CHAPTER 15

Ocean Ecosystems

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CRITICAL CONCEPTS USED IN THIS CHAPTER

CC9 The Global Greenhouse Effect
CC14 Phototrophy, Light, and Nutrients
CC16 Maximum Sustainable Yield
CC17 Species Diversity and Biodiversity
CC18 Toxicity

FIGURE 15-1. Coral reef ecosystems have a species diversity that rivals, and perhaps exceeds, the species diversity of tropical rain forests. In this photograph of Deacon's Reef in Papua New Guinea, several species of fishes are easily seen. However, the majority of species that live on this reef live in or on the reef itself, or live hidden in the seafloor substrate. The beautiful red and white coral "tree" is a colony of the soft coral Dendronephthya sp. Less obvious are many species of hard corals, crinoids, sponges, tunicates, hydroids, and algae. Even this profusion of species is only a tiny fraction of the species that live on this reef. Hidden from view in or among the corals and other large animals, there are literally thousands or tens of thousands of species of algae, shrimp, crabs, sea stars, brittle stars, urchins, fishes, barnacles, worms, snails and other mollusks, and other less familiar types of animals and countless microbial species.

The term **ecosystem** encompasses both living organisms and the physical **environment** of a particular volume of space. Within the ecosystem, the components and characteristics of the living and nonliving environment are interdependent, each influencing the other. Hence, conceptually the global environment can be broken down into separate ecosystems within which the **species** that are present, the physical environment, and the relationships among the species and with their environment are distinct and different from those in adjacent areas. For example, we can define each geographically distinct **coral reef** as a separate ecosystem. However, all coral reef ecosystems have common characteristics in terms of the types of organisms they sustain, their physical environment, and processes driven by biological–physical interactions. These common characteristics are different from those of other ecosystems, such as **mangrove** swamps, the **rocky intertidal zone**, and the open-ocean **photic zone**.

This chapter briefly reviews several ocean ecosystems, emphasizing the relationship between their individual physical environmental conditions and their biological **communities**. However, the classification of separate ecosystems in the oceans is not precise. In reality, all such ecosystems are linked and interdependent.

COMMUNITIES AND NICHES

The world ocean can be considered a single ecosystem, but it is too large and complex to be studied as a whole. Consequently, marine ecologists often separate the oceans into ecosystems that have common biological and physical characteristics. Because even the simplest of these is complex, marine **ecologists** study the relationships of species with each other and their environment at a number of different levels, ranging from ocean-sized ecosystems to individual species. These levels are generally not well defined or distinct from each other.

Within an ecosystem, species are distributed in a nonuniform way because of small-scale variations in the physical environment and competition and other interactions among species. Species are often clustered in their communities. The term community is inexact and can refer either to all organisms that coexist in a specific location or to groups of species that are found together in many different locations. Thus, a community can be all the species within an entire coral reef, or a specific species of **sea fan** and all species that commonly live in or on it wherever this sea fan is present.

The distribution of species and their relationships with each other and the physical environment can be studied at the species level. In such studies, a very useful concept is the biological **niche**. Each species has evolved to take advantage of certain characteristics of the physical environment. Hence, each species has a range of environmental variables within which it can survive. These variables include **salinity**, temperature, **suspended sediment** concentration, substrate **grain size**, light intensity, and **nutrient** and other chemical concentrations. The combination of the ranges of each of these environmental variables within which the species can survive is the species' survival niche. Figure 15-2a shows how such a niche can be defined by two environmental parameters. In practice, niches are defined by many more parameters and cannot be fully represented in a two-dimensional diagram.

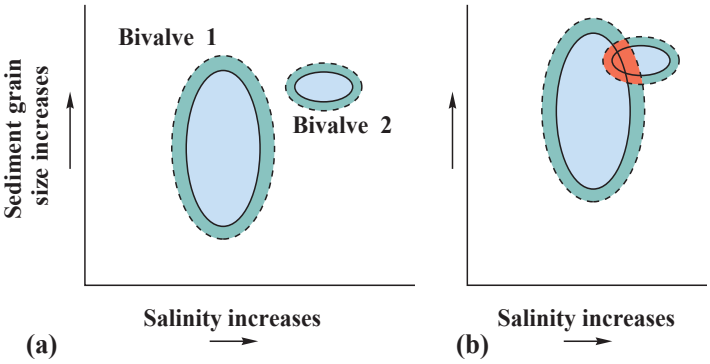


FIGURE 15-2. Ecological niches can be defined in several ways and by many parameters. These diagrams illustrate the concepts using just two such parameters: salinity and sediment grain size. (a) The fundamental niches of two bivalves are defined by the range of values of the two parameters defined by the blue areas. The survival niches are defined by a wider range of environmental conditions and include both the blue and green areas within each dotted line. Because the niches of these two species do not overlap, they would not occur in the same environment. (b) If the niches of the two species overlap, as they do in the red area, they may both occur in environments within this range of the two parameters, but they may also compete so that one species may be excluded from this part of its niche.

Within the survival niche of a particular species is a somewhat smaller range of environmental variables within which the species can both survive and successfully reproduce (Fig. 15-2a). This range is often referred to as the organism's **fundamental niche**. Species rarely, if ever, occupy every area within the marine environment where environmental parameters are within their fundamental niche. Two factors restrict the distribution of a species within its fundamental niche. First, each species has a smaller niche within its fundamental niche in which it finds optimal conditions. Second, species with overlapping niches may compete, and one species may be excluded from parts of its fundamental niche (Fig. 15-2b).

The interaction of species with each other and with the environment is wonderfully complex and may never be fully understood for all species in the oceans. Thus, descriptions of ecosystems in the discussion that follows represent only a cursory view of the factors that contribute to the amazing profusion and **diversity** of species in the oceans.

CORAL REEFS

Although some types of corals are present in all parts of the oceans, including Arctic seas, species of **corals** that build coral reefs, called **hermatypic corals**, grow only in areas where the water temperature never falls below about 18°C. Coral reefs are thus restricted to a broad band of mostly tropical waters between about 30°N and 30°S (Fig. 15-3). The range of coral reef occurrence extends into somewhat higher **latitudes** on the western side of each ocean because warm **western boundary currents** flow poleward.

Environmental Requirements for Coral Reef Formation

Reef-building corals require an appropriate substrate on which to attach, and they have a **symbiotic** relationship with **zooxanthellae**, a nonmotile form of dinoflagellate that lives within the coral's tissues. Because zooxanthellae need light to **photosynthesize** (CC14), living coral reefs are present only in waters where the seafloor is within the photic zone. In clear waters, corals can grow to depths of about 150 m, but in high-turbidity waters coral growth is reduced or prevented by two mechanisms: First, the higher **turbidity** reduces light penetration and limits the depth at which zooxanthellae can photosynthesize and, therefore, also limits the depth at which corals can grow. Second, large quantities of suspended sediment that cause high turbidity may smother the corals. Corals can clear away a certain amount of deposited sediment material, but they must use energy to do so, and they lose additional energy because they must also stop feeding in order to do so. When these energy costs are too high, the corals cannot survive. Therefore, coral reefs do not grow in coastal areas near river mouths or near other sources of large amounts of suspended matter, such as dredging projects. Corals also grow poorly in water of low or variable salinity.

The physical conditions necessary for coral growth (clear, warm, shallow waters with relatively invariable normal ocean salinity) are present primarily between about 23.5°N and 23.5°S. This is a region that we might expect to be a biological desert because surface waters are isolated by a steep permanent **thermocline** throughout most of the tropical oceans. In contrast, instead

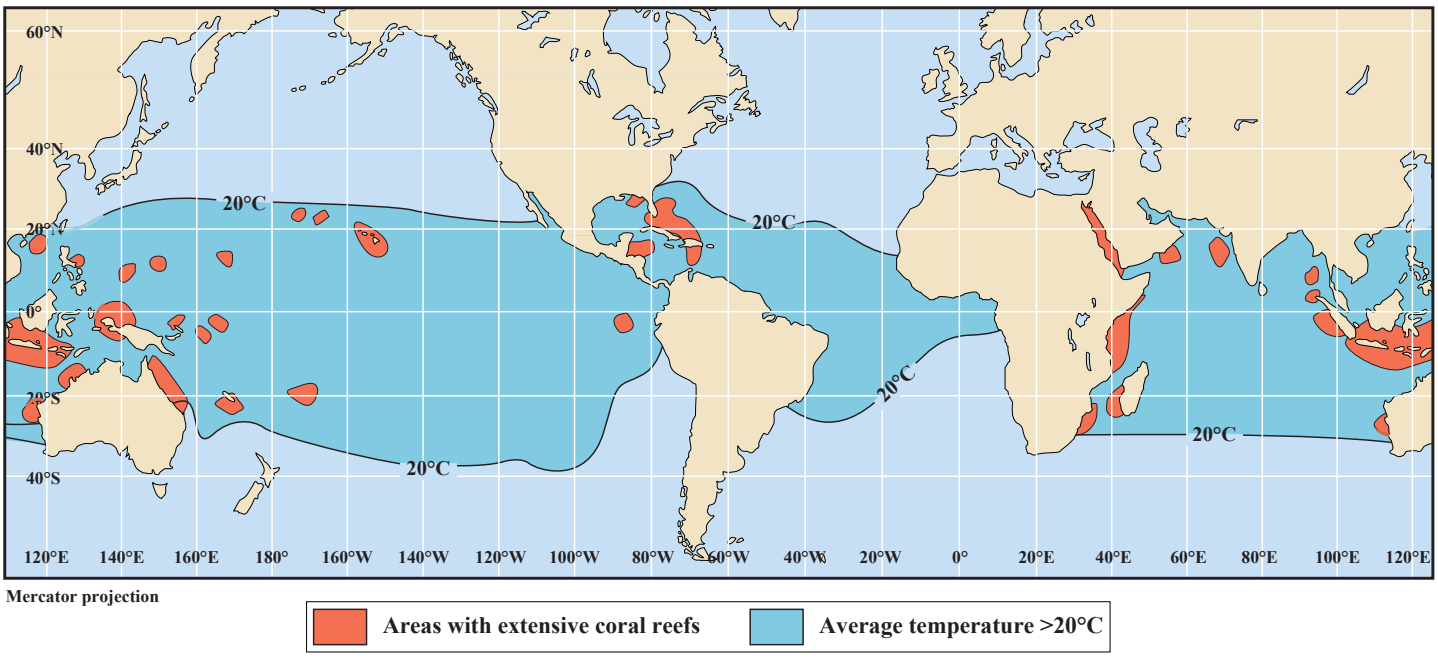


FIGURE 15-3. The area of the oceans with average sea surface temperatures above 20°C extends to about 30° north and south of the equator in the Pacific and Indian oceans, and somewhat less in the Atlantic Ocean. The temperature never falls below 18°C in most of this area. Hermatypic corals grow only in these areas and only where other environmental conditions are suitable within these areas. Although many small tropical islands have extensive coral reefs, they are too small to show in this figure.

of biological deserts, coral reefs are areas of high productivity with an amazing diversity (CC17) of fish and **invertebrate** species. In what may seem to be a paradox, waters surrounding reefs are clear blue and have extremely small populations of **phytoplankton**. The waters over the reef itself have somewhat higher phytoplankton populations and **primary productivity**, but these populations are extremely small in comparison with those in **upwelling**-zone ecosystems and cannot account for the high productivity of coral reefs.

Factors Affecting Coral Reef Productivity

The reasons for the anomalously high productivity of coral reefs are somewhat complex and not fully understood, but they appear to be related to a combination of physical conditions and the unique relationships among the reef organisms.

First, hermatypic corals and their associated zooxanthellae act together in a mutualistic (mutually beneficial) relationship to create a very effective mechanism for collecting, concentrating, and rapidly recycling nutrients. Zooxanthellae live embedded in the coral's tissues and use solar energy that penetrates the coral's transparent tissues to produce food by chemically recombining the coral's waste products. Carbon dioxide and nutrients, which are released by the coral through its digestive processes, are transferred directly to zooxanthellae and converted by photosynthesis into organic matter. In turn, as much as 60% of the organic matter created by the zooxanthellae through photosynthesis is released through the zooxanthellae cell wall directly into the coral tissue, providing food for the coral. In this way, nutrients are continually recycled, and food is continually produced by the **algae** and consumed by the coral. The coral–zooxanthellae association ensures very little loss of either nutrients or food to the surrounding water. Corals feed on **zooplankton** to supplement the food supplied by their internal zooxanthellae. Thus, the small amounts of nutrients that are lost from the coral–zooxanthellae partnership are continuously replaced. This efficient nutrient retention and recycling mechanism is believed to be the main reason for the high productivity of coral reefs.

The second reason for their high productivity is that most reefs are built on the sides of submarine mountains or on the fringes of landmasses with very narrow **continental shelves**. Indeed, the growth of corals off coasts where sea level has risen during the past several thousand years has created very steep drop-offs at the outer edges of many reefs (Figs. 4-28, 15-4). Ocean **currents** that flow past such steep continental shelves and islands form **eddies**. The eddies create vertical water movements that can bring nutrient-rich deep water, at least episodically, into the photic zone of the reef.

The third reason for the high productivity of coral reefs is that many reef ecosystems are partially closed systems, within which most nutrients not retained in the coral–zooxanthellae association are continually recycled. Most of the reef floor is shallow and within the photic zone. Hence, organic **detritus** created on the reef settles largely on the reef floor, where it is consumed by **decomposers** that release nutrients to be recycled. In addition, most fishes are permanent residents of the reef. Nutrients in their urine and feces are released almost entirely back to waters of the reef, where they are rapidly recycled and taken up again by zooxanthellae or phytoplankton.

Primary Producers in the Coral Reef Community

Although zooxanthellae are important primary producers in coral reef ecosystems, they account for only a small proportion (generally less than 5%) of the **biomass** of photosynthesizers in these ecosystems. Reef ecosystems are dominated by **benthic** or **encrusting microalgae** and a variety of attached macroalgae (Fig. 15-4). The biomass of these algae generally exceeds the animal biomass in the reef ecosystem by as much as three times. In fact, the **hard parts** of **calcareous** algae are responsible for building much of the reef structure.

