reduced to about 25% of that at the surface; here, corals tend to be smaller branched forms. At 30–40 m, sediments accumulate on the gentle slope and coral becomes patchy in distribution. Sponges, sea whips, sea fans, and ahermatypic corals become increasingly abundant and gradually replace hermatypic corals in deeper and darker water. At 50 m, the slope steepens into deep water. The depth limit for reef-building corals is about 50–60 m in the Pacific, and about 100 m in the Caribbean; the difference is probably related to differences in light penetration.

8.7 MANGROVE SWAMPS

Mangrove swamps, also called **mangals**, are a common feature covering 60–75% of tropical and subtropical coastlines. These forests of trees and shrubs that are rooted in soft sediments occur in the upper intertidal zone. They produce a marine system that is similar to a saltmarsh in having aerial storage of plant biomass and in harbouring both terrestrial and marine species. The euryhaline plants making up this specialized community are tolerant of a wide range of salinities and are found both in fully saline waters and well up into estuaries, but they are restricted to protected shores with little wave action. The distribution of mangroves overlaps with that of coral reefs, but extends farther into subtropical regions. In many areas, mangrove swamps border coastlines protected by barrier reefs.

8.7.1 WHAT ARE MANGROVES?

The term 'mangrove' refers to a variety of trees and shrubs belonging to some 12 genera and up to 60 species of flowering terrestrial plants (angiosperms). Dominant genera include *Rhizophora, Avicennia*, and *Bruguiera*. They have in common the following features:

(a) They are salt-tolerant and ecologically restricted to tidal swamps.

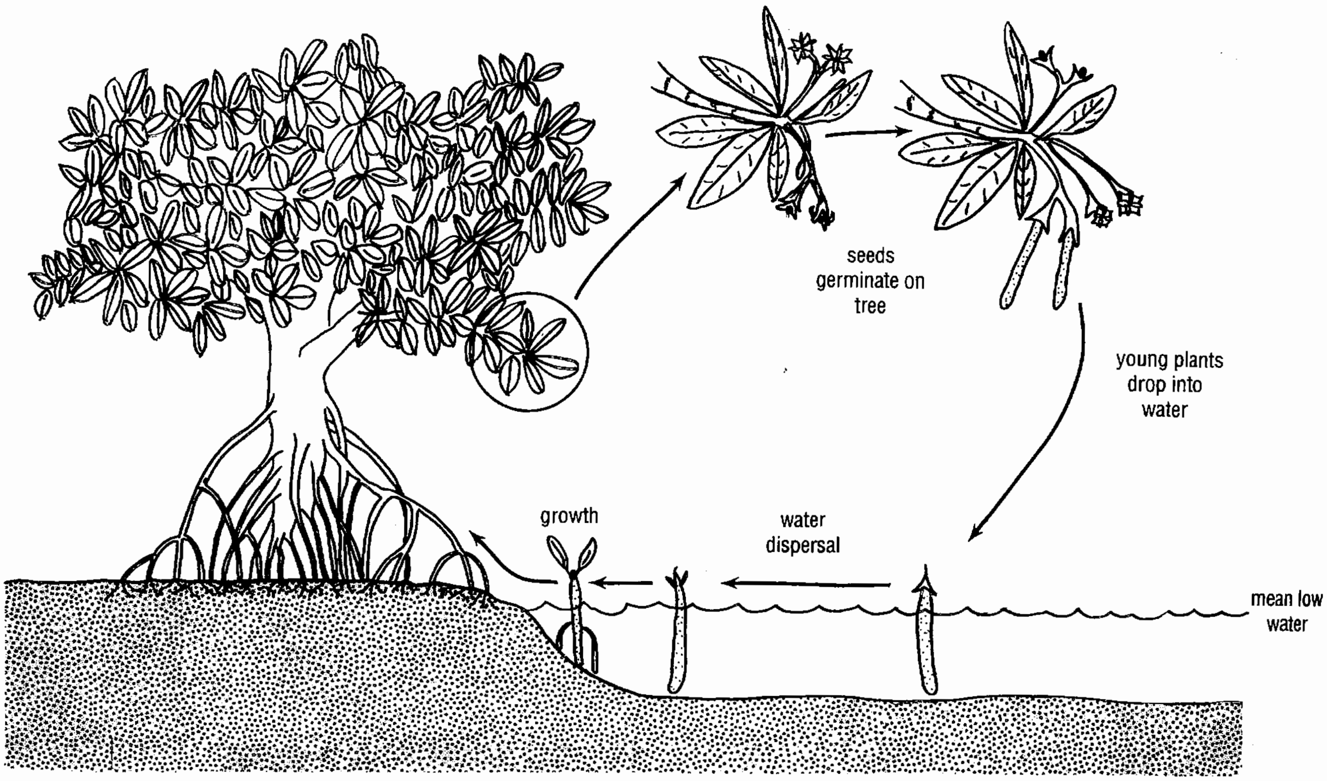
(b) They have both aerial and shallow roots that intertwine and spread widely over the muddy substrate in an impenetrable tangle (Colour Plate 38). The substrate is oxygen-poor, and the aerial roots allow the plants to obtain oxygen directly from the atmosphere. Many of the mangrove species also have special prop roots extending down from the trunk or from branches to serve as extra support.

