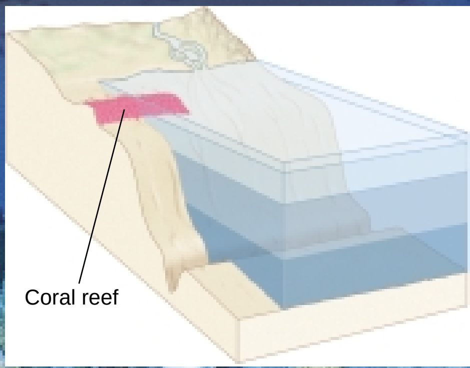
Chapter 14
Coral Reefs

An Indo-West Pacific coral reef.



THERE IS SOMETHING SPECIAL ABOUT tropical coral reefs. The warm, clear water, spectacular colors, and multitude of living things captivate almost everyone who sees a reef. Coral reefs rival that other great tropical community, the rain forest, in their beauty, richness, and complexity. Tropical rain forests and coral reefs are also similar in that the basic physical structure of both communities is produced by organisms. Both reef-building corals and the giant trees of a rain forest create a three-dimensional framework that is home to an incredible assortment of organisms. Coral reefs are such massive structures, in fact, that they must be considered not only biological communities but geological structures, the largest geological features built by organisms.

Oysters, polychaete worms, and red algae can also form reefs, and a deep-water coral (*Lophelia pertusa*) slowly builds mounds up to 30 m (100 ft) high on the northeast Atlantic sea floor. None of these features are as widespread, as large, or as structurally complex as tropical coral reefs.

The Organisms That Build Reefs

Coral reefs are made of vast amounts of **calcium carbonate ($CaCO_3$),** limestone, that is deposited by living things. Of the thousands of species in coral reef communities, only a fraction produce the limestone that builds the reef. The most important of these reef-building organisms, as you might guess, are corals.

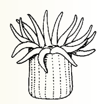
Reef Corals

"Coral" is a general term for several different groups of **cnidarians,** only some of which help build reefs (Table 14.1). In reef-building, or **hermatypic,** corals the **polyps** produce

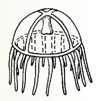
Cnidarians Animals in the phylum Cnidaria; they have radial symmetry, tissue-level organization, and tentacles with *nematocysts*, specialized stinging structures.

• *Chapter 7, p. 116*

Life stages of cnidarians:



Polyp The sessile, sac-like stage, with the mouth and tentacles on top.



Medusa The swimming, bell-like stage, with the mouth and tentacles underneath.

• *Chapter 7, p. 117*

Table 14.1

Major Groups of Corals and Related Cnidarians on Coral Reefs

COMMON NAME	IMPORTANCE AS REEF BUILDERS	NOTES
ANTHOZOANS (GROUP THAT INCLUDES SEA ANEMONES; LACK MEDUSA STAGE AND LIVE ONLY AS POLYPS)		
Scleractinian corals	The main reef builders	Produce a calcareous skeleton; nearly all have zooxanthellae.
Soft corals	Not reef builders	Common on coral reefs (Fig. 14.28); most have zooxanthellae but do not produce a rigid calcareous skeleton.
Organ-pipe corals (*Tubipora*)	Minor	Named for pipe-like structure of skeleton; have zooxanthellae and produce a calcareous skeleton.
Blue coral (*Heliopora*)	Significant in some places	Named for distinct blue color of skeleton; has zooxanthellae and produces a calcareous skeleton.
Gorgonians	Not reef builders	Sea fans (Fig. 7.10) and sea whips; hard skeleton is made mostly of protein and not calcareous; some have zooxanthellae.
Precious corals		Gorgonians with a pink, red, or gold calcareous skeleton used for jewelry; occur mainly in deep water rather than on coral reefs and do not contribute to reef growth; lack zooxanthellae.
Black corals	Not reef builders	Used to make jewelry and sometimes called "precious corals" but are a different group from gorgonian precious corals; hard skeleton is made of protein and is not calcareous; commonly occur in deep and cold surface waters as well as on coral reefs.
HYDROZOANS (GROUP THAT INCLUDES JELLYFISHES; HAVE BOTH MEDUSA AND POLYP STAGES BUT ARE SEEN ON REEF ONLY AS POLYPS)		
Fire corals (*Millepora*)	Significant in some places	Named because touching them produces a burning sensation from their powerful nematocysts; have zooxanthellae and produce a calcareous skeleton.
Lace corals	Insignificant	Named for delicate, branched colonies; lack zooxanthellae but produce a calcareous skeleton; commonly occur in deep and cold surface waters as well as on coral reefs.

calcium carbonate skeletons. Billions of these tiny skeletons build a massive reef. The most important reef builders are a group known as **scleractinian corals,** sometimes called the stony or "true" corals.

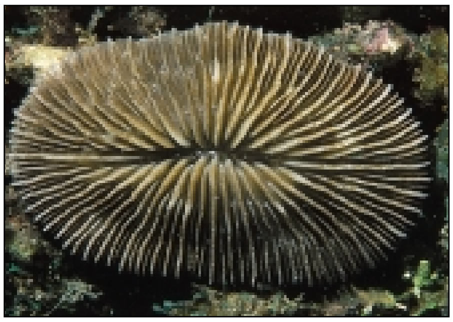
Nearly all reef-building corals contain symbiotic **zooxanthellae** (Fig. 14.1) that help the corals make their calcium carbonate skeletons. Corals can produce their skeletons without zooxanthellae but only very slowly, not nearly fast enough to build a reef. It is the zooxanthellae as much as the corals themselves that construct the reef framework, and without zooxanthellae there would be no reefs. Corals that do not help build reefs, or **ahermatypic** corals, often lack zooxanthellae.

The primary architects of coral reefs are reef-building corals that produce calcium carbonate skeletons with the help of symbiotic zooxanthellae.

The Coral Polyp You have to look closely to see the little polyps that build coral reefs. Coral polyps are not only small but deceptively simple in appearance. They look much like little sea anemones, consisting of an upright cylinder of tissue with a ring of tentacles on top (Figs. 14.2 and 14.3*b*). Like anemones and other cnidarians, they use their nematocyst-armed tentacles to capture food, especially zooplankton. The tentacles surround the mouth, the only opening to the sac-like gut.

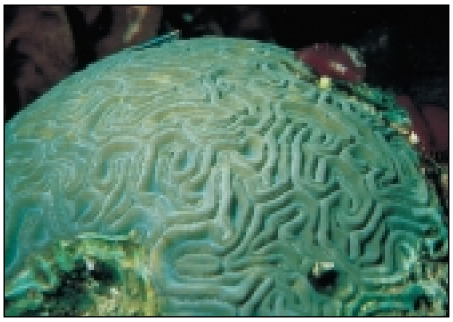
Most reef-building corals are colonies of many polyps, all connected by a thin sheet of tissue. The colony starts when a planktonic coral larva, called a **planula,** settles on a hard surface. Coral larvae generally do not settle on soft bottoms. Immediately after settling, the larva transforms, or **metamorphoses,** into a polyp. This single "founder" polyp, if it survives, divides over and over to form the colony. The digestive systems of the polyps usually remain connected, and they share a common nervous system (Fig. 14.4).