Algae attached to the solid substrate of the reef are favored over phytoplankton in coral ecosystems because nutrients are recycled, made available, and rapidly reassimilated at these sur-

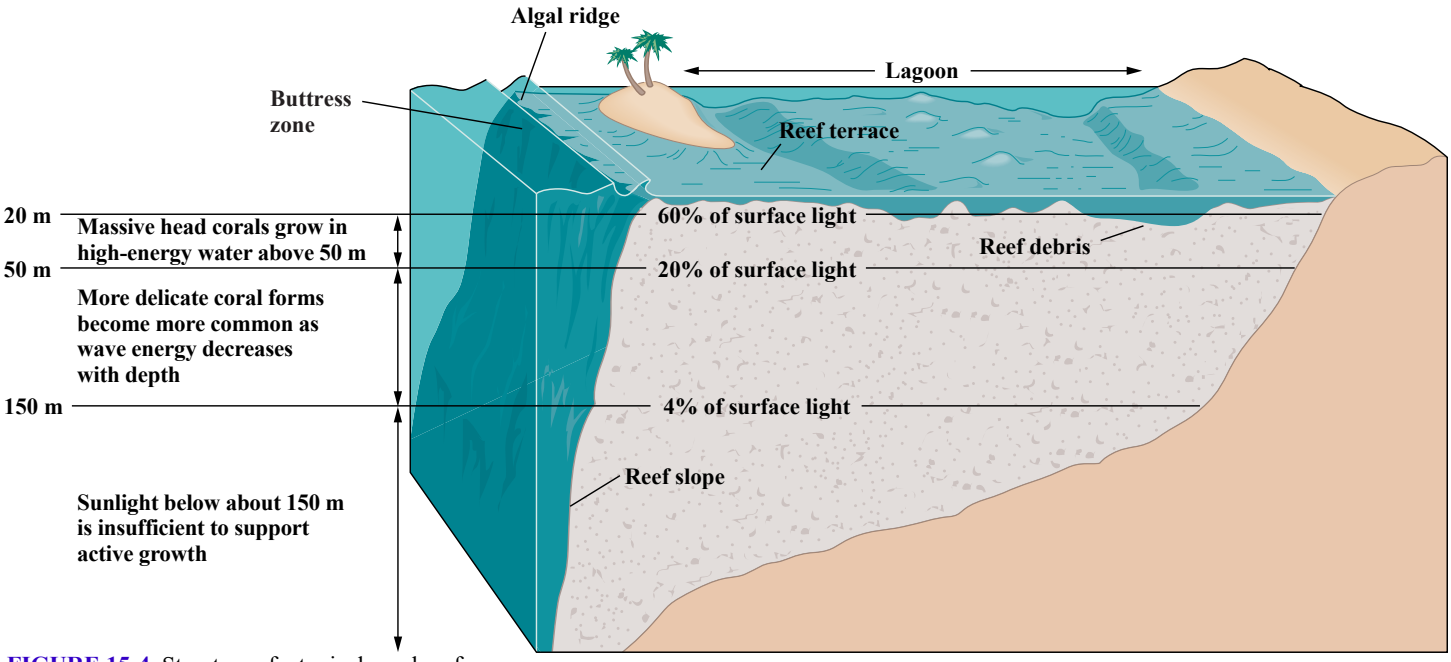


FIGURE 15-4. Structure of a typical coral reef

faces. Attached algae remove most of the recycled nutrients before they can **diffuse** into the water column and become available to phytoplankton. In addition, attached algae remain in the reef ecosystem, where nutrients are available, whereas phytoplankton may be transported away from the reef into nutrient-depleted adjacent deep water.

Coral Reef Niches and Topography

Coral reef ecosystems contain a bewildering variety of species. These species are distributed in niches that are defined by current and wave action, and by variations in salinity, water depth, turbidity, temperature, and other factors.

Figure 15-4 shows the general **topographic** features of a typical coral reef. In shallow waters of the **lagoon**, currents are generally weak and there is little wave action. Hence, sediments tend to accumulate in the lagoon and are removed primarily during major storms. Lagoon **sediments** sustain a wide variety of invertebrates that feed on suspended or deposited detritus. These detritus feeders include **suspension feeders** such as sea pens (Fig. 14-6a), and a variety of bivalve **mollusks** that live in the sediment and extend their feeding apparatus into the water column. Also present are many species of **deposit feeders**, including mollusks and worms that live in and sift through the sediment, **sea cucumbers** (Fig. 15-5a), urchins (Fig. 15-5c), sand dollars (Fig 15-5d), and other species that feed on benthic algae growing on the sediment surface, and predators such as goatfishes (Fig. 14-13d) and **sea stars** (Fig. 15-5b) that hunt mollusks and other animals living in or on the sediment.

In the lagoon, the growth of most corals is inhibited by the blanket of sediment that covers the seafloor. However, certain corals, such as *Acropora* (Fig. 15-5e,f), that grow up into the water column can prosper if **sedimentation rates** are sufficiently low and sediments are rarely **resuspended** by waves. Once established, these corals provide a sediment-free substrate for other species. Consequently, in quiet lagoons with little suspended sediment input and where salinity is not altered by freshwater input, irregularly shaped mounds of coral and associated species develop. These are called "patch reefs."

At the lagoon's outer edge is a **reef flat**, or **reef terrace**, that is relatively free of sediments because they are swept off the terrace by waves. It is an ideal location for coral growth. Coral grows upward until the reef terrace is only a few centimeters below the **low-tide line**. Further growth is inhibited because corals cannot survive for long periods out of water, although the surface of the reef terrace may be completely exposed to the atmosphere for short periods during low **spring tides** without killing the corals. Reef terrace corals are generally encrusting corals because the water is too shallow and the wave energy too high for corals that grow in other forms (e.g., Figs. 14-8a,b, 15-6e,f). The surface of the reef terrace is not smooth. It has many grooves and holes created primarily by invertebrates that eat or drill into the coral to obtain food or to create safe areas to shelter from larger predators.

On some reefs, a low island is formed by sediment accumulated during storms at the landward side of the reef terrace (Fig. 15-6). This island may be well enough established to support palm trees. The seaward edge of the reef usually has an irregular ridge, parts of which are shallow enough to emerge from the water, especially at low **tide**. The ridge is formed by intense wave action that periodically smashes against the reef's outer edge and dislodges large chunks of the **limestone** substrate of the reef. The chunks are cemented back onto the reef by the calcareous algae that live in abundance in this region. Calcareous algae are abundant because wave energy is too intense for corals to grow effectively. The algae cement themselves to the reef surface with their calcium carbonate hard parts. The cemented algae can withstand intense wave action and can quickly colonize any new surface created by storm wave damage. These algae benefit from a continuous supply of very low concentrations of nutrients brought to the reef edge by currents and waves. Because calcareous algae are abundant and help to maintain this ridge, it is called the **algal ridge**.

On the few reefs where wave energy is very low, no algal ridge or reef terrace is present. The outer reef may consist primarily of relatively robust branching corals, such as elkhorn coral (Fig. 15-5f), or the reef terrace may simply end at the reef edge.

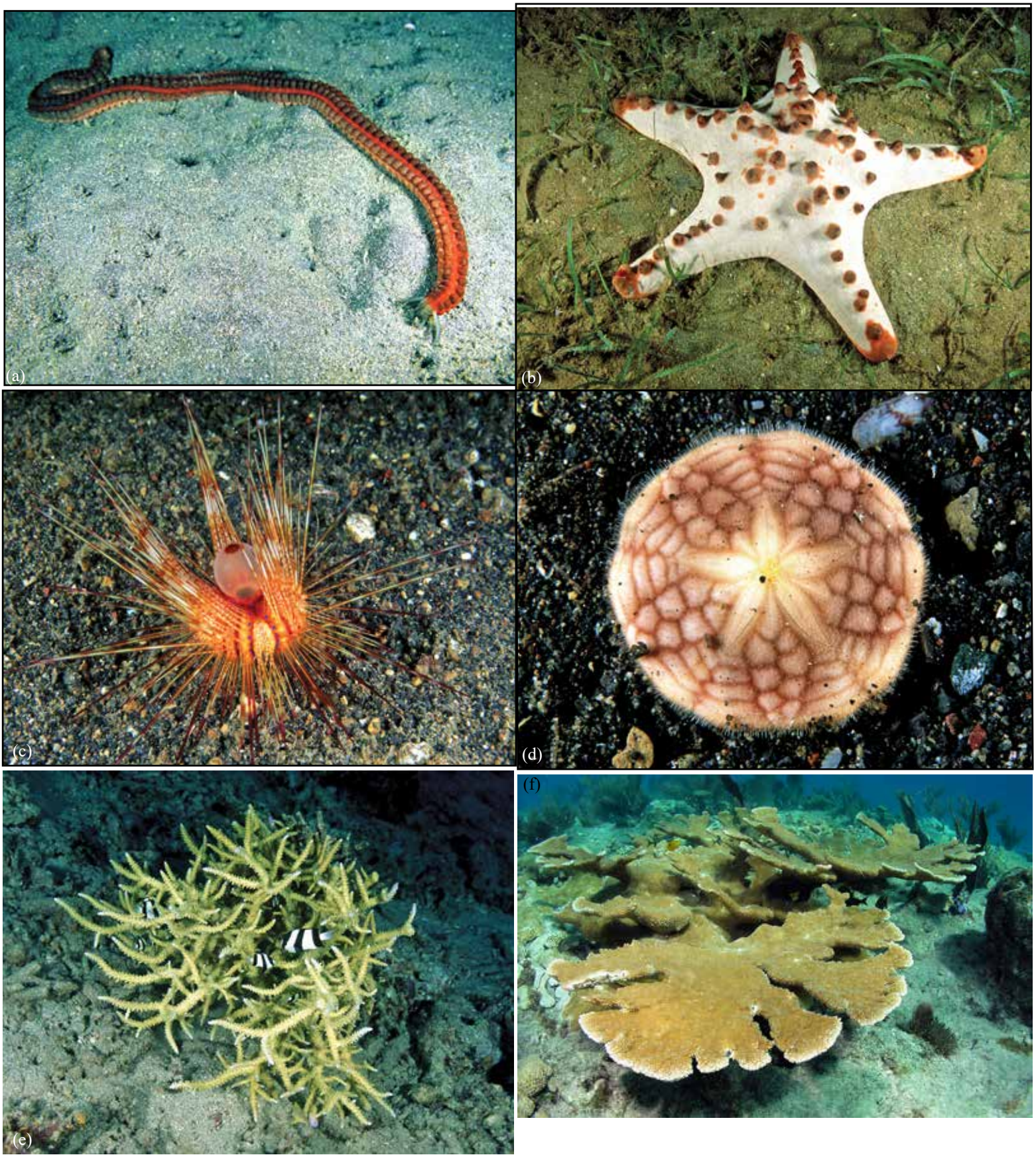


FIGURE 15-3. Inhabitants of the coral reef lagoon and outer reef flat. Many invertebrates—including (a) sea cucumbers (family Synaptidae, Indonesia), (b) sea stars such as this rhinoceros, or horned, sea star (*Protoreaster nodosus*, Papua New Guinea), (c) urchins (*Astropyga radiata*, Indonesia), and (d) the urchins' close relatives the sand dollars (*Clypeaster sp*., Indonesia)—feed on algae, detritus, and microorganisms on sandy seafloors. (e) Spiked forms of hard corals, such as *Acropora sp.* (Papua New Guinea), grow in patches on sandy lagoon floors. (f) Elkhorn coral (*Acropora palmata*, Puerto Rico) grows in many areas on the outer reef flat of reefs that experience low wave energy.

FIGURE 15-6. Islands often form behind the outer reef flat as wave-driven debris accumulates in this area. The island can become high and stable enough to sustain vegetation, such as the palm trees and other plants on this island on a fringing reef in Fiji.

Stands of elkhorn coral characterize the seaward edge of several sheltered Caribbean reefs. Some reefs within tectonically active island chains, such as Palau in the Pacific Ocean, are protected from wave action by a **barrier reef** that surrounds groups of several or many islands. Inside some of these barrier reefs, the sheltered island shore has a **fringing reef** with a reef terrace that simply ends abruptly at the reef wall, which plunges vertically or even undercuts to depths that can exceed several hundred meters (**Fig. 15-4**).

Seaward of the algal ridge (or reef terrace if no algal ridge is present), the downward slope of a reef can range from very gradual to nearly vertical. The upper part of the outer slope (**Fig. 15-4**), called the "buttress zone," is subject to strong scouring action of waves down to about 20 m. It is usually cut across at intervals by deeper channels separated by relatively high ridges, sometimes called a "tongue and groove" formation. The channels or grooves are cut by waves and may also be called "surge channels." Sand and debris created by wave action on the reef are transported seaward through these grooves. Coral growth is limited in the grooves, but many invertebrates and fishes feed on detritus transported along them. Coral growth is more extensive on the relatively sediment-free ridges. However, because wave energy is high, these ridges sustain primarily robust massive varieties of coral, such as brain coral (**Fig. 14-8a**), and encrusting corals and algae.

Farther seaward, on the outer slope between about 20 and 50 m, is a transition from robust massive corals and encrusting species to still strong but less robust forms, such as Acropora (**Fig. 15-5e,f**), and then to more delicate varieties of corals, including black coral (**Fig. 15-7**), sea fans (**Fig. 14-8e**), and **soft corals** (**Fig. 14-8d,f**). The depth at which these transitions occur depends on the intensity of wave action. Delicate corals are present at shallower depths on **leeward** sides of coral-fringed islands than on **windward** sides.

Between about 50 and 150 m, the reef is dominated by delicate coral species that grow outward in slender fingers or arms. Such growth enables hermatypic corals to extend beyond the shadows of their neighbors in the never-ending competition to obtain light for their zooxanthellae. It also enables nonhermatypic corals, including the delicate and beautiful soft corals (**Figs. 14-8d,f**), to extend into the water that flows along the reef face to capture suspended food. Soft corals are most abundant in areas where currents are strongest and thus expose them to the greatest possible food supply.

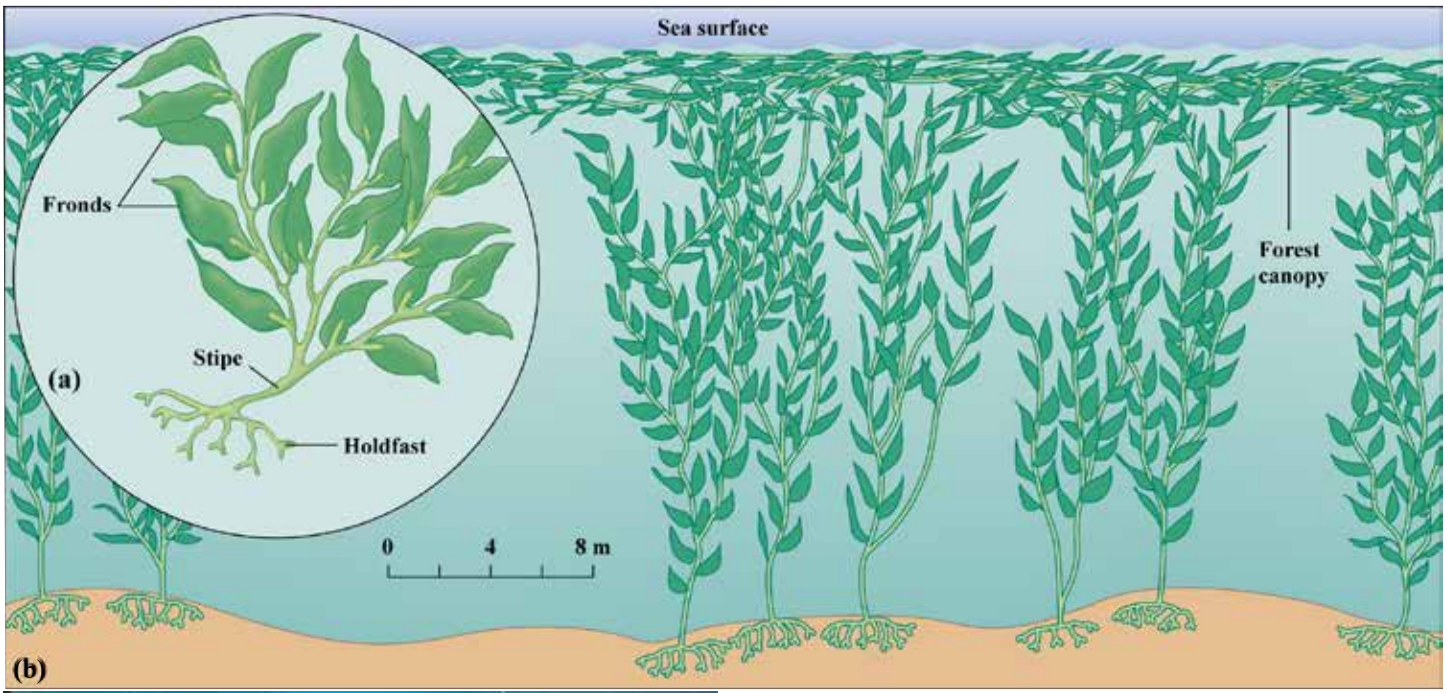
Just as the types of coral that grow on the reef's seaward side are determined primarily by depth and the intensity of wave action, species of invertebrates and fishes that inhabit or feed on the corals change with these factors and in response to changes in coral species. The variations are too complicated to review here but can provide fascinating study for **scuba** divers when no big animals such as sharks, manta rays, or turtles are present to capture their interest.

