CHAPTER 8 BENTHIC COMMUNITIES

This chapter considers different types of benthic communities, ranging from the highest intertidal levels to the deepest trenches. Although these benthic habitats are treated separately here, they are all coupled in a dynamic fashion with the overlying pelagic environment.

In shallow water, both phytoplankton and benthic plants contribute to the primary production of benthic communities. Phytoplankton and zooplankton are consumed by shallow-living filter feeders. Conversely, exudates and detritus from attached benthic plants supply necessary nutrients for the phytoplankton and planktonic bacteria, and bottom currents may cause resuspension of sediments, making benthic microphytes and bacteria-covered sediment particles available as food sources for zooplankton. Some fish and some marine mammals rely on shallow-water benthos for food.

The great majority of benthic communities, however, are located in the aphotic zone, and most are entirely dependent on organic matter that is photosynthetically produced in the euphotic pelagic zone. The only exceptions are certain communities in which the food chain begins with chemosynthetic production by bacteria (see Section 8.9). Part of the organic matter that sinks or is transported from the surface waters is the food source that supplies deep-water benthic communities. Sinking organic and inorganic particles also form the sediments in which the benthos live. Decomposition processes tend to take place in deep water or on the seafloor, and the nutrients that are released are eventually returned to the surface where they are used by the phytoplankton.

Marine organisms may exploit both the benthic and pelagic environments during different stages of their lives. Many invertebrates are benthic as adults, but disperse by producing planktonic larvae. Conversely, some planktonic organisms produce resting stages (spores, cysts, or eggs) that sink into sediments where they remain dormant until favourable water conditions cause them to 'hatch' into swimming or drifting stages.

The concept of **benthic–pelagic coupling** recognizes the many interactions between these two vast environments, and attempts to integrate the ecologies of the seafloor and the water column.

8.1 INTERTIDAL ENVIRONMENTS

The terms littoral and intertidal are synonyms for that coastal area which is periodically exposed to air by falling tides and submerged by rising water levels. Included in this general area are a variety of distinctive ecosystems such as rocky shores, sandy beaches, and mudflats, each supporting specially adapted assemblages of species. Rocky intertidal areas support a preponderance of epifauna, whereas the soft-substrate sand and mud communities have higher proportions of infaunal species. The intertidal regions mark the transition from land to sea, and although they make up only a very small part of the total world ocean, they support rich and diverse communities of marine plants and invertebrates as well as birds and inshore species of fish. Even some land mammals (e.g. mink, skunks, and raccoons) visit this area to feed on easily accessible shellfish, and many shorebirds depend on the rich food supply to be found in these habitats.

8.1.1 TIDES

Tides are the periodic rise and fall of sea level over a given time interval, and they are caused by the interaction between the gravitational attraction of the Moon and Sun on the Earth, and the centrifugal force resulting from the rotation of the Earth and Moon. On most coasts, **semidiurnal tides** result in the intertidal zone being exposed and covered by water twice each day. However, because of certain physical conditions, there is only one tide per day (a **diurnal tide**) in some regions such as the Gulf of Mexico.

Tidal range is greatest during **spring tides** which occur twice each month when the Earth, Sun, and Moon are aligned. At the other extreme, tidal range is minimal during the **neap tides** which occur at the first and the third quarters of the Moon, when these planetary bodies are not in alignment. The high water mark is the greatest height to which the tide rises on any day, and the low water mark refers to the lowest point to which the tide drops.

The extent of the littoral zone in any particular locality is governed by the slope of the shoreline and by local tidal ranges, which are partly determined by the configuration of coastlines. Tidal range varies from barely perceptible in places such as Tahiti and the Baltic Sea, to as much as 15 m in the Bay of Fundy in eastern Canada.

8.1.2 ENVIRONMENTAL CONDITIONS AND ADAPTATIONS OF INTERTIDAL ORGANISMS

The littoral regions experience the greatest variations in environmental conditions of any marine areas. Here, organisms are periodically exposed to air, and they encounter wide fluctuations in temperature and salinity. Rainfall and land runoff both contribute to lowering salinity. In cold climates, intertidal organisms are subjected to ice formation and ice scouring. In addition, many intertidal regions are exposed to heavy wave action and current motion.

Intertidal plants and animals show a variety of special adaptations to the changing conditions of their environment. Whereas inhabitants of sand and mud tend to burrow into the soft substrates to escape desiccation, temperature and salinity extremes, and wave action, organisms living on rocky shores exhibit more diverse adaptations to these environmental features. Rocky-shore species of bivalved molluscs (e.g. clams, mussels) and barnacles close their shells tightly during emersion, enabling them to retain moisture around the gills and thus preventing desiccation as well as exposure to freshwater. Many snails also retreat into their shells, sealing the shell aperture with a horny or calcareous operculum on the foot. On the other hand, many benthic plants and some of the intertidal animals have no particular mechanisms to avoid water loss. Algae like *Fucus* and *Enteromorpha*, for example, tolerate as much as 60–90% loss of water from their tissues.