Figure 14.1 The microscopic, golden-brown zooxanthellae that pack these polyp tentacles help corals build reefs. They also occur in giant clams, some sea anemones (see Fig. 11.26), and other invertebrates. Cells in the white, bulbous tips of the tentacles are packed with nematocysts.



(a)

(b)



(c)

Figure 14.3 Coral polyps. (*a*) A few corals, like the mushroom coral (*Fungia*) from the Indo-West Pacific, consist of a single polyp. Most are colonies of many individual polyps. (*b*) In some of these, like the large-cupped boulder coral (*Montastrea cavernosa*) from the Caribbean, each polyp has its own individual cup, called a corallite. (*c*) In coral colonies like this brain coral (*Diploria*) from the Caribbean, meandering lines of polyps lie in a common corallite.

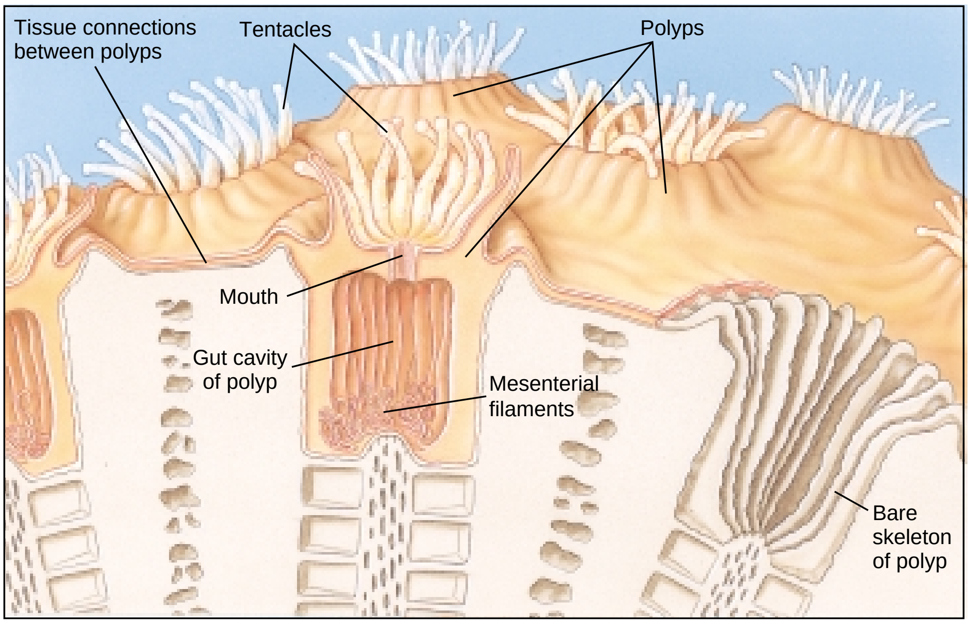


Figure 14.2 Cutaway view of one of the polyps in a coral colony and of the calcium carbonate skeleton underneath. The polyps are interconnected by a very thin layer of tissue.

Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.

- *Chapter 10, p. 222; Figure 10.21*

Zooxanthellae Dinoflagellates (single-celled, photosynthetic algae) that live within animal tissues.

- *Chapter 5, p. 95*

Symbiosis The living together in close association of two different species, often divided into *parasitism,* where one species benefits at the expense of the other; *commensalism,* where one species benefits without affecting the other; and *mutualism,* where both species benefit.

- *Chapter 10, p. 212*

Figure 14.4 The polyps in a coral colony are interconnected. If you touch an extended polyp, it will contract, and so will its neighbors, followed by their neighbors, and so on, so that a wave of contraction passes over the colony. In this colony of the coral *Goniopora lobata* the wave of contraction is moving up from the bottom.

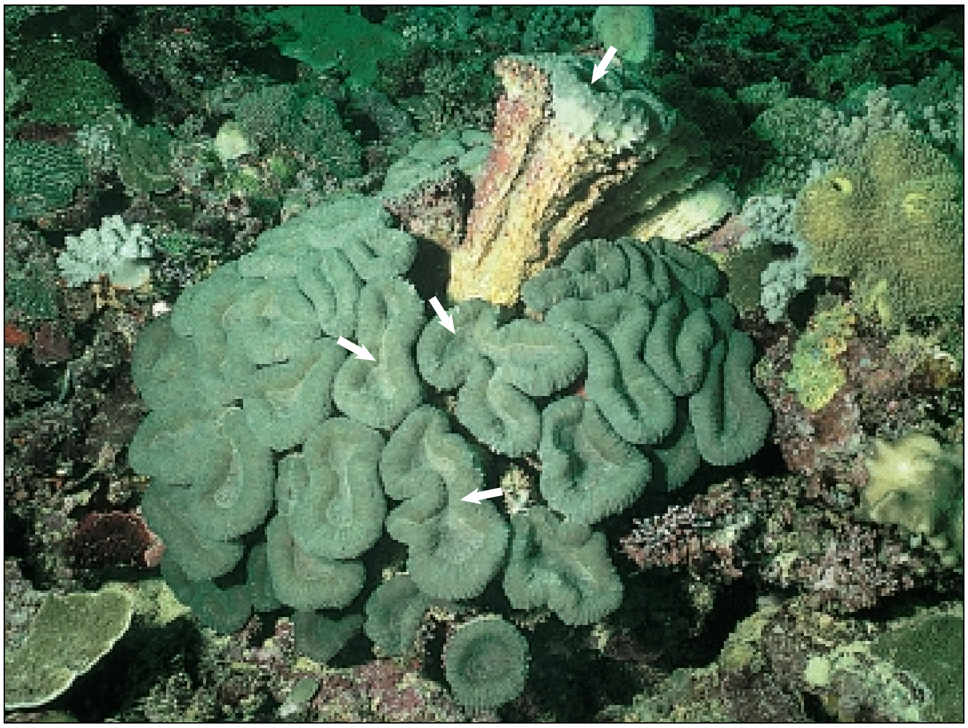


Figure 14.5 This coral (*Lobophyllia hemprichii*) shows particularly well how corals build up their skeleton. Each of the irregular rings (arrows) is a single polyp that has built up a column of calcium carbonate skeleton.

A few reef-building corals consist of only a single polyp (Fig. 14.3a).

Coral polyps lie in a cup-like skeleton of calcium carbonate that they make themselves. The polyps continually lay down new layers of calcium carbonate, building up the skeleton beneath them so that it grows upward and outward (Fig. 14.5). The skeleton forms nearly all of the bulk of the colony (Fig. 14.6) and can take many different shapes (Fig. 14.7). The actual living tissue is only a thin layer on the surface. It is the calcareous coral skeletons that form the framework of the reef.