KELP FORESTS

The name **kelp** is given to a number of species of brown macroalgae that are attached to the seafloor at depths as great as 30 to 40 m, where the water is clear enough to allow light to penetrate to that depth. Once established, kelp fronds grow toward and eventually reach the ocean surface. Where conditions are suitable, kelp grows so densely that it forms forests (**Fig. 15-8**).

Extensive forests of one such kelp, *Macrocystis pyrifera*, are present off the west coast of North America. Kelp fronds are **buoyant**. *Macrocystis pyrifera* fronds, for example, have gas-containing sacs or bladders distributed along them (**Fig. 12-4b**). Once a frond reaches the surface, it continues to grow, but the

FIGURE 15-7. Black coral colony (probably *Cirrhipathes sp.*) with a longnose hawkfish (*Oxycirrhites typus*, Papua New Guinea) hiding among its branches. The hard parts of black corals are a deep black color and are often used to make jewelry, but the polyps may be a variety of colors in the living coral.



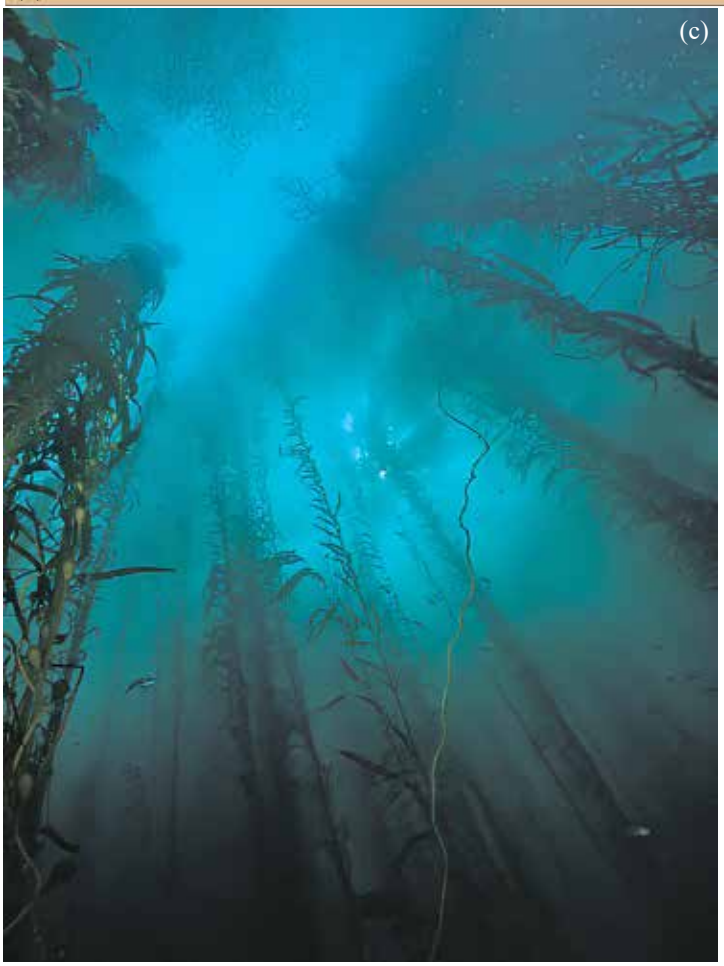


FIGURE 15-8. Kelp forest. (a) Kelp, such as this *Macrocystis pyrifera*, is attached to the seafloor by holdfasts and has long flexible stems, called "stipes," that support the fronds in which photosynthesis occurs. (b) In some areas of abundant kelp, the ocean surface is covered by a canopy of kelp fronds, and the kelp growing upward from the seafloor forms an underwater forest. (c) The sunlight filters through the canopy and kelp forest in this underwater photograph from about 8 to 10 m depth in Monterey, California.

new growth floats on the surface to form dense mats or a canopy. These canopies can cover the entire ocean surface within the species' depth range along substantial stretches of coast.

Kelp Community Environmental Characteristics

Kelp forests grow where the temperature and nutrient characteristics of the water column are very different from those required for coral reef formation. Kelp requires water cooler than 20°C and high nutrient concentrations. Although kelp is attached to the seafloor by holdfasts, it obtains its nutrients from the water column through the surface of its fronds. Kelp fronds grow as much as half a meter a day, and kelp forest primary productivity ranges from 500 to 1500 g of carbon per square meter per year. This rate exceeds the primary productivity in all but the most highly productive phytoplankton-based ecosystems and is approximately the same as primary production rates of terrestrial farms. Large quantities of nutrients are necessary to sustain such growth rates. Consequently, kelp forests are almost exclusively restricted to areas of intense upwelling. The fact that upwelled waters are cold probably accounts for kelp's temperature niche requirements.

Besides low temperatures and high nutrient concentrations, kelp needs a stable, generally rocky, seafloor to which it can attach. In addition, kelp can grow only in shallow waters where sufficient light penetrates to the seafloor to support the growth of newly settled kelp spores.

Kelp Life Cycle and Communities

The kelp life cycle consists of two distinctly different stages. Although the large kelp that form kelp forests grow vegetatively (asexually), they also produce microscopic swimming **spores** that enter the plankton and eventually settle on the seafloor. These spores grow into microscopic male and female plants, which produce eggs and sperm and reproduce sexually near or on the seafloor. If they encounter suitable conditions, the resulting embryos then grow into the large, mature kelp.

Kelp forests support amazingly diverse populations of invertebrates, fishes, and **marine mammals**. The kelp provides several benefits to species that live within its forests. First, kelp produces large quantities of detritus, which forms the base of the

FIGURE 15-9. Members of the kelp holdfast community. (a) These small brown cup corals (*Paracyathus stearnsii*, California) cover many of the rocks at shallow depths. (b) Anemones, such as this rose anemone (*Tealia lineata*, California), are abundant on the kelp forest floor. (c) Many species of crabs, such as this northern kelp crab (*Pugettia producta*, California), feed on the abundant detritus and other animal life. (d) A kelp shrimp is camouflaged to look like the algae in which it lives and on which it feeds (Monterey, California). (e) Sea stars of many species live on the kelp forest floor, and sea pens are often found in the patchy areas of seafloor that are located in and around the forest (Monterey, California). (f) This horned nudibranch species (*Hermissenda crassicornis*, California) is common in the kelp community, together with many other nudibranch species. (g) Many rockfish species live and hunt in the kelp forest, such as these two: the quill-backed rockfish (*Sebastes maliger*) on the lower left, and the copper rockfish (*Sebastes caurinus*, California) swimming above, further to the right.

food web. Surprisingly, only a few animals, including only a few fish, snail, and **sea urchin** species, eat kelp itself, but kelp is easily torn apart, particularly at the ends where new growth occurs. Therefore, kelp releases large amounts of detritus, which is first modified by decomposers and only then consumed by animals. Second, the kelp canopy provides a hiding place and protection from predators, particularly seabirds. The fronds afford many escape routes that enable agile harbor seals and sea lions to evade their shark and killer whale predators, which are less agile and less able to maneuver through the kelp forest. In addition, kelp fronds and holdfasts provide substrate for encrusting organisms and their **grazers** or predators and many secluded places for small fishes and invertebrates to hide from predators.

The rocky seafloor and holdfasts of the kelp forest also sustain a surprisingly diverse community of nonhermatypic corals, **anemones**, crabs, shrimp, sea stars, **nudibranchs**, fishes, and other animals (**Fig. 15-9**). In many ways, kelp forest communities rival those of coral reefs in complexity and beauty.

Kelp, Sea Otters, and Sea Urchins

Two of the most important residents of the kelp community are sea otters (**Fig. 15-10a**) and sea urchins (**Fig. 15-10b**). Sea urchins eat kelp, and sea otters eat sea urchins. Because of this relationship, healthy and abundant kelp forests depend to a large extent on a healthy population of sea otters. In areas where otters are abundant and many sea urchins are eaten, sea urchin populations are low and dominated by small, young individuals. Such populations are too small to affect the kelp significantly (**Fig. 15-10c**). However, if otters are scarce, the sea urchin population multiplies, and many large sea urchins are present to graze heavily on the kelp and reduce its abundance (**Fig. 15-10d**). Large sea urchins, in particular, feed preferentially on the kelp holdfasts and may destroy the forest by cutting the kelp loose from the seafloor, even if they do not consume it.

The California coast was once almost completely fringed by kelp forests, but they were severely depleted by the early years of the twentieth century and have only recently begun to recover. The primary reason for the kelp forest decline is now understood to be hunting of sea otters during the eighteenth and nineteenth centuries, which drove the otters almost to extinction. Once the otters were removed, sea urchin populations increased and steadily overwhelmed and destroyed the kelp forests. Now sea otters are protected and their populations are slowly recovering. As

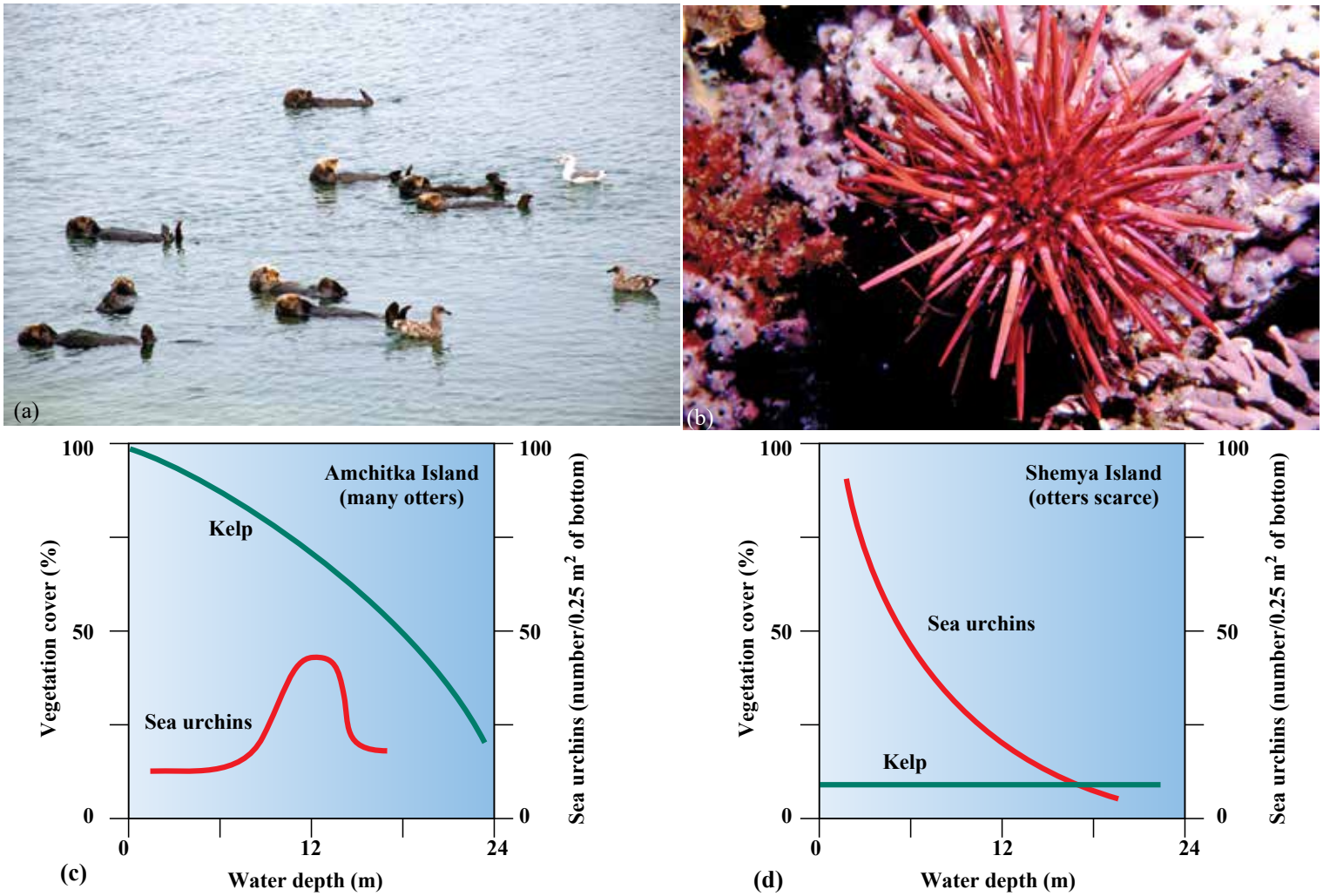


FIGURE 15-10. The sea otter–urchin–kelp relationship. (a) Sea otters (*Enhydra lutris*) were at one time abundant in the kelp forests of California, but their numbers plummeted during the nineteenth century because they were exploited for their pelts. Their populations are now recovering. (b) The sea otter's favorite and most important food is sea urchins, such as this red urchin (*Strongylocentrotus sp.*, California). (c) At Amchitka Island, Alaska, where sea otters are abundant, sea urchins are rare in shallow water because they are preyed upon by the otters. As a result, there is little browsing of the kelp forests by urchins and the kelp is abundant. (d) In contrast, at nearby Shemya Island, where otters have become scarce, urchins are abundant and kelp is very sparse as a result of browsing by the urchins.

a result, sea urchin populations are declining and kelp forests are gradually returning, although their future is threatened by climate change-driven warming of ocean waters. The sea otter is called a "keystone predator" because, without it to prey on urchins, the urchin population growth produces large and fundamental changes in the ecosystem. Keystone predators are found in many ecosystems.

ROCKY INTERTIDAL COMMUNITIES

The rocky intertidal community that lives between the **high-tide line** and the low-tide line on rocky coasts is unique in two important respects. First, this community can be easily observed and studied by anyone who visits a rocky coast at low tide. Second, the community is normally arranged in well-defined depth zones that run parallel to the shore at different heights above the low-tide line. Each zone is populated by different species. Species that live in each zone are determined by a combination of physical conditions of the environment and competition among species that have different tolerances to these conditions.

The most important characteristic of the rocky intertidal zone is the degree of exposure of the substrate to the atmosphere when the tide recedes. Unlike organisms that inhabit sandy **beaches** or mudflats, most rocky intertidal species cannot bury themselves in the rocky substrate to survive periods when they are exposed by the tide. Once exposed to the atmosphere, organisms are subjected to a number of stresses, such as:

- Temperature variations and extremes that far exceed those in seawater
- Variable water exposure (spray or rain) and **humidity**, and the consequent variable tendency to lose body fluids by evaporation
- Variable salinity because the remaining pockets or pools of water may be subject to evaporation and/or dilution with rainwater or snow
- Variable oxygen concentrations and **pH** because physical and biological processes quickly alter these conditions in the small volume of seawater that remains in contact with the organism, and this water is not renewed until the water level rises again
- Predation by birds and terrestrial animals

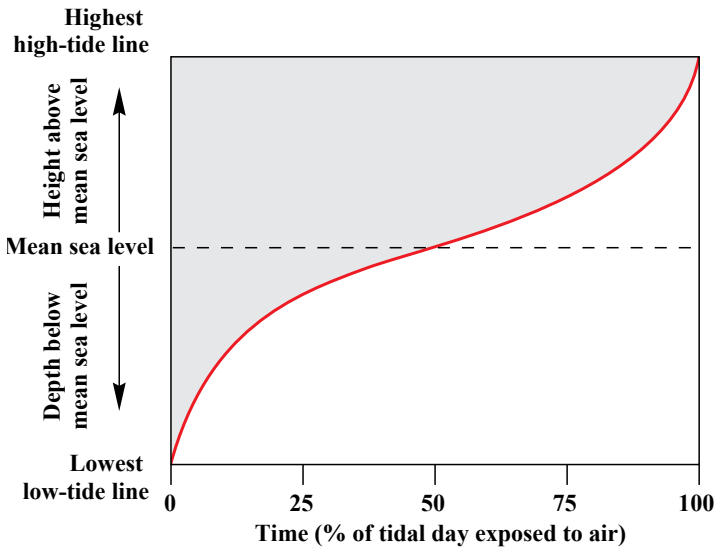


FIGURE 15-11. The length of time that a particular depth in the intertidal zone (and the organisms that live at that point) are exposed to the air during the tidal cycle varies with height above the low-tide line.