Shells, or other types of rigid exoskeletons like those of sea urchins, also protect animals from mechanical injury in areas where wave action can be severe. In some sea urchins and molluscs, the shell is much thicker in populations exposed to heavy wave action than in populations which are sheltered. Strong attachment to rock surfaces or other firm substrates prevents plants and animals from being washed away by waves and currents. Benthic algae attach to rocks by special holdfasts. Barnacles, oysters, some tubeworms, and tunicates secrete cementing substances for firm attachment. Mussels secrete tough elastic byssal threads from a special gland in the foot and these secure their positions. The broad, flattened foot of limpets, abalones and chitons provides a suction-like attachment, and their low, streamlined profiles also help to resist wave impact. Certain animals (e.g. some sea urchins and rock-boring clams) are equipped to bore into hard surfaces by mechanical abrasion, chemical secretions, or both. Many of the more mobile intertidal animals, like crabs and isopodes, seek out rock crevices where the wave action is reduced; this sheltering behaviour also permits them to remain in moist refuges at low tide. Rock pools form similar refuges for animals such as starfish, crabs, and small intertidal fish, all of which avoid desiccation by remaining in these pools at low tide.

8.2 ROCKY INTERTIDAL SHORES

Much is known about the inhabitants and ecology of rocky shores compared with other marine habitats. The accessibility of these densely-populated marine communities has permitted researchers to make long-term direct observations, and to conduct *in situ* experiments on factors determining community structure.

8.2.1 ZONATION

A striking characteristic of all rocky shores is that the resident plants and animals are grouped in distinctive bands, with some species living high in the intertidal zone and others being grouped at lower tidal levels. This vertical **zonation** of species applies to all rocky intertidal communities, although the specific pattern of zonation and the species composition of the zones varies according to geographic location, tidal range, and whether sites are exposed to severe wave action or are protected. Zonation is largely based on sessile species, like algae, barnacles and mussels, although some mobile animals also tend to be zoned but with less sharp demarcation. In general, many of the larger motile animals move with the tides and often remain in a relatively constant water depth, or retreat to rock pools at low tide.

On rocky shores, the supralittoral zone (see Chapter 7) is inhabited by encrusting black lichens (which are combinations of algae and fungi) and blue-green algae, certain species of *Littorina* (periwinkles) that graze on the vegetation, and relatively large (3–4 cm long) isopods (*Ligia*). Primitive insects (e.g. *Machilis*) may also be present.

Just below the supralittoral zone, periwinkles (*Littorina* species) are usually found in extraordinarily dense populations, with numbers ranging from several hundred to 10 000 snails per square metre. Lower in the intertidal, barnacles form a sharply demarcated belt, and these crustaceans may also have densities of thousands per m^2. In many localities, mussels crowd together in dense aggregations below the barnacle zone. There is intense competition for the limited space among the attached algae and sessile animals as shown in Colour Plate 31.

Gregariousness is an adaptive feature in many of these intertidal species. By crowding together, periwinkles create microhabitats in which more moisture is retained during exposure at low tides. They reproduce by internal fertilization, and crowding also increases their chances of finding mates. Mussels freely release gametes into the sea, where fertilization occurs; in this case, gregariousness increases synchrony of spawning among many individuals. Barnacles are hermaphrodites that cross-fertilize, and high population densities are necessary for reproduction. The penis of a barnacle can only reach about twice as far as the diameter of its exoskeleton, so it is essential that the animals be in close proximity.

Intertidal zonation of organisms is not determined simply by tidal levels, but results from a variety of physical and biological causes. The upper limit of a particular zone is often determined by physical factors and the ability of particular plants and animals to deal with exposure to air and with temperature and salinity variability. The upper limit of any one species may also be set by biological factors such as the absence of suitable food, or grazing or predation pressure. The lower limit of a particular zone is usually determined only by biological factors.

How can the causes of vertical zonation be determined?

Sessile animals, like barnacles and mussels, make ideal subjects for studies of vertical zonation because the same individuals can be monitored over long periods. Photographs taken at successive intervals record the size and position of individuals and enable researchers to follow growth, interactions with neighbouring individuals, and death. The accessibility of the intertidal zone also makes experimental manipulation possible, and individual animals may be removed from sites, or whole rocks with attached organisms may be relocated to different tidal levels. It is also possible to exclude predators by enclosing study populations within wire cages. The results of such techniques are described below.

Barnacle populations on rocky shores in Scotland are composed of two species (Figure 8.1). Adults of the small *Chthamalus montagui* form a distinct band high on the shore, above the mean high water mark of neap tides, with only a few adults being found down to the mean tide level. The larger *Balanus balanoides* has a much wider distribution for both adults and larvae, extending above and below the mean neap tide marks. Long-term observations indicated that the larvae of *Chthamalus* actually settle throughout most of the *Balanus* zone, but only survive to adulthood in the upper areas. This is because young *Chthamalus* are eliminated from areas below the mean high water neap mark by competition for restricted attachment space with the faster growing *Balanus*. *Balanus* either overgrows, undercuts, or crushes *Chthamalus*. The observation that the lower limits of *Chthamalus* zonation are dictated by biological competition was confirmed by experimental work in which all newly settled *Balanus* larvae were removed from rocks containing young *Chthamalus*; in such studies, *Chthamalus* survived well at all tidal levels. On the other hand, the upper zonation levels for both barnacle species are determined by physical factors, with *Chthamalus* being more tolerant to heat and/or desiccation than *Balanus*. Further, intraspecific competition may be an important mortality factor for *Balanus*; if larval recruitment is high, the growing barnacles begin to compete for space, and the younger or slower-growing individuals of the species are eliminated.