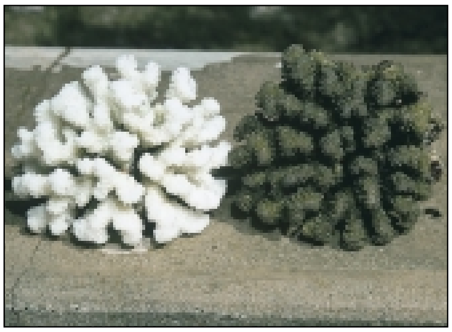


Figure 14.6 The calcium carbonate skeleton makes up most of a coral colony. A live colony (*Pocillopora verrucosa*) is shown on the right. On the left is a colony with the living tissue removed. The main difference is the color; the live part is only a thin layer of tissue on the surface. The "corals" sold in shell and aquarium shops are actually only the skeletons of live corals that were taken from the reef and bleached. Some reefs have been devastated by the collectors who supply these shops in order to feed their families.

Coral Nutrition Zooxanthellae nourish the host coral as well as help it deposit its skeleton. They perform **photosynthesis** and pass some of the organic matter they make on to the coral. Thus, the zooxanthellae feed the coral from the inside. Many corals can survive and grow without eating, as long as the zooxanthellae have enough light.

Although corals get much of their nutrition from their zooxanthellae, most eat when they get the chance. They prey voraciously on zooplankton. The billions of coral polyps on a reef, along with all the other hungry reef organisms, are very efficient at removing zooplankton brought in by currents. Indeed, the reef has been called a "wall of mouths."

Coral polyps catch zooplankton with their tentacles or in sheets of mucus that they secrete on the colony surface. Tiny, hair-like cilia gather the mucus into threads and pass them along to the mouth. Some corals hardly use their tentacles and rely on the mucus method. A few have even lost their tentacles altogether.

Corals have still other ways of feeding themselves. There are a number of long, coiled tubes called **mesenterial filaments** attached to the wall of the gut (Fig. 14.2). The mesenterial filaments secrete digestive enzymes. The polyp can extrude the filaments through the mouth or body wall to digest and absorb food particles outside the body. Corals also use the mesenterial filaments to digest organic matter from the sediments. In addition, corals can absorb **dissolved organic matter (DOM)** (see "The Trophic Pyramid," p. 216).

Corals nourish themselves in a remarkable number of ways. Zooxanthellae are the most important source of nutrition. Corals can also capture zooplankton with tentacles or mucus nets, digest organic material outside the body with mesenterial filaments, or absorb dissolved organic matter (DOM) from the water.

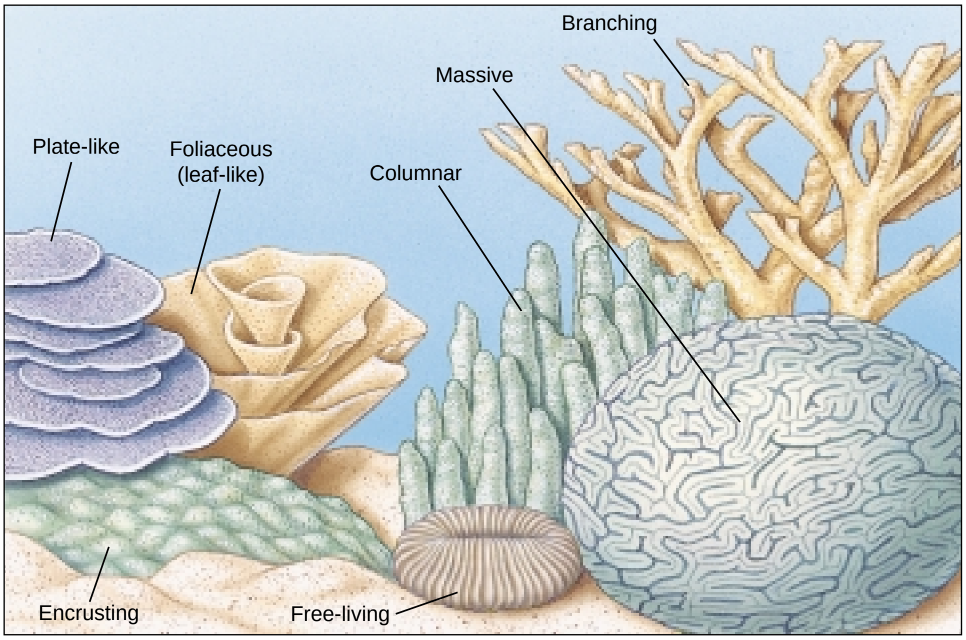


Figure 14.7 Corals come in a multitude of shapes, or growth forms.

Other Reef Builders

Although they are the chief architects, corals cannot build a reef alone. Many other organisms help make a coral reef. The most important of these are algae, which are essential to reef growth. In fact, some marine biologists think that coral reefs should be called "algal reefs" or, to be fair to both, "biotic reefs." One reason for this is that zooxanthellae, which are algae, are essential to the growth of corals. There are other algae, however, that also have key roles in building the reef. Encrusting **coralline algae** (*Porolithon, Lithothamnion*) grow in rock-hard sheets over the surface of the reef. They deposit considerable amounts of calcium carbonate, sometimes more than corals, and thus contribute to reef growth. Coralline algae are more important on Pacific reefs than Atlantic ones.

Encrusting coralline algae not only help build the reef but also help keep it from washing away. The stony pavement formed by these algae is tough enough to withstand waves that would smash even the most rugged corals. The algae form a distinct ridge on the outer edge of many reefs, especially in the Pacific. This **algal ridge** absorbs the force of the waves and prevents erosion from destroying the reef.

Encrusting algae do yet another job that is vital to reef growth. Coral skeletons and fragments create an open network, full of spaces, that traps coarse carbonate sediments (Fig. 14.8). Sediment, especially fine sediment, damages corals when it settles directly on them, but the buildup of coarse sediment in the reef framework is an essential part of reef growth. The structure of a reef is formed as much by the accumulation of calcareous sediment as by the growth of corals. Encrusting algae grow over the sediment as it builds up, cementing the sediment in place. Thus, encrusting coralline algae are the glue that holds the reef together. Some invertebrates, notably sponges and **bryozoans,** also help bind the sediments.

Encrusting coralline algae help build the reef by depositing calcium carbonate, by resisting wave erosion, and by cementing sediments.

Nearly all the sediment that accumulates to help form the reef comes from corals and the shells or skeletons of other organisms. In other words, nearly all the sediment is **biogenous. Coral rubble,** fragments of broken coral, is one important source of sediment on reefs. Another important sediment-forming organism is a calcareous green alga called *Halimeda* (Fig. 14.9). *Halimeda* deposits calcium carbonate within its tissues to provide support and to discourage grazers—a mouthful of limestone is pretty unappetizing. The remnants of *Halimeda* accumulate on reefs in huge amounts, to be bound together by encrusting organisms.