Zonation of communities on a rocky intertidal shore is critically dependent on the frequency and duration of their exposure to the atmosphere and, therefore, to these stresses (Fig. 15-11).

The shore can be divided into four zones on the basis of atmospheric exposure time (Fig. 15-12). The highest zone, the **supralittoral zone**, is above mean higher high water (Chap. 10) and thus essentially permanently out of the water, but it is frequently wet with seawater spray from breaking waves, at least during high tides. Below the supralittoral zone, the **high-tide zone** is covered with water for parts of the tidal cycle but remains exposed to the atmosphere most of the time. The **middle-tide zone** is usually covered by water, but it is exposed to the atmosphere during all or most low tides. Finally, the **low-tide zone** is water-covered almost permanently and exposed to the atmosphere only briefly during the lowest low tides. The boundaries between these zones are sometimes sharp, as revealed by abrupt changes in the biological communities that they support.

Even when covered by water, the zones of the rocky shore are subject to different physical conditions, particularly wave-induced turbulence and scour. Wave-induced **turbulence** decreases with depth but can still be substantial well below the low-tide zone.

Rocky coasts are present throughout the oceans, and each has its own unique communities with different species and species interactions. Consequently, only the general types of **flora** and **fauna** in rocky intertidal zones are described here. For most coastal areas, easy-to-read guides to shore and **tide pool** creatures can be found in local bookstores.

Supralittoral Zone

The supralittoral zone is either permanently exposed to the atmosphere or covered by water only during occasional extreme high tides or **storm surges**. Hence, this zone can be considered land and not part of the ocean ecosystem. Nevertheless, the continuous or frequent spray of seawater that reaches this zone provides moisture and nutrients that support the growth of **lichens**, encrusting **blue-green algae**, and small tufts of various green algae. These autotroph communities are sparse but provide food for a variety of animals, including species of periwinkles (marine snails), other marine snails, **limpets**, **isopods**, and crabs (Fig. 15-12).

Periwinkles, other snails (Fig. 15-13a), and limpets are grazers that feed on algae encrusting the rocks. The periwinkles are often species of the **genus** *Littorina*. Many *Littorina* species are well adapted to life in the supralittoral zone. Some "breathe" air and may even drown if fully immersed in water for long periods. Supralittoral species of *Littorina* are **viviparous**, giving birth to live young. In contrast, the marine species of this genus that live completely submerged deposit eggs on the rocks or release them to the water. Periwinkles can completely withdraw into their shell and seal off the opening with an operculum, a rigid disk of horn-like material. This seal is watertight and provides protection from predators and especially from dehydration during long periods of exposure to the atmosphere.

Limpets (Fig. 15-13b) are not able to withdraw entirely into their shell. Instead, they cling to the rocks with their bodies and pull their shells tightly down on top of them. If the shell edge fits well with the surrounding rock, the animal is sealed inside, where it is protected from predators and desiccation. Some limpets rasp the rock away or release acidic secretions to create a perfectly fitted platform for their shell. When immersed or wet, limpets may

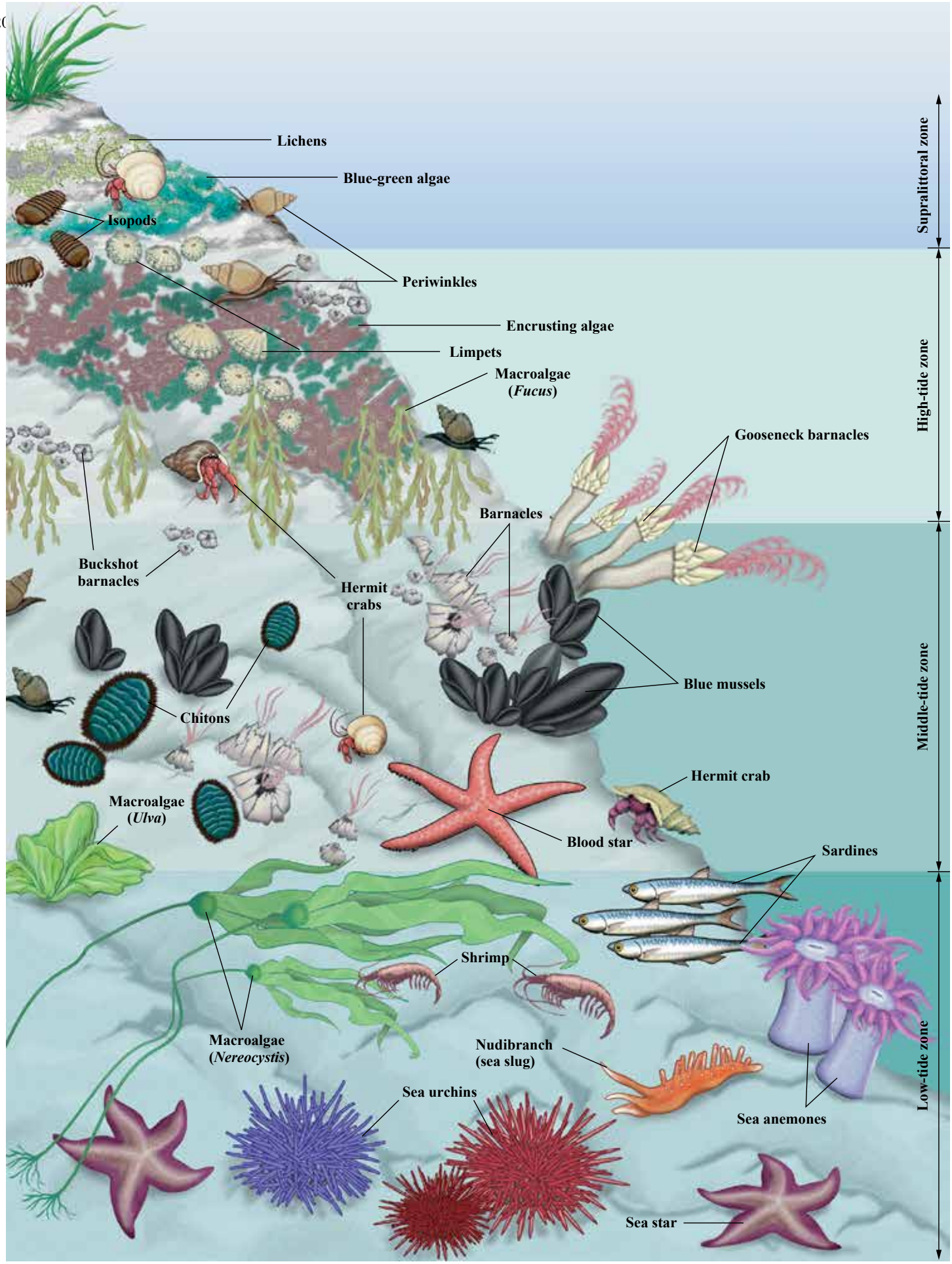


FIGURE 15-12. The rocky intertidal shoreline can be separated into four zones based on length of time exposed to the atmosphere. Many species have ecological niches that restrict them to only one of these zones, although closely related species may occupy different zones. The flora and fauna in this figure are typical of a mid-latitude, cold-water, rocky shoreline. Generally, many more species occur in each zone than are shown here. Competition between species often determines the vertical limits of a particular species' distribution within the zone that it occupies.

FIGURE 15-13. Animals and algae of the rocky intertidal zone. (a) Group of black turban snails (*Tegula funebralis*, Monterey, California). (b) A limpet (order Archaeogastropoda, California). (c) Barnacles in the high intertidal zone, often called buckshot barnacles. These are probably primarily *Chthamalus sp.*, with some interspersed Balanus glandula. (d) Lined chiton (probably *Tonicella lineata*, California). (e) Dense bed of California mussels (*Mytilus californianus*, Monterey, California). (f) These green algae are in the upper intertidal zone and have been out of water and in the sun for several hours. The algae survive this experience on a regular basis with no harm (south of San Francisco, California). (g) A hermit crab (*Pagurus sp.*, California) living in its borrowed gastropod shell.

move over the rocks to graze, but they return to their prepared location during periods of prolonged exposure to the atmosphere. The limpet's bond to the rock is so strong that it cannot easily be turned over, and thus its soft body is protected from predators such as birds. The limpet's defensive action of clinging tightly to the rock is easy to observe. Limpets can be surprised and easily removed from their rock location by a quick sideways stroke of a chisel or blade. However, if the limpet is warned, perhaps by a light tap from a finger, it clamps down and is impossible to remove without breaking the shell.

Isopods often live in the supralittoral zone in great numbers. These animals are **scavengers** that feed on organic debris. They are rarely seen by most visitors to the shore because they remain in hiding places within the rocks by day and emerge to feed only at night. Various species of crabs also inhabit the supralittoral zone. Many are scavengers, but some are grazing **herbivores** or predatory **carnivores**.

Each zone of the rocky intertidal ecosystem varies in width according to factors that include the slope of the rocks and the **tidal range**. The width of the supralittoral zone is also affected by factors that determine the degree of wetness of the rocks, including the intensity of wave action, the average air temperature and humidity, and the location, roughness, and orientation of the shore (which control the degree of shading from the sun). For example, the supralittoral zone is wide in areas such as central California and Maine, where cool, damp, and foggy days are common.

High-Tide Zone

In the high-tide zone, organisms are exposed to the atmosphere for long periods and, like inhabitants of the supralittoral zone, must be able to withstand extremes of temperature and salinity and must be protected from dehydration. In addition, these organisms must be able to withstand severe wave-induced turbulence. To offset these disadvantages, a reliable supply of nutrients, plankton, and suspended organic particles becomes available each time the rocks are covered by ocean water. Consequently, the high-tide zone can support species that cannot tolerate the limited nutrient supply and prolonged dry periods of the supralittoral zone.

Rocks of the high-tide zone support many species of encrusting algae, particularly in the upper parts of the zone. In contrast to the supralittoral zone, the high-tide zone has several species of macroalgae. All these species have thick cell walls, which give them a leathery feel and protect them from excessive loss of water by evaporation when exposed to the atmosphere (**Fig. 15-13f**). They are firmly attached to the rocks by holdfasts, and their stipes (branches) are extremely flexible, enabling them to withstand wave turbulence. Although they are eaten by some species of snails, crabs, and other animals, these algae are tough and difficult to digest, and they contribute to the food web primarily in the form of detritus. The detritus is formed when parts or all of the algae are first broken loose from the rocks by waves or grazers and then broken down or modified by decomposers.

FIGURE 15-14. On this shoreline at Rialto Beach in Washington State, you can see the zonation of species in the middle tide zone. There is a band of barnacles (the light greenish gray) above a band of mussels (black and shiny). The band of mussels extends down to a depth determined by sea star predation. Sea stars cannot survive the long air exposure between tides that occurs in the mussel zone.

In many areas, the top of the high-tide zone is marked by a band dominated by small **barnacles** called "buckshot barnacles" (**Fig. 15-13c**). Several larger species of barnacles are present lower on the shore in the middle-tide zone. Because barnacles are suspension feeders, they cannot live above the highest high-tide line. However, they can survive in locations where they are able to feed for only a few hours on the few days of spring tides each month when they are immersed in water. When exposed to the atmosphere, the barnacle withdraws into its hard shell, which protects it from dehydration, predators, wave impacts, and wave-induced turbulence.

Because organisms of the high-tide zone, like species in the supralittoral zone, must withstand extended exposure to the atmosphere, the two zones sustain many similar species, including periwinkles and limpets. Toward the lower end of the high-tide zone, periwinkles and limpets become less abundant, whereas chitons and mussels become more abundant. This change marks the transition from the high-tide zone to the middle-tide zone. Chitons (**Fig. 15-13d**) feed and attach themselves to the rocks in the same way as limpets, but they have shells made up of eight separate connected plates. Mussels (**Fig. 15-13e**) are suspension feeders like barnacles, but they have a two-piece shell attached to the rocks by a network of strong threads called "byssal threads." These threads are formed by a liquid secreted from the mussel's foot that hardens in seawater. The threads are attached between the mussel shell and the rocks or, in dense mussel beds, between one shell and another. Periwinkles, barnacles, limpets, mussels, and other species living attached to rocks of the high- and middle-tide zones tend to have rounded shells, which can best withstand and dissipate the turbulent impacts of waves.

The lower limit of the zone inhabited by a rocky intertidal species is determined for many species by competition from other species. In contrast, the upper limit of the inhabited zone is normally determined by the tolerance limits of the species' fundamental niche.

Middle-Tide Zone

Macroalgae are generally less abundant or absent in the middle-tide zone because of competition by mussels and barnacles. In a middle-tide zone newly formed by vertical movements of the coast during earthquakes or by **lava** flows, or in a middle-tide zone partially denuded by extreme storms, macroalgae quickly establish themselves and cover the rocks. However, as mussel and barnacle **larvae** settle and grow into new colonies, the macroalgae are steadily overcome and eventually disappear from the zone.

Within the middle-tide zone, the lower limit of mussel beds is determined by competition from predatory sea stars, which can grip and slowly pull open a mussel with the many tube feet on

their undersides. As you can see in **Figure 15-14**,, mussel beds terminate abruptly at their lower limit on many shores, almost as though the mussels were incapable of growing below that depth. However, this limit is simply the depth at which recolonization by mussels is less effective than predation by sea stars (whose fundamental niche does not extend as high up the middle-tide zone as the fundamental niche of the mussels does). Although some sea stars do prey on mussels within the mussel bed zone, they must withstand stresses associated with being at the limits of their fundamental niche (e.g., atmosphere exposure and turbulence), or they must migrate up and down the shore's zones with the tides. Hence, mussels are able to outcompete the predatory sea stars in this upper zone.

The mussel beds on many rocky intertidal shores are ideal **habitat** for a variety of algae and animals that include **hydroids**, worms, snails, clams and other mollusks, and crabs and other **crustaceans**. Acorn barnacles are interspersed in the mussel beds. These barnacles, and to a lesser extent the mussels, are eaten by snails that drill through the barnacle plates or mussel shell or force the mussel shell open to get to their prey. The middle-tide zone is also populated by numerous species of **hermit crabs** (**Fig. 15-13g**) and a number of species of anemones that can withstand periodic exposure to the atmosphere.

Low-Tide Zone

The low-tide zone sustains a variety of macroalgae and encrusting algae nourished by nutrients brought to them with each tide. In this shallow zone, algae have ample light, even when turbidity is relatively high. In addition, because they are exposed to the atmosphere for only short periods at low tides, they do not need the protection against desiccation that algae in higher zones require. Although the low-tide zone, unlike zones higher on the shore, is dominated by algae, it sustains numerous species of animals, many of which use the abundant mats of algae for shelter. Animals in the low-tide zone are similar to those of the kelp community (**Fig. 15-9**) and include anemones, **sponges**, sea urchins, nudibranchs, shrimp, sea stars, crabs, sea cucumbers, and fishes. These organisms are infrequently exposed to the atmosphere, so they include delicate forms that would be dehydrated or thermally shocked if exposed for more extended periods.

The principal physical hazard in the low-tide zone is wave-induced turbulence. Some species withstand this turbulence by attaching themselves to the rocks. Other species are active swimmers or simply use macroalgae or cracks and holes in the rock as protection from wave action. Because the low-tide zone has abundant macroalgae and a continuous supply of suspended detritus and plankton, the low-tide community comprises many species of **filter feeders**, detritus eaters, scavengers, grazers, and carnivores.