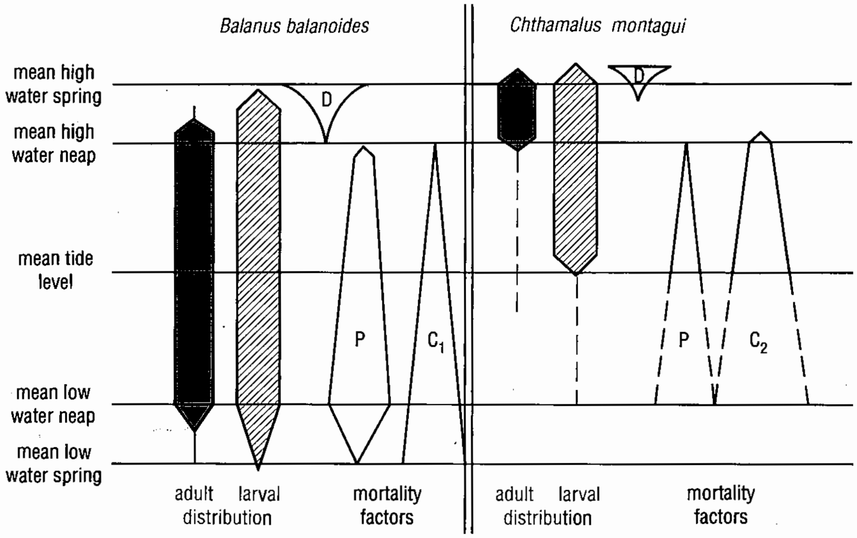

Figure 8.1 The effects of competition and predation on barnacle distribution in Scotland. C_1, intraspecific competition; C_2, interspecific competition between *Chthamalus* and *Balanus*; D, desiccation; P, predation by *Nucella*, a predatory snail. The widths of the distribution bars indicate relative abundance; the widths of the mortality bars indicate relative importance of the factors concerned. Note that the upper limits of distribution for both species are determined by physical factors (i.e. tolerance to dessication). Snail predation and intraspecific competition for space are the major causes of mortality for *Balanus*, and both factors become increasingly important at lower tidal levels. For *Chthamalus*, the major cause of mortality of newly settled larvae is intraspecific competition for space with the faster-growing *Balanus*. Few *Chthamalus* larvae settle below mean tide level, but those that do are eliminated by predation and interspecific competition.

Predation too may be an important determinant of zonation patterns. The whelk *Nucella lapillus* is a major predator of barnacles in Scotland. Like many predators, this snail prefers to eat larger prey, and thus prefers *Balanus balanoides* over *Chthamalus*. When cages were used to exclude *Nucella* from natural populations of barnacles, it became evident that snail predation was a major cause of mortality for larger (and older) *Balanus*, especially those living in the lower intertidal zone where *Nucella* was most abundant. Thus the lower limit of the *Balanus* zone is determined largely by predation.

Similar predator-prey relationships can be found on the west coast of North America between three barnacle species (*Chthamalus dalli, Balanus glandula* and *B. cariosus*) that are preyed upon by three different species of *Nucella*. In this area, most of the mortality of young *Balanus glandula* is the result of predation rather than crowding and competition for space, and *B. cariosus* attains an adult size that is too great to be eaten by *Nucella*. However, here too predation and competition for space act to set the lower limits on the barnacle distributions.

Physical and biological factors also act in concert or independently to set the zonation patterns of benthic algae. Algae compete for sunlight (see Section 7.1) and for restricted space with other plants and with animals, and these biological factors partly establish the position of plants on shores. Upper zonation limits of algal species are often set by tolerances for exposure and desiccation, and may also be determined by the grazing pressure of herbivores. As an example, the *Torrey Canyon* oil spill in 1967 killed the dominant grazing molluscs in the intertidal areas of parts of south-western England, and subsequently there was a rise in the upper zonation limits of several intertidal algae. With eventual recovery of the grazers, the higher reaches of the algae were once again grazed down and the original zonation pattern was re-established.

8.2.2 TROPHIC RELATIONS AND THE ROLE OF GRAZING AND PREDATION IN DETERMINING COMMUNITY STRUCTURE

Both benthic algae and phytoplankton are important primary producers supporting rocky intertidal communities, but production figures are relatively low. The intertidal zone is a difficult habitat for benthic algae in several respects. In tropical regions, heavy rainfall, high light intensities, and exposure to high air temperatures with resulting desiccation are major problems. Freezing and scouring by ice limit algal production in arctic and subarctic intertidal areas. In temperate climates, where benthic algae reach their full potential, there is competition between algal species for access to sunlight, and competition for attachment sites with other algae and with sessile animals. The average annual productivity of the rocky intertidal areas of the world is of the order of 100 g C m^{-2}. However, production rates of around 1000 g C m^{-2} yr^{-1} may occur in particularly favourable areas.