Many other organisms make calcium carbonate sediments and thus contribute to the growth of the reef. The shells of **forams,** snails, clams, and other molluscs are very important. Sea urchins, bryozoans, crustaceans, sponges, bacteria and a host of other organisms add or help bind carbonate sediments. Reef growth is truly a team effort.

The accumulation of calcium carbonate sediments plays an important role in reef growth. A calcareous green alga, Halimeda, *and coral rubble account for most of the sediment, but many other organisms also contribute.*

A great deal of the sediment on reefs comes from the activities of organisms that do not deposit calcium carbonate themselves but instead break down the solid reef structure. Many animals scrape or bite their food off the reef with some sort of hard structure. Parrotfishes, for example, are named for their fused teeth that form a parrot-like beak (see Fig. 8.13*d*). Sea urchins scrape algae off the reef with their **Aristotle's lantern.** In the process, these and many other grazers remove bits of calcium carbonate from the reef to form sediment. The erosion caused by

Photosynthesis $CO_2 + H_2O +$ sun energy $\rightarrow$ organic matter (glucose) $+ O_2$

• *Chapter 4, p. 68*

Coralline Algae Red algae that deposit calcium carbonate ($CaCO_3$) in their tissues.

• *Chapter 6, p. 106*

Bryozoans Small, colonial, encrusting animals that make delicate, often lace-like, skeletons.

• *Chapter 7, p. 134; Figure 7.40*

Foraminiferans (Forams) Protozoans, often microscopic, with a calcium carbonate shell.

• *Chapter 5, p. 98; Figure 5.10*

Aristotle's Lantern A complicated set of calcium carbonate ($CaCo_3$) teeth and associated muscles that is found in sea urchins.

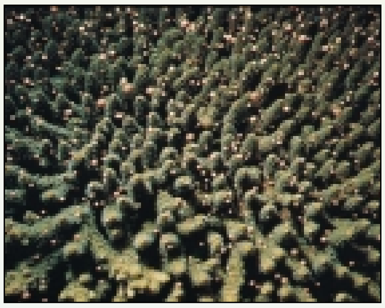
• *Chapter 7, p. 138*

Coral Reproduction

Corals are amazingly adaptable animals. They come in all shapes and sizes and have many ways to feed themselves. It should come as no surprise, then, that they also have more than one way to reproduce.

One form of reproduction in corals is essentially the same as growth. As individual polyps reproduce vegetatively by dividing into new polyps, the colony as a whole grows. The process is taken a step further when a piece of a coral colony breaks off and grows into a new "daughter" colony. This reproduction by fragmentation seems to be quite important for some coral species, which may even be adapted to break easily to produce more fragments. The growth of broken coral fragments into new colonies is also an important part of the recovery of reefs from storm damage and other disturbances, and transplanting fragments is one way that scientists and conservation groups help restore damaged reefs (see "Restoration of Habitats," p. 407).

Corals can also reproduce sexually. Like other animals, they produce eggs and sperm, which fuse and develop into planula larvae, the characteristic larvae of cnidarians. Some coral species have separate sexes, but about three-quarters are hermaphrodites and make both eggs and sperm. The method of fertilization also varies. In some corals, whether or not they are hermaphrodites, the egg is fertilized and develops inside the polyp. Most corals, however, are broadcast spawners and release eggs and sperm into the water.



The release of sperm and egg bundles during the mass coral spawning on the Great Barrier Reef. Photographs courtesy of the Great Barrier Reef Marine Park Authority.

The most spectacular form of sexual reproduction in corals is mass spawning, in which many different coral species on a reef all spawn at the same time. Mass spawning was first reported from the Great Barrier Reef, where it takes place for a few nights a year between October and early December just after a full moon. At a given place the time of the mass spawning event can usually be predicted down to the night. Since its discovery on the Great Barrier Reef mass spawning has been observed on many other reefs around the world.

Spawning corals release their eggs and sperm through the mouth. In some species the gametes are packaged into little bundles, which may contain both eggs and sperm or only one or the other. The bundles float to the surface and break up, allowing the eggs and sperm to mix.

Nobody knows why the corals all spawn together. Maybe egg predators get so full that most of the eggs go uneaten. Maybe it has something to do with the tides. There may be an explanation that no one has thought of. Another interesting thing is that although mass spawning happens on some reefs it does not occur on others. Is there something different about these reefs? Finding answers to these questions is likely to occupy coral reef biologists for some time to come.

such organisms, or **bioerosion,** tends to wear the reef away, although some of the sediment they create does get reincorporated into the reef structure. Many other organisms—including sponges, clams, polychaete and other worms, and algae—cause bioerosion by burrowing into or through the reef limestone, either scraping it away to form sediment or dissolving it. A reef grows only if corals, coralline algae, and sediment-forming and -binding organisms accumulate limestone faster than the bioeroders wear it away.

Conditions for Reef Growth

Other organisms may be important, but coral reefs do not develop without reef-building corals. Corals have very particular requirements that determine where reefs develop. Reefs are rare on soft bottoms, for example, because coral larvae need to settle on a hard surface.

Light and Temperature Corals can grow only in shallow water, where light can penetrate, because the zooxanthellae on which they depend need light. Calcareous algae require sunlight as well. Particular types of coral and algae have different depth limits—some can live deeper than others—but reefs rarely develop in water deeper than about 50 m (165 ft). Because of this, coral reefs are found only on the continental shelves, around islands, or on top of seamounts. Many types of coral live in deep water and do not need light, but these corals do not contain zooxanthellae or build reefs. Corals also prefer clear waters, since water clouded with sediment or plankton reduces light penetration.

Reef-building corals are limited to warm water and can grow and reproduce only if the average water temperature is above about 20°C (68°F). Most reefs grow in considerably warmer areas. Figure 14.10 illustrates the relationship between coral reefs and water temperature.

Corals need light and warm temperatures, so reefs grow only in shallow, warm waters.