Tide Pools

On many coasts, the rocky shore is convoluted or pitted sufficiently that seawater remains in many depressions, even when the tide recedes. These depressions are called "tide pools." Depending on the size, location, and permanence of the tide pool, any of the species of any part of the rocky shore, from the high-tide zone to the low-tide zone, may be present.

Each tide pool is unique because evaporation, rainfall, solar heating, winter cooling, and other factors affect the physical properties (e.g., salinity, temperature, pH, oxygen concentration) of the water in each tide pool differently. Tide pools high on the shore are isolated for long periods between tides and are subject to the greatest changes. Deep tide pools have a greater volume of seawater per unit area than shallow ones and are less affected by evaporation, rainfall, heating, and cooling. Consequently, small tide pools tend to support only microscopic algae and highly tolerant **copepods** and other microscopic animals. In contrast, large tide pools may contain many species of algae, sea urchins, anemones, crabs, shrimp, small fishes, and other animals that are tolerant to relatively small changes in salinity, temperature, and other physical characteristics of the tide pool water. The next time you visit a shore with tide pools, you can see which species are more tolerant by simply examining several different tide pools.

SARGASSO SEA

The Sargasso Sea is the region of the North Atlantic Ocean surrounded by the North Atlantic **subtropical gyre**. The permanent thermocline in the Sargasso Sea is steep, persistent, and deep (**Chap. 8**). Hence, upwelling does not occur, and the surface layer is depleted of nutrients. Furthermore, there is little exchange between Sargasso Sea surface waters and adjacent surface waters from which nutrients could be resupplied. Consequently, primary productivity is very low, and we would expect the Sargasso Sea to be an ocean "desert." The phytoplankton-based **food chain** in the Sargasso Sea is indeed very limited. However, parts of the Sargasso Sea surface are covered by dense mats of floating brown macroalgae (**Fig. 15-15a,b**), within which lives a diverse community of animals. These mats often cover areas of many square kilometers.

Why do these vast quantities of algae grow in what should be a desert? The answer illustrates the infinite adaptability of nature. The brown algae in the Sargasso Sea are species of the genus *Sargassum*. These species grow extremely slowly and are thought to have lifetimes of decades or even centuries. The very small amounts of nutrients available in Sargasso Sea surface waters are adequate to sustain the very slow growth of *Sargassum*. However, the critical factors that enable *Sargassum* to populate the Sargasso Sea so heavily are very weak currents and very limited wind mixing. Because the surface currents are weak and flow in directions that are oriented partially toward the center of the subtropical **gyre**, they tend to retain the floating algae within the Sargasso Sea, and the mats of the long-lived algae tend to stay together. The algal population therefore can develop a large biomass despite its very slow growth and reproduction rate. In addition, because wind mixing is very limited, nutrients released into the water column by the consumers and decomposers that live in the *Sargassum* are not rapidly diluted, and are available to be recycled back into new *Sargassum* growth.

Within the *Sargassum* mats lives a community of many different species of fishes, crabs, snails, and other animals, including a frogfish called the sargassumfish. Many in this community have a body that mimics the structure and color of the *Sargassum*, and they can cling to the branches of the algae unnoticed by predators or prey that swim by. In contrast to many other ocean ecosystems, the *Sargassum* community has relatively few grazers and a relatively small animal biomass in relation to the algal biomass. This composition reflects the evolution of the community to a stable condition. If there were large populations of grazers or other animals, the algal biomass would be rapidly reduced to the point where the animal populations could not be sustained. The animals that have survived in this community include many long-lived, slow-growing species with sedentary lifestyles. Each

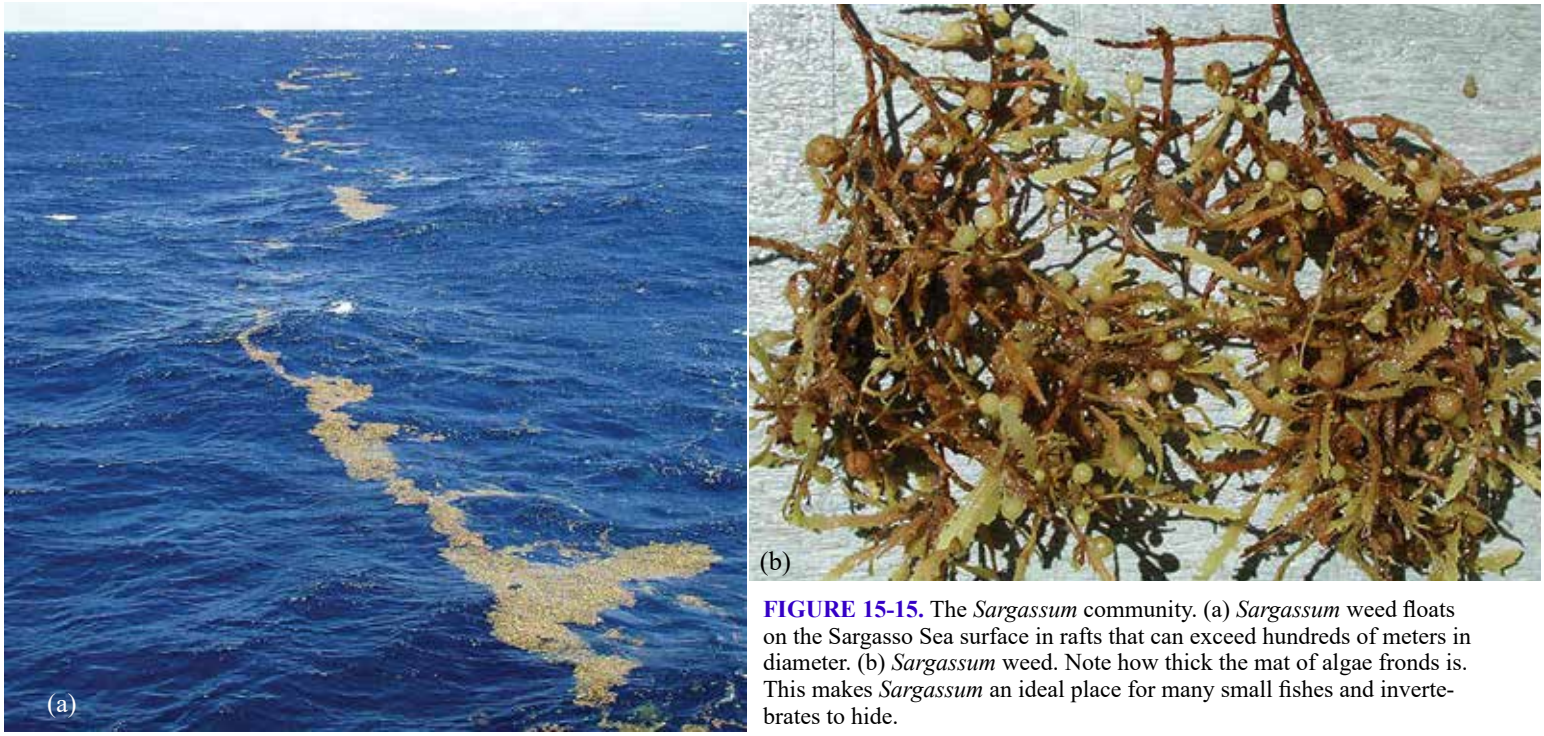


FIGURE 15-15. The *Sargassum* community. (a) *Sargassum* weed floats on the Sargasso Sea surface in rafts that can exceed hundreds of meters in diameter. (b) *Sargassum* weed. Note how thick the mat of algae fronds is. This makes *Sargassum* an ideal place for many small fishes and invertebrates to hide.

of these characteristics represents an adaptation to minimize food intake needs.

Although some species similar to those found in the Sargasso Sea are found within the interior of other subtropical gyres, for reasons as yet not fully understood, none of these other areas sustain the high biomass found in the Sargasso Sea.

POLAR REGIONS

The marine ecosystems of the north and south polar regions differ from one another physically and biologically because of the configuration of the landmasses and because they are separated by warm tropical waters through which most cold-adapted marine species cannot transit. Nonetheless, the two ecosystems have a number of environmental similarities, including extreme seasonal variation in light availability, generally low surface water temperatures, and seasonally variable sea-ice cover.

In both polar regions, cooling of surface ocean waters and vigorous wind mixing caused by storms formed at the polar **front** (Chap. 7) prevent the formation of a permanent thermocline and promote vertical mixing. Therefore, nutrients are generally abundant, especially in surface waters of the upwelling region between the Antarctic **Convergence** and the near-coastal east-wind drift current that flows around Antarctica. Primary productivity in this region apparently is limited by the availability of **micronutrients**, particularly iron, even when light is ample, and nitrogen, phosphorus, and silica are abundant. Iron concentrations are low in this region because there is a very low supply of river inputs and atmospheric dust in this region.

Special Characteristics of Arctic Marine Environments

In the Northern Hemisphere, nutrients are abundant in surface waters of the **marginal seas** that surround the Arctic Ocean, particularly the Bering, Norwegian, and North Seas. Nutrients are less abundant in seasonally ice-free surface waters of the Arctic Ocean itself, because freshwater **runoff** and **ice exclusion** lower surface salinity and establish a strong **halocline** that inhibits the vertical mixing of higher-salinity, nutrient-rich deep water into the surface layer. In addition, the permanent ice cover of much of the Arctic Ocean and its location in an atmospheric **downwelling** zone (zone of weak winds) minimize wind-induced vertical mixing.

In coastal regions of the Arctic Ocean, nutrients are generally available in relatively high concentrations during summer because they are supplied to some extent in freshwater runoff. In addition, nutrients are returned to the water column through decomposition during the darkness of winter, when these regions are covered by ice. Hence, nutrients are readily available during at least the early part of the short spring–summer ice-free season.

Common Characteristics of Arctic and Antarctic Marine Environments

In both the Arctic and the Antarctic, substantial populations of microscopic ice algae live, or form resting phases, within liquid pockets in the ice or on the underside of the ice. During spring and summer, ice algae can grow in or under the ice as the light increases in intensity and begins to penetrate the ice. As the ice melts, the resting spores of many species of phytoplankton are released into the water column, where they grow rapidly in the nutrient-rich and now well-illuminated open water. Both the Arctic and the Antarctic have a zone of maximum productivity that coincides with the edge of the floating ice. Each spring, this zone moves poleward with the melting ice edge.

Several important characteristics of polar ecosystems determine the species that are able to live there. First, because nutrients are generally available, phytoplankton usually grow quickly and are abundant when light is also available. Second, the extreme seasonal variation of light intensity and duration, and in some areas the extent of sea-ice cover, limit the period of ideal conditions for phytoplankton growth to only a few weeks or months in summer. Third, upwelling and wind mixing, which supply nutrients to surface waters and at the same time affect the **residence time** of phytoplankton in the nutrient-rich photic zone, are particularly variable because of eddies, turbulence induced

FIGURE 15-16. Some examples of seal species that inhabit the Antarctic ecosystem. (a) Crabeater seals (*Lobodon carcinophagus*, Antarctic Peninsula) have specialized teeth (not shown in the image) to filter out krill, their principal food source. They are somewhat misnamed since they do not eat crabs. (b) Antarctic fur seals (*Arctocephalus gazella*, South Georgia Island), heavily hunted for their fur during the 18th and 19th century, feed mostly on krill squid fish and penguins, (c) Leopard seal, (*Hydrurga leptonyx*, Antarctic Peninsula) a voracious predator that will eat krill, fish, squid, penguins and other seals.

by seafloor topography, and especially changes in weather and **climate**.

As a result of the unique physical characteristics of their environment, many animals that live in polar regions must migrate seasonally or be able to obtain all the food they need for the year during the short productive summer period. In addition, they must be capable of ensuring the survival of their species during years when climatic extremes may result in a partial, or even total, loss of their food supply. The evolutionary response to these constraints is for the animals to be long-lived, to reach sexual maturity late, and to bear only one or a few offspring each year for several years. This response ensures that the species will survive if one or more successive years are poor years in which none of the offspring survive. In addition, the animals must be able to store the food energy needed to survive the winter when food is unavailable or to migrate to warmer regions for the winter. The food energy is stored as fat. Many species that live in polar ecosystems, including certain fishes, marine mammals, and birds, have these characteristics.

Many of the characteristics shared by polar animals make them more susceptible than the marine species of lower latitudes to the adverse effects of certain chemical compounds that can cause **contamination**. Because fat-**soluble** chemical compounds are concentrated in an animal's fatty tissues, they can accumulate for several years before polar animals reach reproductive age. This buildup maximizes the possibility of **carcinogenic**, **mutagenic**, and **teratogenic** effects in the species or its offspring (**CC18**). Fortunately, the Arctic and Antarctic marine ecosystems are substantially less contaminated than marine ecosystems at lower latitudes.

Antarctic Communities

The pelagic food web of the Southern Ocean is described in **Chapter 12** (**Fig. 12-12**). It consists of many species of whales, seals, and penguins that feed on the abundant **krill** and other zooplankton (many of which can be found at the ice edge feeding on phytoplankton populations). Most of the penguin and seal species live year-round in Antarctic waters and haul themselves out on the continent or one of the nearby islands to breed and bear their offspring (**Fig 15-16**). Like many polar species, most of these mammal and bird species mature only after they are several years old, normally have one or two offspring per year for several years, and build up heavy layers of fat during summer, when food is abundant.

Although fat layers act as insulation against the Antarctic cold, particularly when the animal is on land, their most important function is to provide energy during the period when the animal is not feeding. For example, the majority of whale species in the Antarctic are **baleen** whales that visit the region only during summer, when food supplies are abundant. The huge store of fat that they build up during this time is used to supply them with energy during the remainder of the year, when most of these species migrate to breeding grounds in the tropical or subtropical ocean. During the migration and breeding season, the whales feed little or not at all.

Human hunting has dramatically reduced the populations of many seal and whale species in the Antarctic (**CC16**). These species are now protected, and most populations are showing signs of slow recovery.

Although fishes of the Antarctic ecosystem are much less well

Hatchetfish

Saccopharynx

Viperfish

Lanternfish

FIGURE 15-17. Mid-water fish species are often very strange-looking and have unusual adaptations, such as unhingeable jaws and hugely expandable stomachs, strange eyes, lures, and light-emitting photophores. Many of these adaptations aid these species to cope with the scarcity of food and difficulty of locating mates and prey.

studied than the marine mammals and birds, we know that a high proportion of these species are present only in Antarctica and appear to be adapted to the cold and seasonally variable food supply in much the same way that Antarctic marine mammals are. Some species have evolved a unique blood chemistry that enables them to live at temperatures below freezing. The natural antifreeze of these fishes is the subject of considerable research because it could have commercial and medical applications.

Arctic Communities

The biological populations of the Arctic region are similar in some ways to those of the Antarctic, particularly in their concentrations of marine mammals. However, species found in the Arctic are different from those found in the Antarctic. Many seal species live year-round in the Arctic and its adjacent seas and haul themselves out on land to breed, as other seal species do in the Antarctic. Most northern whale species migrate between their Arctic feeding grounds and tropical or subtropical breeding grounds. Penguins and leopard seals are not present in the Arctic. However, the Arctic is populated by polar bears and walrus (**Fig. 12-27d**), which are not present in Antarctica. Polar bears are voracious predators and superb swimmers, but they are land animals. However, because they range across the sea ice to hunt seals, they are primarily dependent on food from the marine environment, and so they are considered a part of the marine ecosystem.

Susceptibility to Climate Change

Global climate models all predict that climate changes will be amplified in the polar regions, and this conclusion is supported by historical data and by observations during the past several decades. The reasons for this special susceptibility are many and complex, but they include the positive feedback (**CC9**) due to reduced snow and ice cover. A covering of snow and ice is a good reflector of the sun's energy. Warming reduces snow and ice cover, which increases the amount of the sun's energy absorbed by land and ocean, causing further warming.