Attached algae are grazed by a variety of molluscs and sea urchins. Mussels, barnacles, clams, tunicates, tubeworms (polychaetes), and sponges are among the many filter feeders that are dependent on plankton. Intertidal carnivores include starfish, which eat limpets, snails, barnacles, mussels, and oysters; predatory snails, which consume a variety of prey including clams, mussels, and barnacles; and sea anemones, whose prey includes shrimp, small fish, and worms. Important scavengers include isopods and crabs. Shorebirds may also have considerable predation impacts on intertidal life (see Sections 6.5 and 8.5).

Experimental work has demonstrated that herbivores such as sea urchins, limpets, chitons, and littorine snails may control both the level of primary production and the species composition of benthic plants. For example, removal of limpets from experimental areas results in the appearance of different species of algae and in heavier algal growth compared with undisturbed sites. Removal of sea urchins from intertidal and subtidal regions also tends to create a greater initial diversity of algal species, although this may eventually change to lower diversity as other determinants of community structure come into play. The species composition of the algae in a community may also result from competition for space and light between different algal species, with the dominant species being those that are fastest growing in the particular locality.

Competition and predation are also important determinants of species composition and diversity among intertidal animals. Along the north-west Pacific coast of North America, the rocky intertidal community is dominated by mussels, barnacles, and the carnivorous starfish *Pisaster ochraceus*. *Pisaster* feeds on a variety of molluscs and barnacles, as illustrated in Figure 8.2. Experimental removal of the starfish from the community resulted in lowering species diversity from about 30 species to one dominant species, the mussel *Mytilus californianus*. When *Pisaster* is present, its feeding activities control the numbers of dominant sessile prey (barnacles and mussels) so that space is kept open and none of these species becomes dominant; at the same time, primary production is also enhanced by the provision of space for benthic algae. When the top predator is removed, competition for space is intensified and, in this region, *Mytilus californianus* overgrows and outcompetes all other macrobenthos to take over the available space throughout most of the mid-intertidal zone. *Pisaster* is referred to as a **keystone species** because its activities disproportionately affect the patterns of species occurrence, distribution and density in the communities in which

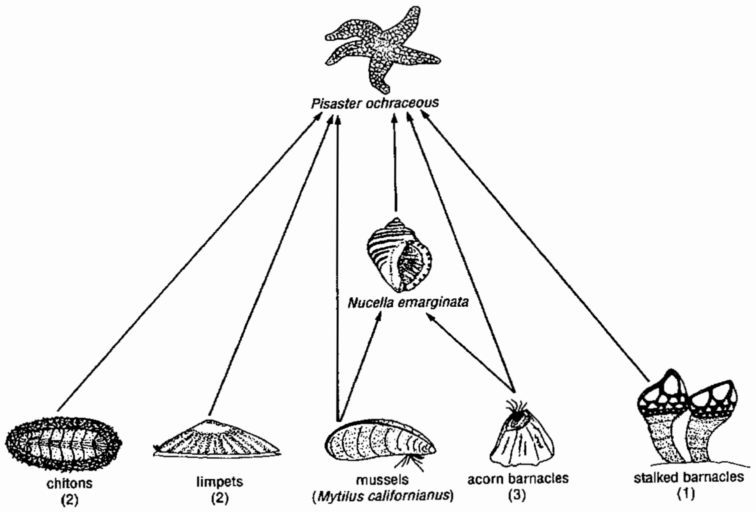

Figure 8.2 The food of the starfish *Pisaster ochraceus*, a keystone species of rocky intertidal communities along the Pacific coast of North America. Numbers in parentheses indicate the number of species in a particular group. (Animals are not to scale.)

it lives. Similar types of interactions control rocky intertidal community structure in other areas of the world. In New England, for example, the mussel *Mytilus edulis* is the competitively dominant sessile species, whose numbers are usually kept in check by two species of starfish (*Asterias forbesi* and *A. vulgaris*) and by the snail *Nucella lapillus*.

QUESTION 8.1 Would you expect to find a greater biomass per unit area benthic organisms in intertidal areas with a high tidal range (e.g. >2 m in those with a small tidal range (e.g. <0.5 m), and why?

8.3 KELP FORESTS

In cold temperate regions, intertidal rocky-shore communities merge subtidally into kelp forests. The term **kelp** refers to a variety of very large brown algae that are usually found only outside the limits of the 20°C summer isotherms. These algae form distinctive subtidal communities in areas of upwelling, fast currents, or heavy surf. Kelp require a hard substrate for attachment, and they grow off rocky shores to depths of 20–40 m, depending on water clarity. Kelp beds occur along the western coasts of North and South America, extending into subtropical latitudes in upwelling areas. In the western Pacific, extensive kelp beds are found off Japan, northern China, and Korea. In the Atlantic, large kelp beds occur off the Canadian east coast, and off the coasts of southern Greenland, Iceland, and northern Europe including the United Kingdom. The highest biomass levels of kelp are around subantarctic islands like the Falklands. New Zealand and South Africa are also localities that support kelp in quantities sufficient for exploitation.