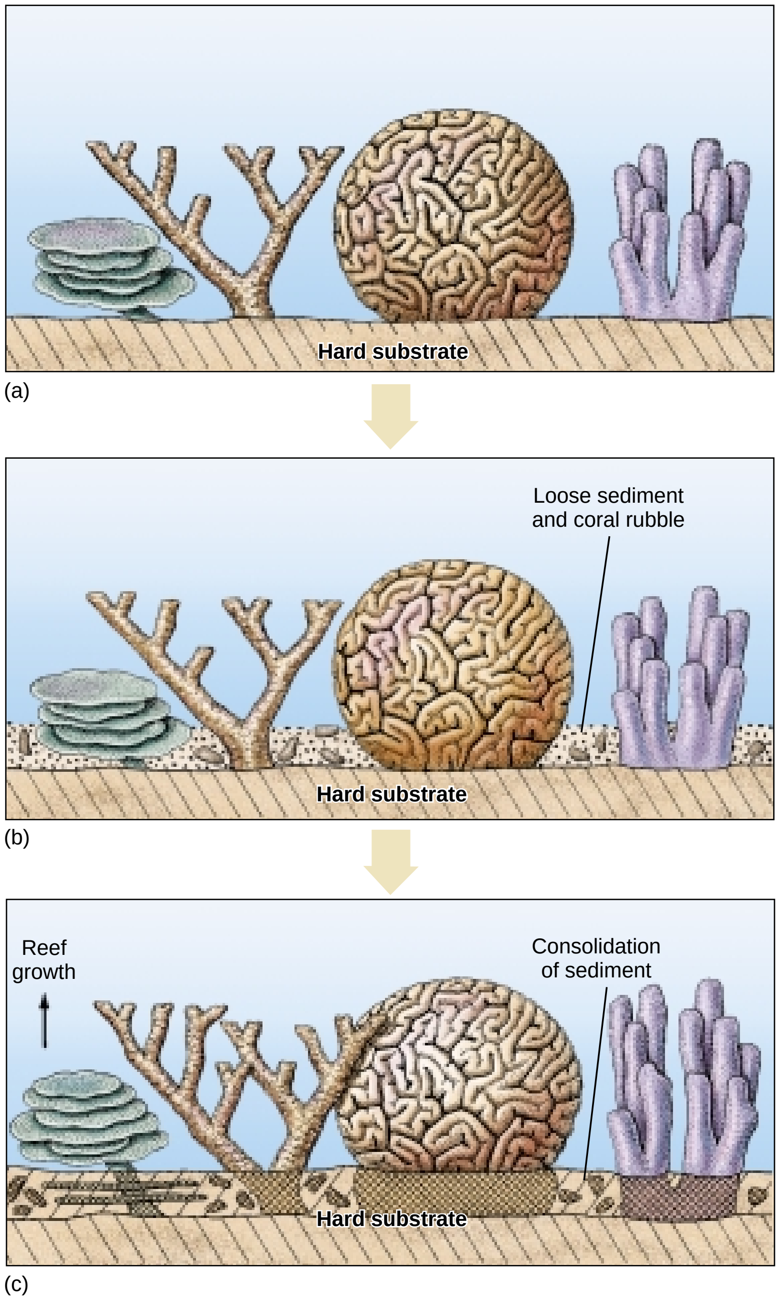


Figure 14.8 Reef growth involves several processes. (*a*) The framework is made when reef-building corals settle and grow on some hard surface, usually a preexisting reef. (*b*) The spaces in this framework are partially filled in by coarse carbonate sediments. (*c*) When the sediments are glued together by encrusting organisms, new reef "rock" is formed and the reef has grown. On a real reef all three steps go on at the same time. Reefs are not actually completely solid as depicted here but are porous, with many holes and crevices that serve as home to a multitude of organisms.

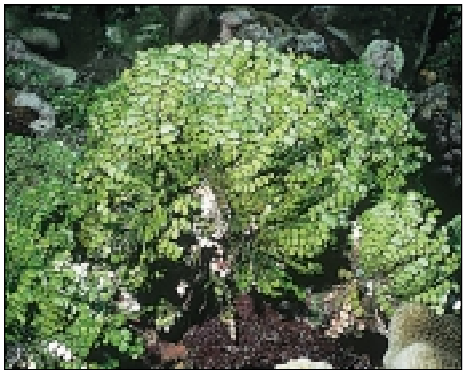


Figure 14.9 This calcareous green alga (*Halimeda*) is one of the main sediment-forming organisms on most reefs. About 95% of the plant's weight is calcium carbonate, and there is only a thin layer of live tissue on the outside. When the tissue dies the segments separate, each leaving a piece of limestone.

Water that is *too* warm is also bad for corals. The upper temperature limit varies, but is usually around 30° to 35°C (86° to 95°F). The first outward sign of heat stress, or stress of other kinds, is **bleaching,** in which the coral expels its zooxanthellae (see Fig. 18.3). It is called bleaching because the golden-brown or greenish zooxanthellae give the coral most of its color; without them, the coral is almost white. Corals also slough off large amounts of slimy mucus when stressed. Corals often recover from bleaching, regaining their symbionts either from the regrowth of the few that remain or by acquiring new ones from the water. If the warm conditions last too long or the temperature gets too high, however, the coral dies.

Temperature limits vary among coral species and from place to place. Corals from warm locations, for example, tolerate higher temperatures than corals from cooler waters (Fig. 14.11). Corals can also adapt to fluctuating conditions. For instance, reefs grow in parts of the Persian Gulf where the water temperature ranges from 16° to 40°C (60° to 104°F). The symbiotic zooxanthellae, different species and strains of which vary in their temperature tolerances, may be partly responsible for this temperature adaptation. Bleaching may occur simply because one partner or the other is weakened or damaged by stress, or be caused by viruses or other disease-causing organisms. Some biologists have proposed, however, that corals bleach to expel zooxanthellae that are poorly adapted to the prevailing conditions, on the chance that they will be able to acquire better-adapted symbionts.

In any case, the upper temperature tolerances of corals are usually not far above the normal temperature range where they live. Corals suffer when exposed to temperatures outside this normal range. This sometimes happens during extreme low tides, when shallow pools on the reef may be cut off from circulation. Heated by the sun, the water can warm up to fatal temperatures. By discharging heated water, power plants can also kill corals.