The polar climate has warmed during the past 30 years, resulting in substantial reduction in the area of permanent sea ice in the Arctic Ocean, and causing ice sheets to be reduced in size in the Antarctic, and glaciers to retreat in both polar regions. If sustained, this trend will not only cause sea level to rise worldwide, but will also have profound effects on polar biological communities. For example, polar bear populations are already adversely affected and are likely to be devastated because the bears hunt mostly on floating summer sea ice, which is steadily reducing in area and retreating farther from the coast. Similarly, many species of seals and penguins are already and likely will be much further affected by changing ice and snow cover in their traditional breeding grounds on the Antarctic coast. Furthermore, changes with unknown effects are likely to take place because a reduction in ice cover favors phytoplankton production over ice algae production in both polar regions. Profound changes in both the Arctic and Antarctic marine ecosystems already appear to be well underway.

BEYOND THE SUN'S LIGHT

Below the surface layers of the oceans, organisms must be adapted to extremely low light levels, to uniformly low temperatures, to a detritus-based food supply that decreases steadily with depth, and to increasing pressure. These factors interact to give pelagic and benthic communities of the **bathyal zone** and **abyssal zone** characteristics that are very different from those of communities that live near the surface.

Relatively little is known about bathyal and abyssal communities because the vast volume of the ocean that they inhabit has been visited only for fleeting moments by research **submersibles**, which many denizens of the deep undoubtedly avoid. More is being learned from ROVs but even ROVs are expensive to operate at these depths, and likely also avoided by many species, so progress is slow. In addition, collecting samples from the deep oceans is very difficult and expensive.

The creatures that live in the deep oceans zones range from rather familiar forms that resemble fishes and invertebrates of the shallower ocean to incredibly bizarre-looking creatures that

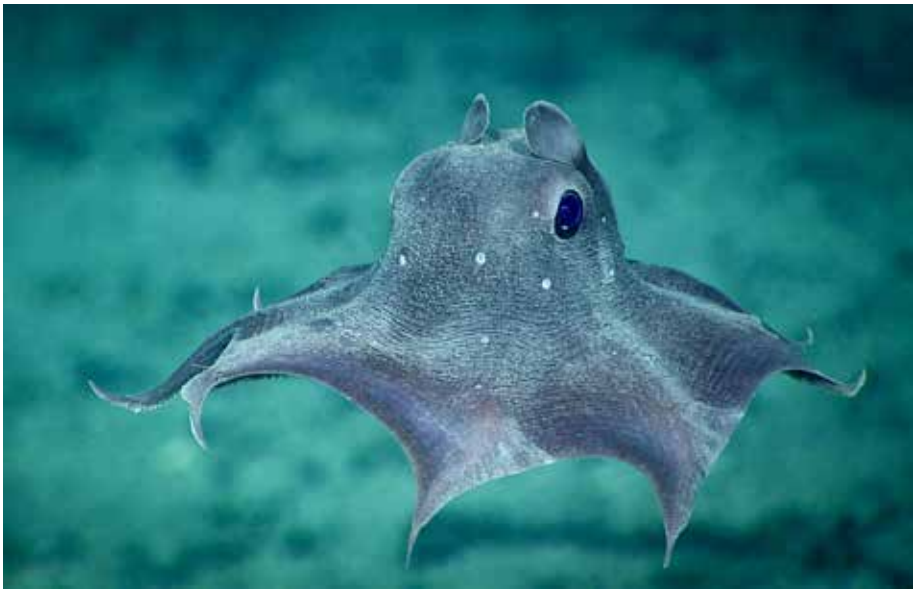


FIGURE 15-18. "Dumbo" octopuses named for their floppy ear-like fins that they use to move through the water, are members of a genus of octopi called *Grimpoteuthis*. The largest Dumbo octopus so far recorded was about 1.8 m in length and weighed about 5.9 kg. They live in the hadal and abyssal zones and have been observed as deep as 7000 m in the Java Trench. As food is rare they eat almost anything including worms, crustaceans, mollusks, and small fish. Unlike other octopuses, they can not swim by jet propulsion and do not produce ink to evade predators. These are likely adaptations that reduce metabolic energy expenditures needed for these functions in response to the relative absence of predators and light for them to hunt by, and the scarcity of food supplies for the octopuses themselves.

would be well suited to science fiction movies. **Figure 15-17** shows just a small selection of the fishes that inhabit the **aphotic zone**.

Organisms living below the photic zone have four potential sources of food: particulate detritus that sinks slowly through the water column, carcasses of large animals that sink rapidly to the ocean floor because of their size, prey species that live in the aphotic zone, and prey species that live in the photic zone above. Of these, only prey species in the photic zone are abundant, so many deep-water species migrate to this zone to feed. All other deep-ocean biota must be adapted to a low and uncertain food supply.

Many species of crustaceans (such as shrimps, copepods, and **amphipods**), other invertebrates (such as squid), and numerous fish species live in the part of the water column immediately below the photic zone, between about 200 and 1000 m. Many of these species migrate vertically up into the photic zone at night to feed and then return to the depths during the day. Other species prey on species that live in their own depth zone. Vertical migrants include the unique *Nautilus* (**Fig. 12-24e,f**), which has a chambered shell to provide buoyancy. To avoid problems with pressure changes as the *Nautilus* migrates vertically, the rigid internal buoyancy chambers contain gas at a low pressure. To adjust its buoyancy it pumps small amounts of water into and out of its internal chambers. Since this increases or decreases its mass, and density is mass divided by volume, this allows the nautilus to control or change its depth. Oceanographers profiling floats achieve the same buoyancy control by applying the same principle but changing their volume rather than their mass by pumping small amounts of oil between their interior and an external expandable membrane.

There is very little or no light below 200 m, and no red light penetrates to this depth. Many organisms of this zone are red or dark colored (**Figs. 15-17, 15-18**), so they do not reflect any of the ambient light, and this makes them difficult to see in the near darkness. However, many fishes and other species that live at these depths have greatly enlarged eyes to enable them to hunt prey in the dim light.

The easiest way to hunt visually for prey in waters below about 200 m where light still penetrates is to look upward into the very dim light filtering down from above and search for the dark silhouette of the prey species. Consequently, many fish species of this zone have eyes that look directly upward. To counter this hunting strategy, many prey species have a series of light-producing organs called "photophores" arrayed along the underside of their body. By illuminating their underside with these photophores, they can reduce the sharpness of their silhouette and blend better into the dimly lit background above. Many species also have photophores arrayed on other parts of their body, presumably as devices to identify members of their own species or to attract prey species.

With increasing depth below 1000 m, fewer and fewer species are present that migrate vertically. Many organisms are brightly colored, although, in the absence of light, color does not advertise their presence and so is irrelevant. Eyes become less prominent and absent in many species, but some species that live in the absolute darkness of the deep oceans do have eyes that, at least in some fishes, are adapted to detect bioluminescent light produced by many animal species and bacteria in this otherwise lightless zone, likely for recognition or mate attraction, and used by predators for prey location. Adaptations, found in some fish species suggest that they may be able to detect a single photon of bioluminescence and even to distinguish between wavelengths (see colors) which no other animals are known to be able to do at such low light levels.

Because of the low abundance and widespread dispersal of organisms, all fishes of mid and deep waters must be adapted to take advantage of any prey species they encounter. Therefore, many of these fishes have unhingeable jaws and soft expandable bodies, so they can swallow and digest prey species as large as, or larger than, themselves. Some also have highly sensitive chemosensory (chemical-sensing) systems that allow them to detect even slight changes in chemical traces coming from live or decaying prey.

On most of the deep-ocean floor, the food supply comes from above as a rain of detrital particles and as occasional carcasses of large animals. Much of the detrital material has already been subjected to substantial decomposition during its slow descent through the water column. Hence, what remains is primarily material that is difficult to digest and that decomposes only very

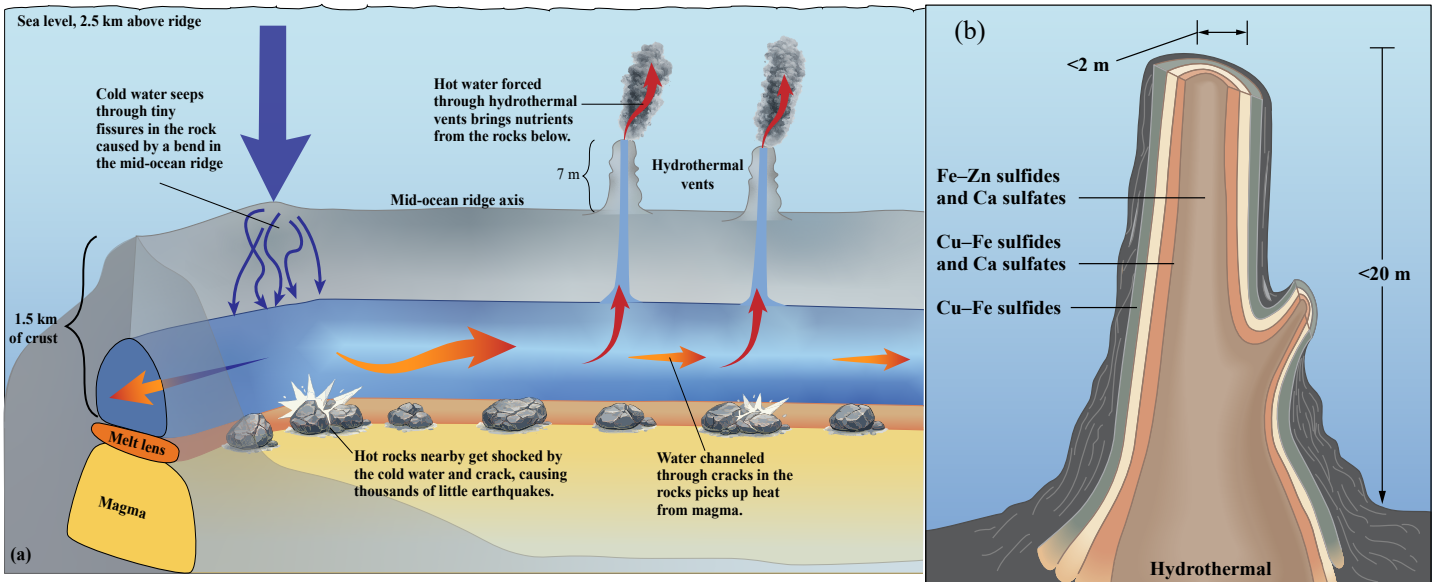


FIGURE 15-19. Black smoker formation and composition. (a) Hydrothermal vents on the oceanic ridges are believed to be formed because heat from magma below the oceanic ridge sets up a convection circulation. In this circulation, water from below the seafloor is heated and rises at the vents and is replaced by water drawn through the cracks in the rocks and sediment on the flanks or an adjacent section of the ridge. (b) At black smoker vents, the discharged water contains no oxygen but does contain high concentrations of iron, manganese, and other sulfides. As water is vented into cold ocean water, metal sulfides are deposited around the vent and often form a chimney-like structure.

slowly. This material has little immediate food value for animals. This detritus is normally consumed by **bacteria** in the surface sediment, and it is the bacteria that become food for larger animals. Because the suspended particulate food supply near the deep seafloor is at very low concentrations and is of low nutritional value, there are few suspension feeders. Most animals of the deep seafloor are deposit feeders, including many species of sea cucumbers and **brittle stars**. The particulate food supply in some areas near the continents may be supplemented by detritus carried to the deep seafloor in **turbidity currents**.

Although we have little direct information about such events, it is known that bodies of large animals must sink rapidly to the seafloor with some frequency. When bait is lowered to the deep seafloor, a variety of fishes, sharks, crustaceans, and other invertebrate scavengers (Fig. 15-17) arrive to feed on the bait within as little as 30 min. Once the bait has been eaten, these animals disappear into the darkness. Some bait, such as a massive whale fall can create an ephemeral, yet long lasting ecosystem that can provide energy for decades. They can also act as "stepping stones" across the barren seafloor, providing energy for the gathering scavengers to disperse and colonize new areas. How these scavengers find the bait or their normal food is not known, but the speed at which they appear suggests that they must have extremely sensitive chemosensory organs for this purpose. It has been observed that many of these scavengers can sense, but cannot find, bait if it is suspended even a meter or less above the seafloor, which demonstrates that they are completely adapted to feeding on material that lies on the seafloor.

The speed with which food is found by deep-ocean scavengers after it reaches the seafloor indicates fierce competition for food, because food does not decompose rapidly at such depths. Bacterial decomposition is inhibited by high pressures, so food items that fall to the deep-ocean floor would decompose only very slowly if they were not immediately consumed. Inhibition of bacterial decomposition by high pressure was first discovered when the research submersible *Alvin* sank unexpectedly in more than 1500 m of water. A lunch box containing an apple and a bologna sandwich was inside the submersible when it sank. A year later, when *Alvin* was recovered, these food items were wet but almost undecomposed. They did decompose within weeks after their return to the surface, despite being refrigerated. Inhibition of bacterial decomposition by high pressures has been confirmed by a number of experiments conducted since the *Alvin* discovery.

HYDROTHERMAL VENTS

Until 1977, it was thought that all areas of the abyssal oceans werUntil 1977, it was thought that all areas of the abyssal oceans were biologically impoverished because of the limited availability of food that rains down from above. However, in 1977 the research submersible *Alvin* made a number of dives on the Galápagos Ridge that would change those ideas. The purpose of the dives was to study the geology and chemistry at this **oceanic ridge**. The researchers were looking for evidence that the high heat flow through the seafloor at the center of the ridge creates hydrothermal circulation. In hydrothermal circulation, seawater sinks through sediments or cracks in rocks of the seafloor and is heated, convected upward, and vented to the water column to be replaced by more seawater drawn through the rocks and sediments (Fig. 15-19a, Chap. 6). The heat comes from the upwelling **magma** and cooling volcanic rocks beneath the seafloor.

The researchers found much more than they expected. In fact, their findings may represent one of the most surprising and profound scientific discoveries ever made. They found not only hydrothermal vents, but also dense communities of marine organisms surrounding those vents. The communities include **tube worms**, clams, mussels, and many other invertebrates, most of which belonged to previously unknown species and many of which were very large in comparison with similar known species. The biomass in these vent communities is hundreds of thousands of times greater than that in any other community at comparable

depths in the ocean. However, even this finding of abundant oases of life in the "desert" of the abyss was to prove less surprising than the subsequent discovery that these communities do not depend on photosynthesis. In fact, they were found to be dependent on chemosynthesis for primary production of their food.

Hydrothermal Vent Environments

Initially, hydrothermal vents were thought to be rare and to occur only on fast-spreading oceanic ridges. We now know that hydrothermal vents and their associated biological communities are present in many locations, dispersed irregularly along the oceanic ridges in all oceans. Vents have even been found on the ultraslow-spreading Gakkel Ridge in the Arctic Ocean.

Vents have also been found on the submerged volcanoes at island arc **subduction zones** such as the Mariana Arc. These **back-arc** volcano vents are especially interesting to scientists because many are at much shallower depths than the oceanic ridge vents. The shallower depth makes them much easier to study, and the fluids they discharge are dispersed in the upper layers of the oceans, where they may have greater immediate effects on marine species that live in, or migrate periodically to, the photic zone. Some estimates now suggest that vents are abundant enough that a volume of ocean water equal to the entire volume of the world oceans may be processed through high-temperature vents about every 10 million years, which is a relatively short period in geological time.

Each vent differs from the others in terms of the temperatures and chemical characteristics of the water it discharges. Two general types of vents are known to occur along the oceanic ridge axis. Vents of the first type, called black smokers, discharge hot water, usually about 360°C (but can be up to about 460°C) The second type of vent, called white smokers discharges somewhat cooler water (about 260 to 300°C), usually at flow rates lower than those at black smokers.