Each kelp plant typically has a holdfast for attachment to the substrate and a flexible stipe (or stalk) (Figure 8.3). Large, thin blades (equivalent to leaves) are attached to the stipe. Kelp may also have gas-filled floats (or pneumatocysts) which keep the blades near the water surface where solar radiation is highest. Because of their large photosynthetic surface and the constant supply of nutrients in the surrounding turbulent water, kelp are highly productive plants. Common Pacific genera include *Nereocystis, Postelsia*, and *Macrocystis. Macrocystis pyrifera* is commonly known as the

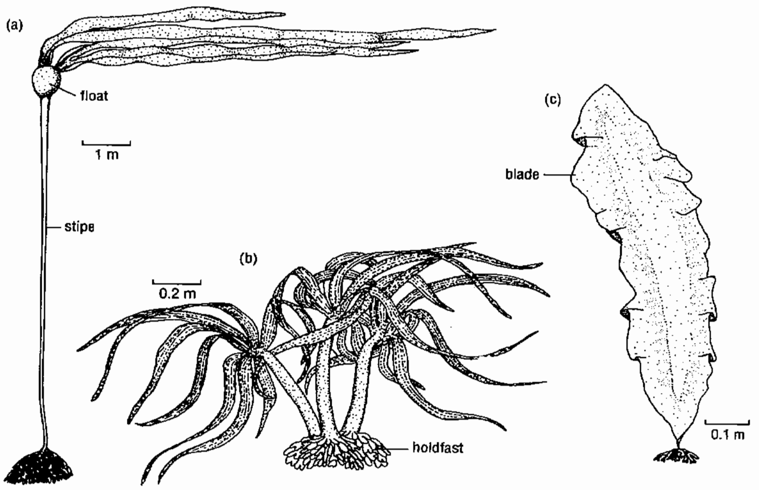

Figure 8.3 A number of kelp species illustrating diversity of structure in this group of brown algae. (a) *Nereocystis luetkeana*; (b) *Postelsia palmaeformis*; (c) *Laminaria saccharina*

giant kelp as it may exceed 50 m in length, and it forms aquatic forests off California. Various species of *Laminaria* (usually 3–5 m in length) are the dominant kelp along coastal areas of the North Atlantic, and they also occur as an understory species in the temperate Pacific.

Kelp not only are the largest of all algae, but some are considered to be among the world's fastest-growing plants. Growth rates of 6–25 cm per day are common, and *Macrocystis pyrifera* grows as much as 50–60 cm per day off California. Kelp can be either annual or perennial species, some regrowing new stipes and blades from the original holdfast either yearly, or every few years. All kelp reproduce via production of spores.

The high growth rates of kelp translate into productivities of from about 600 to more than 3000 g C m^{-2} yr^{-1} (compare with production values for rocky intertidal areas in Section 8.2.2). Off Amchitka Island in the Aleutians, annual kelp production is from 1300 to 2800 g C m^{-2}. This high production once supported populations of the giant Steller's sea cow (see Section 6.4). Off Nova Scotia, in Atlantic Canada, *Laminaria* forests produce about 1750 g C m^{-2} yr^{-1}. Kelp beds off South Africa have a production of about 600 g C m^{-2} annually. In some locations, kelp are harvested for fertilizer, iodine salts, industrial chemicals, and alginates used as food additives. The commercial harvest of the California giant kelp amounts to 10 000–20 000 tonnes dry weight per year.

Kelp communities provide spatial heterogeneity and diverse habitats and thus support a highly diverse association of animals. The large surface area of the kelp blades provides space for numerous epiflora and epifauna, including diatoms and other microflora, and colonial bryozoans and hydroids. A variety of molluscs, crustaceans, worms, and other animals live on the plants, or on the substrate between plants. In some areas, much of the primary production may be consumed by herbivores such as sea urchins. Some snails and sea slugs (e.g. *Aplysia*) also feed on kelp directly, but usually consume only very small amounts of the total production. This habitat also supports a variety of fish that feed on kelp-associated animals and that find protection from predators such as seals, sea lions, and sharks.

In many areas, however, as much as 90% of the kelp production is not consumed but enters the detritus food chain. The edges of the kelp are continually abraded by wave action, with small fragments being torn off, and there may be self-thinning with some plants losing the competition for available light, space, and nutrients. Annual kelp species (e.g. *Nereocystis* spp.) may attain a summertime biomass of more than 100 tonnes per hectare, all of which may be destroyed in the first winter storm. This material enters the detrital pool of the kelp bed or is exported to other areas. Kelp that is uprooted in storms may wash up in large quantities on beaches, where it is eaten by amphipods or isopods. Kelp also release considerable quantities of organic matter into solution, and this exudate is utilized by bacteria and thereby converted into particulate biomass (see Section 5.2.1).