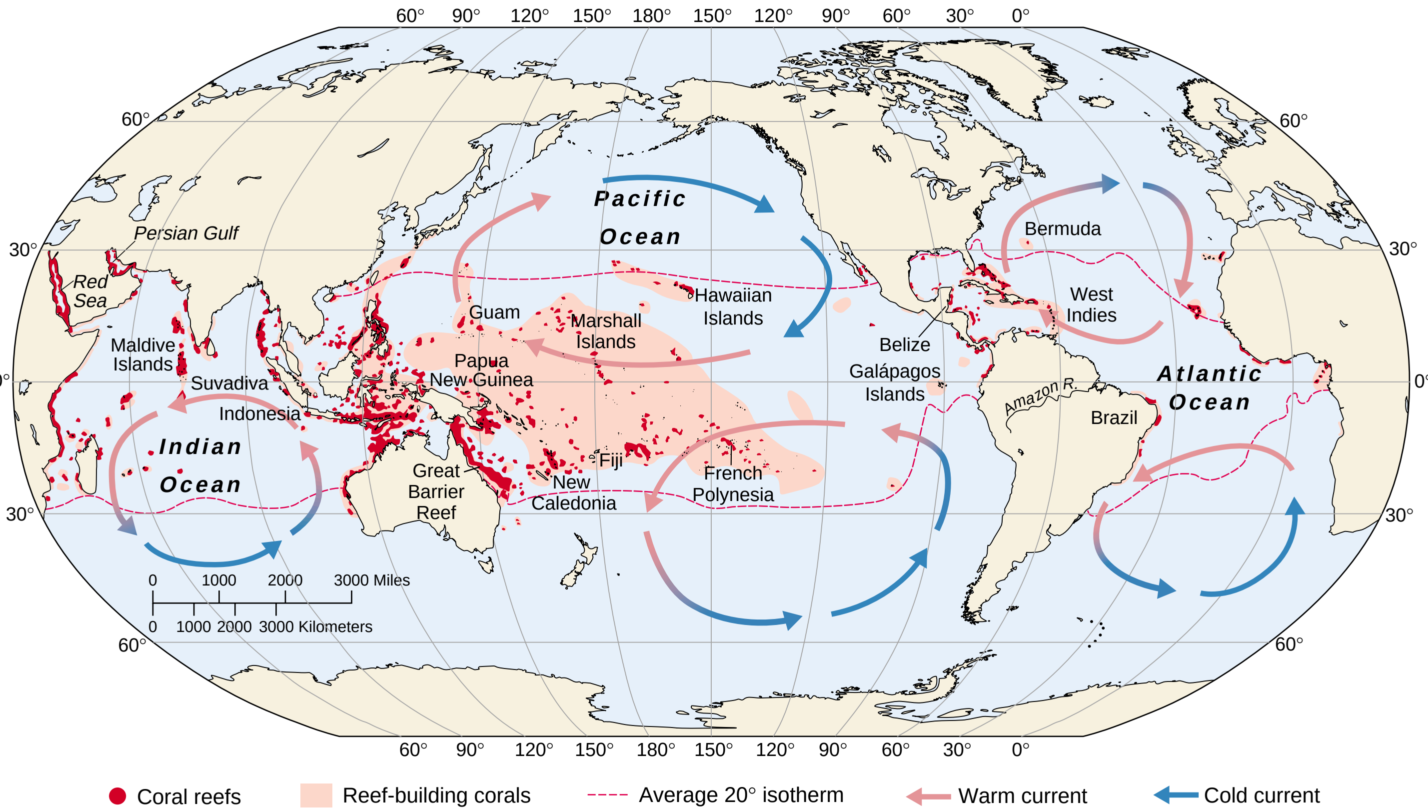


Figure 14.10 The distribution of reef coral communities, including those that do not form structural reefs. Note that the distribution of reef corals, like that of kelps, is related to temperature. Reef corals require warm water, however, while kelps need cold water. Compare the distribution of reefs with that of kelps shown in Figure 13.21. Note that because of warm surface currents corals extend further north and south on the east sides of continents than on the west sides.

El Niño (see "The El Niño–Southern Oscillation Phenomenon," p. 336), brings unusually warm water to many parts of the ocean. Widespread coral bleaching and mortality also occur during El Niño events. During the unusually strong El Niño of 1997–98, severe bleaching occurred on many reefs around the world, probably as a direct result of the unusually warm water. In some places, including the Caribbean and parts of the Great Barrier Reef, bleaching did not kill many corals, and reefs quickly recovered after the water cooled. In other areas, such as the Indian Ocean, Southeast Asia, and the far western Pacific, many corals died after bleaching and some reefs were severely damaged. Many of these reefs have recovered slowly or not at all.

High water temperatures have led to other major, though more localized, bleaching events since the 1997–98 El Niño. Reef scientists are increasingly concerned that bleaching is becoming more frequent and more intense as a result of global climate change (see "Living in a Greenhouse: Our Warming Earth," p. 394). On the other hand, bleaching is natural and past events probably often went unreported because many reefs are in remote locations. Today scientists continually monitor sea surface temperatures by satellite and can use the Internet to immediately report bleaching when it occurs. El Niño is also a natural event, and the unusually strong recent El Niños that have brought such widespread coral bleaching are to some extent probably just normal, random fluctuation. Temperature records stored in the oxygen isotopes of fossil corals, in fact, show that the most intense El Niño events of the last millennium took place in the mid-17th century, long before the smokestacks of the industrial revolution began belching huge quantities of **carbon dioxide** (CO_2) and other greenhouse gases. Nonetheless, the sea has steadily warmed in many reef areas over at least the last 50 to 100 years, and climate scientists predict that with global warming this trend will continue. Combined with other human-induced stresses (see "Coral Reefs," p. 391), this warming threatens coral reefs around the world.

Salinity, Sediments, and Pollution

Most corals are quite sensitive to reduced salinity and do not do well near river mouths, for example, where there is a lot of freshwater input. This is not only because of the lowered salinity but also because rivers bring in a lot of silty sediment, which is generally unfavorable to corals. It clouds the water, cutting down light for the zooxanthellae. Sediment on the colony surface can smother the coral or cause disease, though the coral can clean itself to some extent by sloughing off mucus that carries the sediment away.

Some corals tolerate high levels of sediment and build reefs in silty environments, where some even feed on the organic-rich sediment particles. Most reefs, however, develop in clear, low-sediment waters and are vulnerable to high levels of sediment unless there is enough wave or current action to wash the sediment away **(Fig. 14.12)**. Many reefs around the world have been damaged by human activities like mining, logging, construction, and dredging that greatly increase the flow of sediment onto the reef.