(c) Mangroves have special physiological adaptations that prevent salt from entering their tissues, or that allow them to excrete excess salt.

(d) Many mangrove plants are **viviparous**, producing seeds that germinate on the tree. Young plants drop from the tree into the water, and the floating plants are dispersed by water. The life cycle of these long-lived plants is illustrated in Figure 8.12.

Some Indo-Pacific mangrove forests may contain 30 or more species of mangroves. There are fewer in Atlantic areas; a total of 10 species is distributed throughout the New World, and mangrove swamps in Florida, for example, support only three species.

Figure 8.12 The life cycle of viviparous mangrove trees.



8.7.2 ECOLOGICAL FEATURES OF MANGROVE SWAMPS

The physical environment of mangals is characterized by considerable fluctuation in salinity and temperature. This is also a region that is strongly influenced by tidal action. Water exchange transports nutrients into mangrove areas, and exports material out. Tidal flow also results in an inflow and outflow of animals, such as fish and shrimp, into the tidal area. Animals living high in the intertidal zone are subjected to the greatest environmental variation and to potential desiccation. Nevertheless, the plants and animals are adapted to tidally-induced fluctuation, and the largest mangrove swamps are in areas with a large vertical tidal range.

Mangroves are found in regions of little wave action, and the intertwining roots of the plants further reduce water velocities. This results in trapping of suspended sediments and organic material (particularly leaves) which settle on the bottom to form black mud. The sediments tend to be anoxic because of high bacterial activity and because of poor circulation within the fine-grained substrate.

There is a progressive change from marine to terrestrial conditions from the seaward side of a mangrove area to the landward edge. There is a corresponding zonation of different mangrove species, based at least partly on their respective salt tolerances.

Ecologically, a mangrove community can be divided into (a) the above-water forest, (b) the intertidal swamp, and (c) the submerged subtidal habitat. These distinctive zones support unique combinations of species which are described below.

The **above-tide forest** formed by the trunks and leaf canopy of the mangroves is an arboreal environment inhabited by terrestrial species. Birds, bats, lizards, tree snakes, snails, land crabs and mangrove crabs, spiders, and insects are all common residents, with insects being the most diverse and most abundant. The birds and bats are mostly insectivores or are piscivorous, feeding on small fish. The crabs are detritivores or omnivores and may feed on marine prey during low tide. In some areas, domestic animals (cattle, goats, or camels) may graze on the mangrove leaves. A study of Florida mangroves showed that about 5% of the total leaf production was consumed by non-mammalian terrestrial grazers, the rest entering the aquatic system as debris and becoming available for marine detritivores, either fish or invertebrates.