The sea otter (*Enhydra lutris*) (Colour Plate 32) is considered to be a keystone species in North Pacific kelp forests. Otters eat a wide variety of prey including crabs, sea urchins, abalone and other molluscs, and slow-moving fish, and a single otter may eat 9 kg of food per day. Off Amchitka Island, otters at a density of 20–30 km^{-2} annually consume about 35 000 kg km^{-2} of prey. Otter predation on sea urchins regulates the ecological balance between kelp production and the destruction of the kelp by the herbivorous urchins.

Sea urchins (*Stronglyocentrotus* spp.) graze directly on living kelps, and they are capable of eating through the holdfasts that anchor the algae to the seafloor. The detached kelp is then swept away from the area in ocean currents. Otters, by direct predation, maintain relatively low densities of sea urchins and thus protect the kelp from overgrazing. The importance of otters in maintaining healthy kelp forests was revealed from ecological comparisons of different islands in the Aleutian chain. Certain islands off the Alaskan coast were found to have lush kelp communities with thriving populations of otters, seals, and bald eagles; other nearby islands had no kelp or otters, and few seals or bald eagles. The depauperate islands were the focus of extensive hunting expeditions during the eighteenth and nineteenth centuries, and historical records document the elimination of otters from many kelp beds during this time. Only those islands which had been repopulated with the few surviving otters had flourishing kelp forests. Since 1911, sea otters have been protected by law, and populations have recovered in some areas of Alaska and British Columbia. They have also been deliberately reintroduced into other depopulated regions, including along the California coast. Where otter populations have recovered, sea urchin numbers have decreased, and kelp production has increased. Despite protection, otters remain a vulnerable species. They are disliked by fishermen, who often perceive them as competitors for fish or shellfish (especially the valuable abalone). Otters are also particularly vulnerable to oil spills, as the *Exxon Valdez* experience of 1989 demonstrated when at least 5000 otters were killed by exposure to crude oil spilled off the Alaskan coast.

Wherever sea urchins occur in very high densities in kelp beds, they are capable of eliminating the kelp as illustrated in Figure 8.4. Prior to 1968 there were luxurious beds of *Laminaria* along rocky shores of the Nova Scotian coast (eastern Canada). The kelp beds extended to a depth of about 20 m, and they supported sea urchin populations of about 37 individuals m^{-2}. From 1968 onward, the urchins (*Stronglyocentrotus droebachiensis*) became more and more abundant, and barren areas developed where the kelps were eliminated. By 1980, urchin-dominated barren grounds extended along more than 400 km of coastline. The rocky substrate became encrusted with coralline red algae, which are not controlled by urchin grazing. In the early 1980s, the urchin population was decimated by epidemic disease and

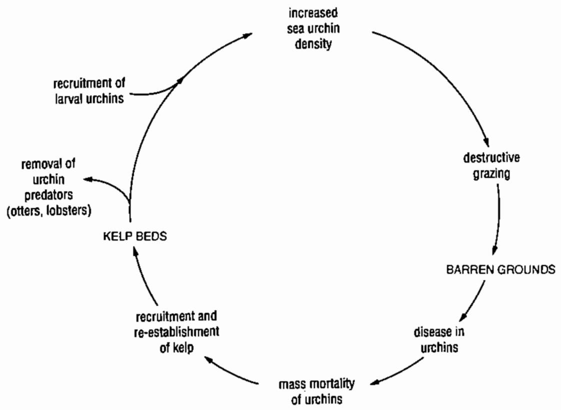

Figure 8.4 The biological events that alternate between productive kelp beds and barren grounds that are dominated by sea urchins.

kelp began to reappear along most of the coast. Within three years of the mass mortalities of urchins, luxuriant kelp beds had been re-established in some areas.

Anecdotal evidence from fishermen suggests that mass mortalities of sea urchins, and reciprocal fluctuations in kelp and urchin abundance, have occurred off the Nova Scotian coast since at least the turn of the century. The population explosions of sea urchins may be related to very high recruitment success of larvae in certain years, and this may be related to changes in local seawater temperature. As well, higher than average water temperatures have been linked with outbreaks of disease in urchins. These facts suggest that fluctuations in kelp and urchins may be natural events triggered by environmental change, and that they may have been occurring over a very long time. In any case, it is clear that urchin grazing and disease regulate the ecological dynamics of these subtidal *Laminaria* communities.

8.4 SAND BEACHES

The intertidal zones of sandy beaches appear barren when compared with rocky shores. In particular, beaches exposed to severe wave action often seem entirely devoid of life. This is because the nature of the substrate sets living conditions which are best met by infaunal organisms that usually remain hidden from direct observation. This makes sand beaches more difficult to study than areas where the activities of the resident organisms can be directly observed. Compounding the problem is the fact that many of the organisms in this environment are of very small size, making their separation from the sediment tedious, and their taxonomic identification difficult.