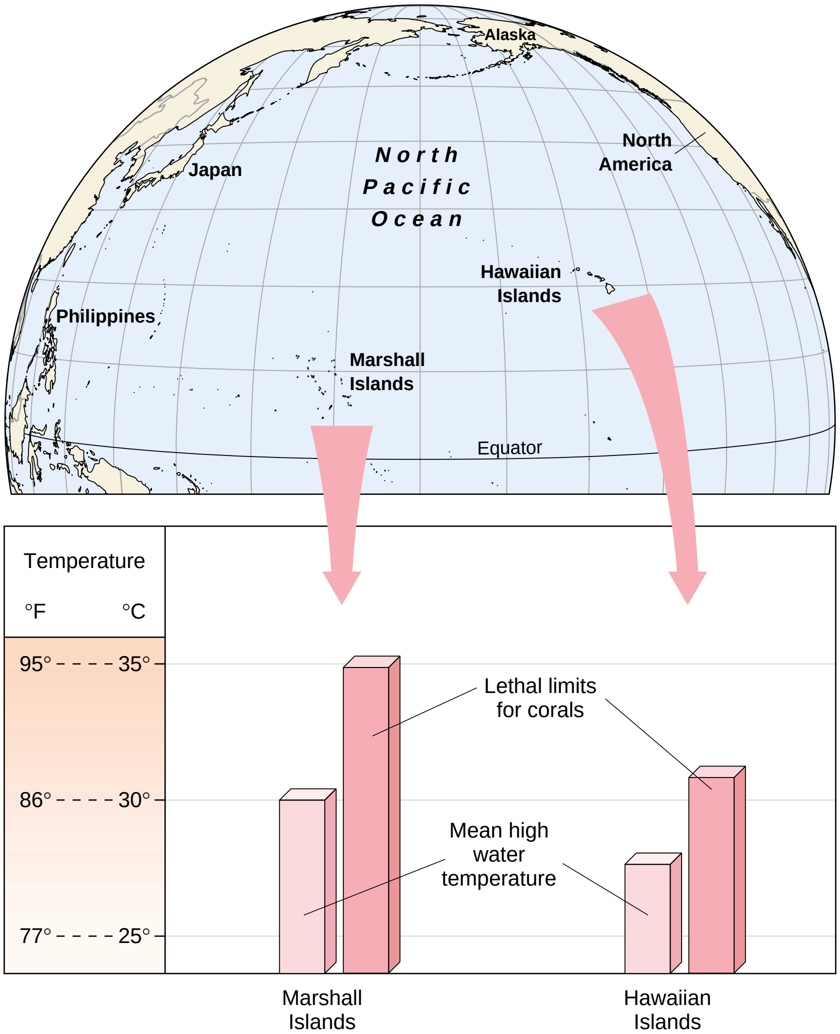


Figure 14.11 The upper temperature limit of corals is related to the temperature at their home sites. For example, the water in the Marshall Islands is warmer on average than that in Hawai'i. During the hottest months of the year the average high temperature is several degrees higher in the Marshalls. Corals from the Marshalls can tolerate correspondingly higher temperatures. Why do you think the highest temperature that the corals can tolerate would be higher than the average high temperature at their location?

Corals are also sensitive to pollution of many kinds. Even low concentrations of chemicals like pesticides and industrial wastes can harm them. The larvae are especially sensitive. In high concentrations, nutrients too can be harmful to reef growth. Humans release tremendous amounts of nutrients in sewage and in fertilizers that are washed from farmland and carried to the sea. The nutrients may harm the corals directly by interfering with the formation of their skeletons. More importantly, increased nutrients can alter the ecological balance of the community. Most coral reefs grow in water that is naturally low in nutrients. In such nutrient-poor water, seaweeds do not grow very rapidly and are kept under control by grazers. This allows corals to compete successfully for space and light. When nutrients are added, seaweeds may grow much faster and shade and choke out the slow-growing corals. This is a particular problem when, as is often the case, fishing has reduced populations of grazing fishes and other organisms.

Corals are very sensitive to fresh water, fine sediment, and pollution, including pollution by high nutrient levels.

The Kane'ohe Bay Story One of the best-known examples of the harmful effects of nutrient enrichment occurred in a partially enclosed bay in the Hawaiian Islands. Kane'ohe Bay, located on the northeast shore of the island of O'ahu, once had some of the most luxuriant reefs in Hawai'i. Until the 1930s the area around the bay was sparsely populated. In the years leading up to World War II, with the military buildup of O'ahu, the population began to increase. This increase continued after the war as the shores of the bay were developed for residential use.

The sewage from this expanding population was dumped right into the bay. By 1978 about 20,000 m^3 (over 5 million gallons) of sewage were being dumped into the bay every day. Long before then, by the mid-1960s in fact, marine biologists began to notice disturbing changes in the middle part of the bay. Loaded with nutrients, the sewage acted as a fertilizer for seaweeds. A green alga, the bubble alga (*Dictyosphaeria cavernosa*), found the conditions particularly to its liking and grew at a tremendous rate, literally covering the bottom in many parts of the bay. Bubble algae began to overgrow and smother the corals. Phytoplankton also multiplied with the increase in nutrients, clouding the water. Kane'ohe Bay's reefs began to die. Such accelerated algal growth due to nutrient input is called **eutrophication** (see "Eutrophication," p. 392).

For a time it appeared that the story had a happy ending. As the once beautiful reefs smothered, scientists and the general public began to cry out. It took a while, but in 1978 public pressure finally managed to greatly reduce the discharge of sewage into the bay, and the sewage was diverted offshore. The result was dramatic. Bubble algae died back in much of the bay, and the bay's corals began to recover much faster than anyone expected. By the early 1980s, bubble algae were fairly scarce and corals had started to grow again. The reefs were not what they once were, but they seemed to be on track to recover.

Then the ghost of pollution past reared its ugly head. In November 1982, Hurricane Iwa struck Kane'ohe Bay. During the years of pollution a layer of the coral skeleton had weakened, becoming fragile and crumbly. When the hurricane hit, this weak layer collapsed and many reefs were severely damaged. Fortunately, the corals were already beginning to recover, and the broken pieces were able to grow back. If the hurricane had hit during the years of pollution, the reefs of Kane'ohe Bay—and their benefits to fishing, tourism, and recreation—might have disappeared forever.

The rapid recovery of Kane'ohe Bay's reefs that was seen during the early 1980s did not continue. By 1990 the recovery seemed to have leveled off. Some areas even began to decline again, with bubble algae once more becoming abundant. There are a number of possible explanations for this. Even though most sewage is now discharged outside the bay, some nutrients continue to enter from boats, the septic tanks and cesspools of private homes, and other sources. Not only that, nutrients from the old sewage outfalls were stored in the sediments, and are still being released even after 30 years. There is also evidence that fishing has reduced populations of fishes that graze on bubble algae. Furthermore, the grazing fishes that remain prefer to eat other species of seaweed that have been introduced from outside Hawai'i, and have shifted away from eating bubble algae. Thus, bubble algae may be abundant because they are not being eaten as fast as they once were. Another introduced seaweed, which like bubble algae is not a preferred food of herbivorous fishes, has also started to proliferate and smother corals in the bay **(Fig. 14.13).** It will be much harder to restore the coral gardens of Kane'ohe Bay than it was to destroy them.

The Kane'ohe Bay story is far from unique. Most of the world's tropical coasts are undergoing increasing development and population growth. As a result, more and more nutrients are ending up in the waters that support coral reefs, and there are many reports of reefs being threatened by eutrophication. New research, however, is showing that the effects of added nutrients on coral reefs are more complicated than we thought. Experiments indicate that algal growth is not nutrient-limited on at least some reefs. There are even suggestions that added nutrients may sometimes be good for the zooxanthellae and help corals grow faster. The bulk of the evidence, though, is that eutrophication is damaging, especially when populations of algal grazers are reduced. Many reef biologists consider it one of the most serious threats to the world's coral reefs.

Figure 14.12 Corals often flourish where there is plenty of wave action. The water motion keeps sediment from settling on the corals and brings in food, oxygen, and nutrients.