The water discharged by black smokers contains no oxygen or nitrate but has high concentrations of hydrogen sulfide and of certain metals, including iron (Fe) and manganese (Mn; **Fig. 15-19**). As the superhot water is discharged into cold, oxygenated seawater, it does not vaporize because of the high pressure. However, as it cools and mixes with oxygenated seawater, metal sulfides are precipitated to form a cloud of tiny black particles. This cloud gives the black smokers the appearance of a dirty smokestack and hence their name. As the black smoker continuously disgorges, precipitated metal sulfides are deposited in the area around the vent exit and may help to construct a chimney at the vent outlet that can be up to 20 m high and several meters wide (**Fig. 15-19b**). The deposits formed at these vents are rich in many metals such as copper, zinc, gold, silver and lead with the quantities of these metals varying with temperature and other characteristics of different vents. These deposits are commercially valuable because the sulfide deposits are rich in these metals and they are now often called seafloor massive sulfide (SMS) deposits (**Chap. 2**). Many of the metal sulfide ores mined on land today are believed to have originated in hydrothermal vent environments and then to have been scraped off and added to the continents at subduction zones (**Chap. 4**).

White smokers were not discovered until 2000. Unlike black smokers these vents are not located along the ridge axis. Instead they lie on the flank of the ridge, where the underlying rock is about 1.5 million years old. The fluids discharged at white smokers are cooler, have a higher pH, contain less sulfide but more silica, calcium, and magnesium than fluids discharged from black smokers. When these fluids are discharged and mix with seawater, calcium, magnesium, and other sulfates are precipitated out and deposited to form chimneys much like those at black smokers. However, some of these chimneys can be up to about 60 m high, much taller than black smoker chimneys. The populations of larger animals, such as crabs, are much less abundant at these vents than are often found at black smokers. However, the white smoker vents do support abundant microbial communities.

Biological Communities Associated with Hydrothermal Vents

Although individual species vary, biological communities that surround ridge axis black smoker hydrothermal vents in the Atlantic, Pacific, and Indian Oceans are composed of generally similar species, and similar communities form in distinct zones around the vent.

At many of the Pacific vents, numerous giant tube worms and clams (**Fig. 15-20**) live closest to the vent. Other invertebrates, such as one or more species of limpets, shrimp, and scale worms, are present but less abundant. Farther from the vent are other plume worms, crabs, amphipods, other shrimp species, and several species of snails. Still farther from the vent are a wide variety of hydroids, species of worms, shrimp, anemones, and snails that are different from those closer to the vent. Many of these species are filter feeders, and others are predators. The biomass decreases progressively and rapidly with distance from the vent, and the more normal sparse fauna of the deep seafloor are present a few tens of meters from the vent.

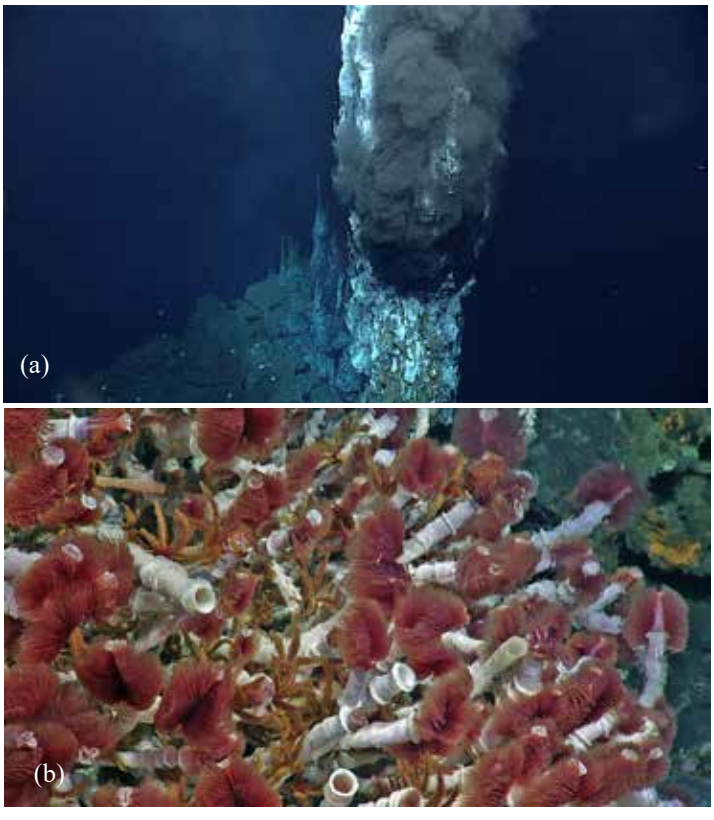


FIGURE 15-20. Hydrothermal vent communities support many species that are not found elsewhere. (a) A typical biological community near a black smoker, like the one seen here, includes tube worms, crabs, mussels, and other invertebrates. (b) One of the most important members of most hydrothermal communities is the tube worm *Riftia pachyptila*, which can be a meter or more in length and which sustains itself by feeding on symbiotic chemosynthetic bacteria.

More than 590 new species have been identified in the hydrothermal vent fauna, representing more than 20 new **families** and more than 100 new genera (plural of genus) and these numbers continue to climb steadily as new species are found at newly discovered vent areas. The discovery of this bewildering array of new species is unique in the history of biological science, rivaled only by the findings of the *Challenger* expedition in the 1870s (**Chap. 2**).

The biomass of many Pacific hydrothermal vent communities is dominated by the giant tube worm, *Riftia pachyptila*, a very strange creature (**Fig. 15-20b**). This species has no mouth and no digestive system, but it can grow to several centimeters in thickness and more than 1 m in length. Like the clams that live in the same region near the vents, it has red flesh and blood. Both species get their red color from hemoglobin in their blood, the same oxygen-binding molecule that is present in human blood.

The food source for the giant tube worm is apparently a population of chemosynthetic bacteria that it cultivates within its body in a symbiotic association similar to that between corals and zooxanthellae. The bacteria oxidize sulfide as an energy source to chemosynthesize organic matter (**Chap. 12**), and the tube worm assimilates either the waste products of this synthesis or the bacterial biomass itself, or both. This partnership is phenomenally successful, because the tube worms apparently grow very quickly. The tube worm also has a unique **enzyme** that is incorporated in its tissues, particularly in its surface tissues. The enzyme detoxifies hydrogen sulfide and protects the hemoglobin that carries oxygen needed for the worm to **respire**. However, this enzymatic protection is carefully adapted to allow a route by which the sulfide can be brought from outside the worm into the part of its body where the chemosynthetic bacteria reside.

Although it is certain that some hydrothermal vent species other than the tube worm have similar associations with chemosynthetic bacteria or **archaea** to provide a portion of their food, most species within the hydrothermal vent community are probably filter feeders. Hence, the bulk of their food must come from suspended particles. The source of these particles appears to be chemosynthetic bacteria and archaea that grow in profusion in the mouth of the vent and deep within the sediments and rocks of the seafloor. Clumps of the microbial biomass are broken loose periodically by the flow of water through the vent. The clumps fragment to form suspended particles that can be captured by the filter feeders. The concentration of these particles quickly declines with distance from the vent as the plume disperses and large particles are deposited.

Unanswered Questions about Hydrothermal Vents

Many questions about hydrothermal vents remain unanswered, not only about the abundance, geographic distribution, and physical/chemical characteristics of the vents, but also about the species that make up vent communities. For example, we do not know how the chemosynthetic bacteria or archaea can survive and grow at temperatures in excess of several hundred degrees. Also we do not fully understand how these species are able to survive the trip across many kilometers of abyssal ocean to colonize new hydrothermal vents. Most vent species are adapted to higher temperatures and different water chemistry than are present in the abyssal ocean through which they would have to travel to colonize a new vent. Thus, vent species, or at least their eggs or larvae, must be able to survive a much greater range of environmental conditions than do most of the living organisms with which we are more familiar.

Most known vents are scattered along the ridges, some separated by substantial distances, and each may operate for a limited period, perhaps less than 20 years or so. However, observations have shown that new vents may be colonized within months or years. Bottom currents that could carry eggs and larvae on some ridges may tend to follow the ridge, but new vents may be upcurrent of the old ones. Thus, the physical mechanisms by which new vents are colonized, which also likely differ for individual species, may be complex and are likely aided by eddies formed as tidal currents flow over the elevated oceanic ridge topography. Also, recent findings have revealed that the types of species present at the vents are influenced greatly by the chemical and physical conditions at each vent so that, contrary to earlier expectations that new vents would be colonized by fauna from nearby vents, they may be colonized by completely different fauna.

Many vent species produce extraordinarily large numbers of larvae. One possible explanation for the very large size of some vent species in comparison with similar species elsewhere in the oceans may be a need to produce very large numbers of larval offspring. It has been suggested that, in some species, these larvae may have an arrested development phase, so they could be transported by ocean currents for many decades or even centuries before encountering a new vent to colonize. Eggs and larvae of vent species may rise into shallower layers of the ocean, perhaps entrained in megaplumes of water heated slightly above ambient temperature that are known to occur in hydrothermal vent areas. In the shallower layers, larvae may be widely distributed before settling to the seafloor for a chance encounter with a new vent. There is also evidence that the partially decomposed carcasses of whales and other large mammals that fall to the ocean floor, or other slowly decomposing organic matter such as wood that reaches the deep seafloor, may be ideal sulfide-containing environments to support vent species during a "stopover" while being dispersed across the deep oceans. Any, all, or none of these mechanisms may be involved in new vent colonization.

Genetic analysis of vent species has begun to reveal the rates and patterns of colonization of vents in different parts of the world ocean. Genetic and other studies of many more species from many more vents, exploration of the vast areas currently unsearched to catalog the distribution of hydrothermal vents worldwide, and studies to obtain much better knowledge of the current patterns, mixing, and dispersion in the deep oceans are all needed to enable us to unravel the mysteries of hydrothermal vent species life cycles. We are likely to have more surprises as these investigations proceed.

Other Chemosynthetic Communities

Since the discovery of hydrothermal vents on the oceanic ridges, several chemosynthetic communities have been discovered in other locations in the deep sea, as well as in shallow-water **anoxic** environments such as marshes. Chemosynthetic bacterial mats have been found at the base of the **continental slope** off the west coast of Florida. These bacteria use hydrogen sulfide in water that seeps out from the limestone underlying sediments of the continental slope. In and around these mats is a diverse community of animals that may obtain some or all of their food from the chemosynthetic bacteria.

Chemosynthetic communities have also been found at oil and gas seeps, also known as cold seeps, at a depth of 600 to 700 m in the Gulf of America (Golfo de México) south of Louisiana and

elsewhere. These communities use either hydrogen sulfide and/or **hydrocarbons** as an energy source for their primary production. In the Juan de Fuca subduction zone and in other subduction zones, methane in **pore waters** squeezed out of the buried sediments provides the energy source for other chemosynthetic bacteria.

In addition to these ocean chemosynthetic communities, chemosynthetic communities that are generally dominated by archaea have been found to exist deep within the rocks of the Earth's **crust**. Studies of the organisms able to live and reproduce in such extreme environments have assumed an important role in the search for the origins of life on the Earth and in the search for life or evidence of life in the past on other planets and moons of the solar system.

CHAPTER SUMMARY

Communities and Niches.

Species within an ecosystem are distributed nonuniformly, but they often cluster into communities with common characteristics. Each species has a survival niche that is defined by the ranges of environmental variables, such as salinity, temperature, turbidity, and nutrient concentrations, within which it can survive. Within its survival niche, each species has a fundamental niche within which it can survive and reproduce successfully. In some instances, a species may not occupy all of its fundamental niche, as a result of competition by other species.

Coral Reefs.

Reef-building corals grow only on the seafloor in the photic zone of tropical waters between about 30°N and 30°S. These corals house photosynthetic zooxanthellae within their tissues. Reef-building corals obtain some food from their zooxanthellae. Productivity is higher in coral reefs than in other, nutrient-poor tropical marine areas because nutrients are recycled between coral and zooxanthellae, the reefs cause some upwelling, and most organisms in the reef community are residents and do not export nutrients. High turbidity adversely affects corals by reducing photosynthesis by zooxanthellae and requiring the corals to expend energy to clear away deposited particles.

Primary production in coral reef communities is performed by zooxanthellae and by benthic microalgae and macroalgae, many of which are calcareous algae whose hard parts help to build the reef. A typical coral reef has a sheltered lagoon where coral growth is patchy because of variable salinity and turbidity and where many detritus, suspension, and deposit feeders are present. At the lagoon's seaward edge is a reef flat swept generally free of sediment by waves where coral growth is active and consists mainly of encrusting forms. Invertebrates live in holes and grooves cut in the reef flat.

Farther seaward, there is sometimes a low sandy island and usually an irregular ridge formed from broken coral thrown up periodically by waves and cemented by calcareous algae. Seaward of the ridge is the buttress zone, which may have a gradual to nearly vertical downward slope. It is scoured by waves to about the 20 m depth, characterized by massive robust corals, and often cut across by grooves in which there is little coral growth. Farther seaward, at depths below the reach of wave action, delicate forms of coral, including soft corals, grow in abundance.

Kelp Forests.

Kelp forests grow where the seafloor is stable, preferably rocky, and within the photic zone, and where the water is cold and rich in nutrients. Kelp fronds grow as much as half a meter a day, and kelp primary productivity is very high. Kelp reproduce both vegetatively and by releasing spores to the water column. Kelp forests provide shelter and habitat for many species of fishes and invertebrates. Only a few of these species eat kelp itself, but kelp releases large quantities of detritus that enter the food chain when it is consumed by detritus feeders.

Sea urchins eat kelp, and sea otters eat sea urchins. In the eighteenth and nineteenth centuries, hunting of sea otters off California reduced sea otter populations and thus their predation on sea urchins. The increased sea urchin populations ate more kelp and destroyed the forest in many areas. Sea otters are now protected, and kelp is slowly returning.

Rocky Intertidal Communities.

Species of the rocky intertidal zone are exposed to the atmosphere part of the time. They are subjected to variable conditions of temperature, water and air exposure, salinity, oxygen concentration, and pH, and they are vulnerable to birds and land predators. The rocky intertidal community is separated into four zones, distinguished by degree of exposure to air. The supralittoral zone is above high water and exposed permanently to air but is reached periodically by spray. It supports lichens, encrusting algae, grazers (including marine snails and limpets), and scavengers, primarily isopods. The high-tide zone is covered in water only during high tides and supports encrusting algae, tough attached macroalgae, filter-feeding barnacles, and periwinkle and limpet species different from those in the supralittoral zone. The middle-tide zone is covered and uncovered by water during most or all tidal cycles, has sparse macroalgae because of competition from mussels and barnacles, and supports a diverse community of invertebrates. The low-tide zone is uncovered only during the lowest tides and supports macroalgae and many species of invertebrates and fishes. The upper limit of each zone is generally determined by tolerance of the species to air exposure and other environmental factors, whereas the lower limit is generally determined by competition with other species.

Tide pools undergo substantial changes in temperature, salinity, and other factors because they are small and isolated from mixing with ocean water for part of the tidal cycle. Because small tide pools tend to have greater changes than large tide pools, they support fewer species, and these species are more tolerant.

Sargasso Sea.

Extensive rafts of *Sargassum*, a macroalga, float on the surface of the Sargasso Sea, which is the interior of the North Atlantic Gyre. Nutrients are extremely limited in this region, and the large Sargassum biomass develops because it is very long-lived and currents tend to concentrate and retain it within the center of the gyre. A variety of small fish and invertebrate species live in the *Sargassum*, many of which are unique to this community. The animal biomass is very small in relation to the algal biomass, and there are few grazers because primary productivity is low and any food that is grazed is therefore replaced slowly.

Polar Regions.