8.4.1 ENVIRONMENTAL CHARACTERISTICS

Beach sand grains are usually formed of irregularly-shaped quartz particles mixed with a high proportion of shell fragments, and with detritus derived from both marine and terrestrial sources. The particle size of sand varies from <0.1 mm to >2 mm and is determined largely by the degree of wave action; protected beaches have finer sand particles than exposed areas, where waves resuspend and transport small-sized grains. There is a gradient in particle size between sand and mud, with mud being composed of finer particles and mudflats being formed in areas of little water movement (see Section 8.5). Some substrates are difficult to characterize, giving rise to terms like muddy sand, or sandy mud. As particle size increases, sand grades into gravel or shingle. These large-particle substrates do not retain water because of their high porosity, and the shifting and abrasion of the large particles also contribute to an absence or low diversity of life on gravel and shingle shores.

Sandy beaches typically have a gradual slope, and this means that the sediment drains and dries out relatively slowly. Although oxygen is plentiful in the overlying water, oxygen content in the substratum diminishes with depth because of the respiration of micro-organisms and the oxidation of chemicals within the sand. Anaerobic conditions are marked by a black sulphide layer beginning at a depth of from a few millimetres to nearly a metre, depending on the organic content of the sand. Chemosynthetic bacteria are present in the sulphide layer (refer to Section 5.5).

Animals require special adaptations to live in an environment where the substrate is physically unstable in the sense that the sand grains are continually moved by turbulent water. The continual shifting of the surface layers of exposed beaches excludes large sessile species and most large epifauna in general. As well, sand beaches contain relatively low concentrations of organic matter. On the other hand, sand buffers against large temperature and salinity fluctuations, and organisms burrowing into sand are kept moist at low tide. Sand also acts as a protective cover from intense solar radiation. Although there are differences in the physical environment and in the distribution of species from high to low tidal marks, the zonation patterns are not as clearly obvious as on rocky shores. Zonation on sandy beaches is also dynamic and variable; as the tide rises, many populations change their positions on the shore, or enter the water column.

8.4.2 SPECIES COMPOSITION

Primary producers

There are no large attached plants below the high tide mark on sand beaches. The dominant benthic primary producers are diatoms, dinoflagellates, and blue-green algae. These are restricted to the near-surface layers of the sediment because light does not penetrate very deep in sand. The primary productivity of these benthic plants is very low (<15 g C m^{-2} yr^{-1}), and the system depends primarily on energy derived from primary productivity in the surrounding water and on organic detritus.

Macrofauna

There is a low diversity of macrofauna compared with rocky shores or mud communities. Burrowing polychaetes and bivalves plus crustaceans are usually the dominant members in terms of biomass. In temperate latitudes, the supralittoral zone is occupied by air-breathing amphipods (beach hoppers or beach fleas) and, sometimes, also by isopods. Amphipods and isopods burrow into the sand during the day, and feed at night on detritus like decaying seaweed that has washed ashore. On tropical sand beaches, the highest reaches are occupied by ghost crabs (*Ocypode*) which are also scavengers.

The mid- and lower tidal zones support a higher diversity of macrofauna. Small, fast-burrowing wedge-shaped clams (*Donax, Tellina*) are often present in vast numbers, some migrating up and down the beach with tidal changes.

Larger razor clams (e.g. *Ensis, Siliqua*) are also confined to sandy shores, and they too are rapid diggers. These mobile bivalves tend to have smooth, thin shells with slender profiles that ease passage through sand. Stouter thicker-shelled bivalves like cockles (e.g. *Cardium*) or *Macoma* also inhabit sand, but they tend to anchor themselves more firmly in the sediment and move less. The bivalves may be either suspension feeders or deposit feeders, with some species capable of taking advantage of both food sources. In general, deposit feeders tend to dominate in fine-particle sands, presumably because the concentration of organic material is higher than in coarser sands. The sand environment is also home to certain snails that plough through the sand; these include the olive shells (e.g. *Olivella*), and the larger moon snails (*Natica, Polinices*), all with smooth, undecorated shells. The majority of olive shells prey on small molluscs. Moon snails are also predators, especially of bivalves, and they gain access to their prey by drilling a hole through the shell. Where they are abundant, moon snails can have important effects on community structure; when *Polinices* is experimentally removed, the numbers of clams and other infaunal prey increase.

Few animals form permanent burrows because wave action and the relatively large particle size of sand cause their collapse. However, exceptions can be found in those polychaete species that line their burrows with mucus or membranous materials. Many of the sand-dwelling polychaetes are deposit feeders, a few are suspension feeders on plankton or resuspended organic material, and some (e.g. *Nephthys, Glycera*) are predators or scavengers that move through the sand actively seeking food.

Characteristic crustacean inhabitants of mid-tidal levels include mole crabs of the genus *Emerita*. They typically lie with their entire body buried and only their antennae projecting above the surface of the sand to capture small suspended food particles from receding waves. Despite being swift burrowers, they are commonly preyed upon by shore birds. Prawns and mysids are other sandy-shore crustaceans; they burrow temporarily but emerge to feed. Predators of this community can include larger epifaunal crabs.