The **intertidal swamp** offers a variety of different substrates and different microhabitats to support a more diverse community of marine species. Some organisms attach to the mangrove roots, others reside in or on the mudflat or mudbanks. Barnacles and oysters are conspicuous epifauna on the roots, with the latter often the dominant contributor to community biomass. Certain species of isopods bore into the woody prop roots, and their activities may sever the roots, although the total impact to the mangrove swamp is usually limited. Periwinkles (snails) are found in abundance crawling over the roots in the upper intertidal zone. Some polychaete worms are also associated with the root system, with some tube-building species attaching to this hard surface. In this area, combined densities of snails, nematodes, and polychaetes commonly exceed 5000 m^{-2}.

The intertidal mudflat is the home of numerous burrowing fiddler crabs (*Uca*), and sea cucumbers commonly are present on the surface of the mud. Both of these groups feed on detritus. Red and green benthic algae are grazed by amphipods and some species of crabs. Pacific mangroves are frequented by large-eyed mud-skippers (genus *Periophthalmus*), fish that burrow into the mud but spend much time out of water, using modified fins to crawl on the mud flat or, in the case of one species, to climb the mangrove roots. Various species of shrimp and fish move in and out of this region with the tides.

Leaf fall is a major source of nutrients and energy in the intertidal swamp, and many of the residents are detritivores. Some remove suspended detritus by filter feeding (e.g. oysters), others feed on organic material in the sediments by deposit feeding (e.g. burrowing polychaetes), and others like crabs, shrimp, and amphipods capture larger particles of debris with their claw-like appendages. Most animals in the community probably consume detritus in addition to living plant and animal tissue.

The **subtidal** zone also has sediments of fine-grained mud with a high organic content, and sand patches may be present as well. The subtidal mangrove roots support a rich epiflora and epifauna of algae, sponges, tunicates, anemones, hydroids, and bryozoans, and their crowded numbers indicate that competition for space is intense on this substrate. In some areas, turtle grass (*Thalassia*) may be the dominant benthic plant, and it serves to stabilize the mud bottom. Burrowing animals (e.g. crabs, shrimp, worms) are common, and their burrows facilitate oxygen penetration into the mud and thus ameliorate anoxic conditions. Fish are most common in this zone, and many of them are plankton-feeders. The fish, as well as crabs, lobsters and shrimp, form the basis for local fisheries.

The primary producers in this system include not only the mangroves themselves, but benthic algae, seagrasses, and phytoplankton. Few production studies have been conducted in mangroves because they are a particularly difficult environment in which to work. However, it is clear that mangrove swamps are rich in recycled nutrients. Although large quantities of detritus may be exported from a mangrove community, the roots also trap organic-rich detritus which is broken down and decomposed in the sediments; the recycled nutrients then become available to be taken up by the roots of the mangroves. Thus the mangrove system is not solely dependent on nutrients dissolved in the surrounding oligotrophic seawater. Mangroves are also located in regions of intense solar radiation, and the combination of high nutrients plus high light should lead to high gross primary production rates. Plant respiration is variable and is possibly related to the degree of salinity stress in particular localities. However, it is estimated that mangrove swamps contribute between 350 and 500 g C m^{-2} yr^{-1} net production to coastal waters.

QUESTION 8.9 How do values of net primary productivity in mangrove swamps compare with those for phytoplankton production in tropical nutrient-deficient oceanic waters? Refer to Table 5.1.

8.7.3 IMPORTANCE AND USES OF MANGROVES

Mangroves figure importantly in the livelihoods of peoples living within or adjacent to these habitats. The trees themselves have traditionally been used for firewood and charcoal. The timber is water-resistant, so it is also used to construct boats and houses. The leaves are used for roof thatching and as fodder for cattle and goats. Even cigarette wrappers are manufactured from the young, unfolded, leaf sheaths of a certain mangrove species.

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