Polar regions have extreme seasonal variation in light availability and ice cover, and generally cold surface waters. River runoff or ice exclusion creates strong haloclines in places, but in all other polar waters, vertical mixing due to storms is intense and nutrients are abundant. Microscopic ice algae are important in both polar regions. They grow rapidly during the ice-melting

season. Phytoplankton bloom during only a few weeks of summer when sufficient light is available. Many animal species are adapted to the short primary production period and the large year-to-year variability by having a long life span, maturing late, bearing only a few offspring each year, and storing food energy as fat to survive the winter.

Beyond the Sun's Light.

Below the photic zone, food sources are limited to particulate detritus, carcasses that fall through the water column, and prey species. However, many species migrate vertically from the aphotic zone to the mixed layer, usually at night, to feed. Species that migrate vertically become less common with increasing depth. Many deep-sea animals are adapted to survive on very infrequent meals, and some are able to swallow prey larger than themselves. High pressures inhibit bacterial decomposition, which helps ensure that detrital food particles remain available.

Hydrothermal Vents.

Hydrothermal vents located along oceanic ridge axes and on submerged volcanoes of volcanic island arcs discharge seawater that has percolated through the seafloor and been heated by magma or cooling magmatic rock. The effluent from black smokers, which discharge the hottest water (270 to 380°C), has no oxygen and high concentrations of hydrogen sulfide and metal sulfides. Chemosynthetic bacteria use the sulfides to fuel primary production. Away from the ridge axis vents discharge cooler water and are called white smokers because they discharge much lower concentrations of metal sulfides, and instead contain abundant precipitated white particles of silica, and calcium and magnesium sulfates and carbonates.

Communities at hydrothermal vents are composed of many species that are unique to these environments. At many Pacific vents, the community closest to the vent is dominated by giant tube worms and clams that feed on chemosynthetic bacteria that they cultivate within their bodies. Various species of other invertebrates occupy zones at different distances from the vent. Most are filter feeders that live on clumps of bacteria and archaea grown at the vent or beneath the seafloor and sloughed off to become suspended particles. Food availability declines rapidly with distance from the vent. Many questions remain about these communities, including how they cross large distances of abyssal ocean to colonize new vents.

White smoker vents lie on the oceanic ridge flank, discharges fluids with little metal sulfide but instead particles rich in calcium and magnesium. Additionally, chemosynthetic communities that use methane or other hydrocarbons as their energy source are present in a few locations in the oceans.

KEY TERMS

You should be able to recognize and understand the meaning of all terms that are in boldface type in the text. All of those terms are defined in the Glossary. The following are some less familiar key scientific terms that are used in this chapter and that are essential to know and be able to use in classroom discussions or on exams.

benthic
biomass
blue-green algae
brittle stars
buoyant
calcareous
carcinogenic
carnivores
climate
communities
contamination
continental shelves
continental slope
convergence
copepods
coral reef
corals
crust
crustaceans
currents
decomposers
deposit feeders
detritus
diffuse
dinoglagellate
diversity
downwelling
ecologists
ecosystem
eddies
encrusting microalgae
environment
enzyme
families
fauna
filter feeders
flora
food chain
food web
fringing reef
front
fundamental niche
genetic
genus
grain size
grazers
gyre
habitat
halocline
hard parts
herbivores
hermatypic corals
hermit crabs
high-tide line
high-tide zone
humidity
hydrocarbons
hydroids
ice exclusion
invertebrate
isopods
kelp
krill
lagoon
larvae
low-tide line
low-tide zone
macroalgae
magma
mangrove
marginal seas
marine mammals
micronutrients
middle-tide zone
mollusks
mutagenic
niche
nudibrachs
nutrient
oceanic ridge
pelagic
pH
photic zone
photosynthesize
phytoplankton
pore waters
primary productivity
reef
reef flat
reef terrace
residence time
respire
resuspended
rocky intertidal zone
runoff
salinity
scavengers
scuba
sea cucumbers
sea fan
sea stars
sea urchin
sedimentation rates
sediments
soft corals
soluble
species
sponges
spores
spring tides
storm surges
subduction zones
submersibles
subtropical gyre
supralittoral zone
survival niche
suspended sediment
suspension feeders
symbiotic
teratogenic
thermocline
tidal range
tide
tide pool
topographic
tube worms
turbulence
turbidity
turbidity currents
upwelling

latitudes
lava
leeward
lichens
limestone
limpets
viviparous
western boundary currents
windward
zooplankton
zooxanthellae

STUDY QUESTIONS

1. Why don't species live in all locations where their fundamental-niche requirements are fulfilled?
2. Why do coral reefs sustain a very large variety of species, and why is the biomass of coral reef ecosystems greater than that of other ecosystems in tropical waters?
3. What factors determine the types of corals that live on different parts of a coral reef?
4. Describe the locations and environmental conditions that are appropriate for the development of kelp forests. Contrast these with the locations and environmental conditions appropriate for the development of coral reefs.
5. Why must rocky intertidal species be more stress-tolerant than many other marine species?
6. Why are rocky intertidal communities distributed in distinct bands of different species that follow depth contours?
7. Why does the Sargasso Sea sustain a community of photic-zone organisms that are different and distinct from those found elsewhere in the oceans?
8. What are the principal differences in physical characteristics between the Arctic Ocean and the ocean around Antarctica, and how do they affect primary production and species composition?
9. Why does the species composition of hydrothermal vent communities change rapidly with distance from the vents?

CRITICAL THINKING QUESTIONS

1. Sea otters are increasing in numbers in California coastal waters, but one of their favorite foods, abalone, is heavily harvested, so they may rely more on urchins for their food supply. Describe what you think will happen to the kelp forests over the next several decades as a result of these changes, and how these changes will affect other species in the ecosystem.
2. Describe the feeding, hunting, defensive, and reproductive characteristics that are desirable for carnivorous species that live in the Sargassum community. Compare and contrast these characteristics with the desirable characteristics for a carnivorous benthic species that lives in the deep oceans. Explain each of the differences.
3. Hydrothermal vent communities throughout the oceans are separated, sometimes by substantial distances. However, some of the same species are found at many of the vents, regardless of their location. In addition, chemosynthetic bacteria species that are identical or very closely related to those found at the hydrothermal vents on oceanic ridges have been found in hydrothermal vent environments at the bottom of Crater Lake, Oregon, and Lake Baikal, Russia.
   (a) What are the possible reproductive strategies that could explain these observations?
   (b) Hypothesize ways that chemosynthetic organisms could be transported between their present locations and the locations of new vents or the locations of new lakes similar to Crater Lake and Lake Baikal.
   (c) What studies do you think would be needed to prove or disprove your hypotheses?
4. If the Earth's climate warms and both polar ice caps melt away completely, which ecosystem is likely to be changed more, the Southern Ocean ecosystem or the Arctic Ocean ecosystem? Explain the reasons for your answer.
5. The temperature and salinity of the abyssopelagic environment vary little with latitude or from ocean to ocean. This environment is also uniformly dark and the pressure uniformly high. Does this mean that, if we were able to sample every species in a cubic kilometer of deep-ocean water, we could be certain that we had sampled a large majority of all abyssopelagic species that exist in the oceans? Why or why not?
6. Coral reefs and kelp forests both have high species diversity compared to some other ocean ecosystems. What are the possible reasons for this high diversity?

CRITICAL CONCEPTS REMINDERS

CC9 The Global Greenhouse Effect: Perhaps the greatest environmental challenge faced by humans is the prospect that major climate changes may be an inevitable result of our burning fossil fuels. The burning of fossil fuels releases carbon dioxide and other gases into the atmosphere where they accumulate and act like the glass of a greenhouse trapping more of the sun's heat. .

CC14 Phototrophy, Light, and Nutrients: Phototrophy (which includes photosynthesis) and chemosynthesis are two processes by which simple chemical compounds are made into the organic compounds of living organisms. Photosynthesis depends on the availability of carbon dioxide, light, and certain dissolved nutrient elements including nitrogen, phosphorus, and iron. Chemosynthesis does not use light energy, but instead depends on the availability of chemical energy from reduced compounds, which occur only in limited environments where oxygen is depleted.

CC16 Maximum Sustainable Yield: The maximum sustainable yield is the maximum biomass of a fish species that can be depleted annually by fishing but that can still be replaced by reproduction. This yield changes unpredictably from year to year in response to the climate and other factors. The populations of many fish species worldwide have declined drastically when they have been overfished (beyond their maximum sustainable yield) in one or more years when that yield was lower than the average annual yield on which most fisheries management is based.

CC17 Species Diversity and Biodiversity: Biodiversity is an expression of the range of genetic diversity; species diversity; diversity in ecological niches and types of communities of organisms (ecosystem diversity); and diversity of feeding, reproduction, and predator avoidance strategies (physiological diversity), within the ecosystem of the specified region. Species diversity is a more precisely-defined term and is a measure of the species richness (number of species) and species evenness (extent to which the community has balanced populations with no dominant species). High diversity and biodiversity are generally associated with ecosystems that are resistant to change.

CC18 Toxicity: Many dissolved constituents of seawater become toxic to marine life when the concentrations go above their natural amount. Some synthetic organic chemicals are especially significant because they are persistent and may be bioac-

cumulated or biomagnified.

REFERENCES

Figure 15-1 – Segar, D., and E. Stamman Segar, 1997: Deacon's Reef in Papua New Guinea.

Figure 15-3 – Adapted from Lerman, M., 1986: *Marine Biology: Environment, Diversity, and Ecology*. Addison-Wesley, 534 pp. – Adapted from Chapmen, V. J., Ed., 1977: *Wet Coastal Systems*. Elsevier Science Publishing, 424 pp.

Figure 15-5a – Segar, D., and E. Stamman Segar, 1997: Sea cucumbers (family Synaptidae, Indonesia.

Figure 15-5b – Segar, D., and E. Stamman Segar, 1997: Rhinoceros, or horned, sea star (*Protoreaster nodosus*, Papua New Guinea).

Figure 15-5c – Segar, D., and E. Stamman Segar, 1997: Urchins (*Astropyga radiata*, Indonesia).

Figure 15-5d – Segar, D., and E. Stamman Segar, 1997: Sand dollars (*Clypeaster sp.*, Indonesia).

Figure 15-5e – Segar, D., and E. Stamman Segar, 1997: *Acropora sp.* (Papua New Guinea).

Figure 15-5f – NOAA, 2023: Elkhorn coral, accessed 23 March 2026, https://www.fisheries.noaa.gov/species/elkhorn-coral.

Figure 15-6 – Segar, D., and E. Stamman Segar, 1997: Palm trees and other plants on this island on a fringing reef in Fiji.

Figure 15-7 – Segar, D., and E. Stamman Segar, 1997: Black coral colony (probably *Cirrhipathes sp.*) with a longnose hawkfish (*Oxycirrhites typus*, Papua New Guinea).

Figure 15-8a,b – Adapted from Estes, J. A., and J. F., Palmisano, 1974: Sea otters: Their role in structuring nearshore communities. *Science*, **185**, 1058–1060, https://doi.org/10.1126/science.185.4156.1058.

Figure 15-8c – Segar, D., and E. Stamman Segar, 1997: Canopy and kelp forest in Monterey, California.

Figure 15-9a – Segar, D., and E. Stamman Segar, 1997: Small brown cup corals (*Paracyathus stearnsii*, California).

Figure 15-9b – Segar, D., and E. Stamman Segar, 1997: Rose anemone (*Tealia lineata*, California).

Figure 15-9c – Segar, D., and E. Stamman Segar, 1997: Northern kelp crab (*Pugettia producta*, California).

Figure 15-9d – Segar, D., and E. Stamman Segar, 1997: Kelp shrimp (Monterey, California).

Figure 15-9e – Segar, D., and E. Stamman Segar, 1997: Sea stars of many species (Monterey, California).

Figure 15-9f – Segar, D., and E. Stamman Segar, 1997: Horned nudibranch (*Hermissenda crassicornis*, California).

Figure 15-9g – Segar, D., and E. Stamman Segar, 1997: Quillback rockfish (*Sebastes maliger*) and copper rockfish (*Sebastes caurinus*, California).

Figure 15-10a – Segar, D., and E. Stamman Segar, 1997: Sea otters (*Enhydra lutris*, California).

Figure 15-10b – Segar, D., and E. Stamman Segar, 1997: Red urchin (*Strongylocentrotus sp.*, California).

Figure 15-10c,d – Adapted from Estes, J. A., and J. F., Palmisano, 1974: Sea otters: Their role in structuring nearshore communities. *Science*, **185**, 1058–1060, https://doi.org/10.1126/science.185.4156.1058.

Figure 15-13a – Segar, D., and E. Stamman Segar, 1997: Black turban snails (*Tegula funebralis*, Monterey, California).

Figure 15-13b – Segar, D., and E. Stamman Segar, 1997: Limpet (order Archaeogastropoda, California).

Figure 15-13c – Segar, D., and E. Stamman Segar, 1997: Buckshot barnacles, probably primarily *Chthamalus sp.*, with some interspersed *Balanus glandula*.

Figure 15-13d – Segar, D., and E. Stamman Segar, 1997: Lined chiton (probably *Tonicella lineata*, California).

Figure 15-13e – Segar, D., and E. Stamman Segar, 1997: Dense bed of California mussels (*Mytilus californianus*, Monterey, California).

Figure 15-13f – Segar, D., and E. Stamman Segar, 1997: Green algae south of San Francisco, California

Figure 15-13g – Segar, D., and E. Stamman Segar, 1997: Hermit crab (*Pagurus sp.*, California).

Figure 15-14 – Brownlee, E., 2024: Mussel beds in Rialto Beach, WA. With permission.

Figure 15-15a – NOAA OER, 2002: Lines of sargassum. Islands in the Sea 2002, accessed 23 March 2026, https://oceanexplorer.noaa.gov/explorations/02sab/logs/aug09/media/lines.html.

Figure 15-15b – NOAA OER, 2002: Small mass of sargassum weed. Islands in the Sea 2002, accessed 23 March 2026, https://oceanexplorer.noaa.gov/explorations/02sab/logs/aug09/media/weeds.html.

Figure 15-16a – Segar, D., and E. Stamman Segar, 1997: Crabeater seals (*Lobodon carcinophagus*, Antarctic Peninsula).

Figure 15-16b – Segar, D., and E. Stamman Segar, 1997: Antarctic fur seals (*Arctocephalus gazella*, South Georgia Island).

Figure 15-16c – Segar, D., and E. Stamman Segar, 1997: Leopard seal (*Hydrurga leptonyx*, Antarctic Peninsula).

Figure 15-18 – NOAA OER: 2019: Dumbo octopus. 2019 Southeastern U.S. Deep-sea Exploration, accessed 23 March 2026, https://oceanexplorer.noaa.gov/image-gallery/welcome.html#cbpi=/okeanos/explorations/ex1907/dailyupdates/nov19/media/dumbo-octopus.html.

Figure 15-19a – Adapted from Detretskey, 2012: Hydrothermal vents. NSF, accessed 23 March 2026, https://www.nsf.gov/news/quakes-under-pacific-ocean-floor-reveal-unexpected.

Figure 15-19b – Adapted from Haymon, R. M., and Macdonald, K. C., 1985: The geology of deep-sea hot springs: Recently discovered hot springs burst from the seafloor in areas of active volcanism and deposit metal-rich minerals on the seabed. *Amer. Sci.*, **73**, 441–449. http://www.jstor.org/stable/27853397.

Figure 15-20a – NOAA OER, 2016: Black smoker, 2016 Deepwater Exploration of the Marianas. Accessed 23 March 2026, https://oceanexplorer.noaa.gov/multimedia/black-smoker/.

Figure 15-20b – NSF-OOI, 2015: Vibrant red tube worms, WHOI. Accessed 23 March 2026, https://interactiveoceans.washington.edu/beautifultubworms_phoemix-sdi1_2015-07-099_27_26_32240/.