Various types of echinoderms may be present at lower tidal levels, including burrowing sea cucumbers, heart urchins, and sand dollars, most of which are deposit feeders. The shortened spines of the sand dollars facilitate burrowing, and the young of some species ingest and selectively accumulate the heaviest sand particles containing iron oxide in their digestive tract. These increase the density of the small sand dollars and act as a weight belt, keeping them in the sediments when wave action is intense. Starfish are not common inhabitants in temperate communities, but some tropical species (e.g. *Oreaster*) are present in low intertidal or subtidal depths where they feed on organic matter contained in the sand.

Vertebrate members of sand beach communities include fish that are permanent residents, like sand eels that burrow into the sand at low tide, and temporary inhabitants (e.g. flatfish) that move into the area only at high tide to feed on smaller animals. Shorebirds are also important predators of the community, and mammals (e.g. rats, otters) may visit this area to obtain food.

Meiofauna

The meiofauna of sand beaches includes some of the most diverse and highly adapted species in this environment. The term **interstitial fauna** is also applied to those animals that live in the interstices, or spaces, between the sand grains. They either attach to sediment particles, or move through the interstitial spaces without dislodging the grains. Many animal phyla are represented in this category, and some groups (e.g. gastrotrichs, see Figure 8.5c,d) are wholly or largely restricted to this particular environment. Biomass of the meiofauna usually ranges between 1 and 2 g m^{-2}, with the average number of individuals being 10^6 m^{-2} (from the sand surface down to the anoxic layer).

Figure 8.5 illustrates some of the characteristic meiofauna of sand. Many of their adaptations are morphological and can be seen in the figure; these include small size (only a few mm in largest dimension even among groups that are usually large, such as echinoderms and molluscs), elongate or wormlike shapes, and flattened bodies. As well, many have a strengthened body wall as protection against crushing in a physically unstable substrate. This may involve the development of spines or scales (e.g. in gastrotrichs), a well-developed cuticle or exoskeleton (as in nematodes or crustaceans), or an internal skeleton of calcareous spicules (some ciliates and sea slugs). Alternatively, soft-bodied animals like ciliates, flatworms, and hydroids have developed the ability to contract strongly to protect against mechanical damage. Many of the interstitial species have special adhesive organs for maintaining a hold on the sediment particles; these may be epidermal glands, hooks, or claws (note Figure 8.5e in particular).

The majority of the sand meiofauna are mobile, but some foraminiferans and hydroids (Figure 8.5h) remain firmly attached to sand particles. All feeding types are present, from animals like ostracods and harpacticoid copepods that graze on benthic diatoms and dinoflagellates, to detritus feeders (gastrotrichs, nematodes), to predators such as hydroids and flatworms. Suspension feeders are the rarest type, and these are sedentary animals like bryozoans and

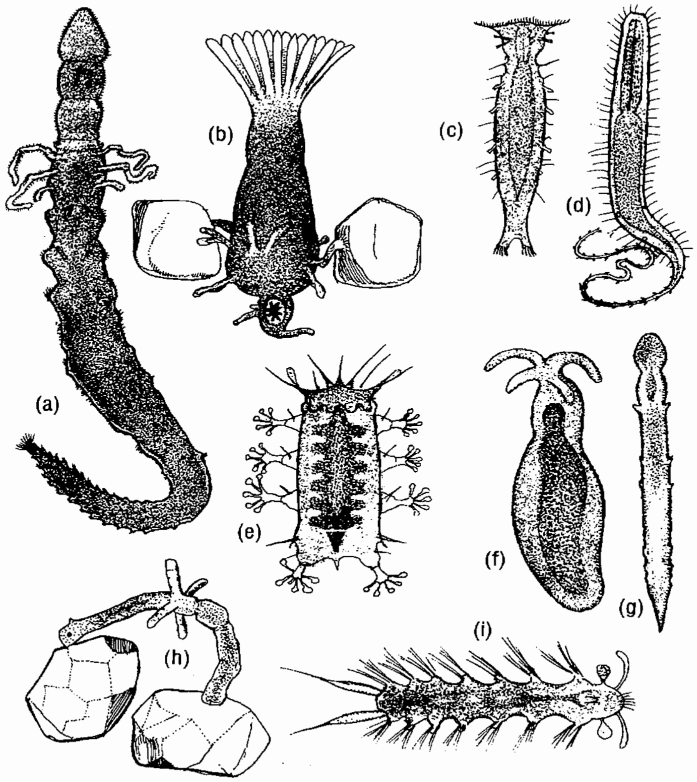

Figure 8.5 Representative meiofauna from sand, all between 0.1 and 1.5 mm in length. (a) *Psammodrilus* (a polychaete); (b) *Monobryozoon* (a bryozoan attached to sand grains); (c) *Dactylopedalia* (a gastrotrich); (d) *Urodasys* (a gastrotrich); (e) *Batillipes* (a tardigrade); (f) *Unela* (a gastropod mollusc); (g) *Pseudovermis* (a gastropod mollusc); (h) *Psammohydra* (a hydroid attached to sand particles); and (i) *Nerillidium* (a polychaete)

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