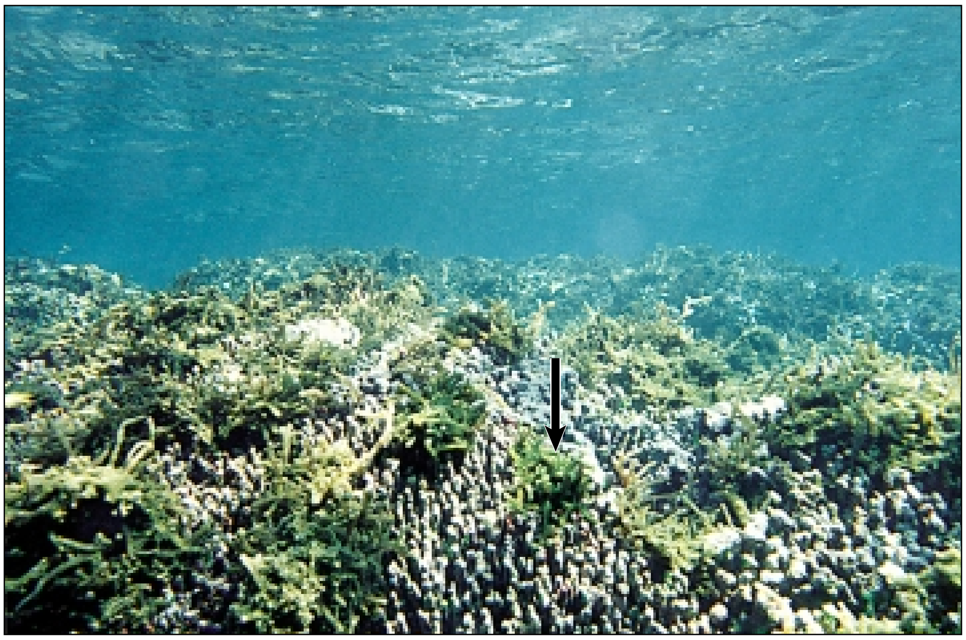


Figure 14.13 The red alga *Kappaphycus striatum,* introduced to Kane'ohe Bay from the Philippines, has gotten out of control. The arrow shows one of many clumps of *K. striata* in this picture that are growing over and smothering reef corals.

Kinds of Coral Reefs

Coral reefs are usually divided into three main categories: **fringing reefs, barrier reefs,** and **atolls.** Many reefs do not fit neatly into any particular category or fall between two categories. Still, the division of reefs into the three major types works well for the most part.

The three main types of reefs are fringing reefs, barrier reefs, and atolls.

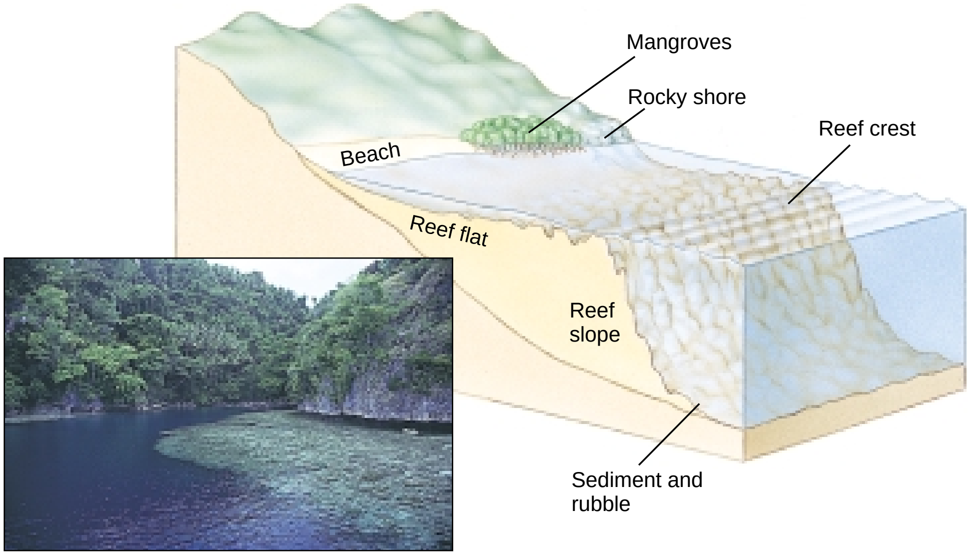


Figure 14.14 Typical structure of a fringing reef. Fringing reefs, like this one in the Bismarck Archipelago in the southwest Pacific (photo), can grow right up to the shore.

Figure 14.15 The upward growth of most reefs is limited by the tides. When extreme low tides occur, shallow areas like this reef flat on the Great Barrier Reef are exposed. If the corals are only exposed for a short time, they can survive, but they will die if exposed for too long. It is this occasional exposure at extreme low tides that keeps reef flats flat because all the corals above a certain depth are killed. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

Fringing Reefs

Fringing reefs are the simplest and most common kind of reef. They develop near shore throughout the tropics, wherever there is some kind of hard surface for the settlement of coral larvae. Rocky shorelines provide the best conditions for fringing reefs. Fringing reefs also grow on soft bottoms if there is even a small hard patch that lets the corals get a foothold. Once they get started, the corals create their own hard bottom and the reef slowly expands.

As their name implies, fringing reefs grow in a narrow band or fringe along the shore (Fig. 14.14). Occurring close to land, they are especially vulnerable to sediment, freshwater runoff, and human disturbance. Under the right conditions, however, fringing reefs can be impressive. In fact, the longest reef in the world (though not the one with the largest coral area) is not the famous Great Barrier Reef in Australia but a fringing reef that runs some 4,000 km (2,500 mi) along the coast of the Red Sea. Part of the reason this reef is so well-developed is that the climate is dry and there are no streams to bring in sediment and fresh water.

The typical structure of a fringing reef is shown in Figure 14.14. Depending on the place, the shore may be steep and rocky or have mangroves or a beach. The reef itself consists of an inner **reef flat** and an outer **reef slope.** The reef flat is the widest part of the reef. It is shallow, sometimes exposed at low tide (Fig. 14.15), and slopes very gently toward the sea. Being closest to land, it is the part of the reef most strongly affected by sediments and freshwater runoff. The bottom is primarily sand, mud, or coral rubble. There are some living corals, but neither as many colonies nor as many different species as on the reef slope. Seaweeds, seagrasses, and soft corals may also occupy the reef flat, sometimes in dense beds.

The reef slope can be quite steep, nearly vertical in fact. It is the part of the reef with the densest cover (Fig. 14.16) and the most species of coral, because the slope is away from shore and therefore away from the effects of sediment and fresh water. Also, the waves that bathe the slope provide good circulation, bring in nutrients and zooplankton, and wash away fine sediments. The **reef crest** is the shallow upper edge of the reef slope. The crest usually has even more luxuriant coral growth than the rest of the reef slope. If there is intense wave action, however, the crest may consist of an algal ridge, with the richest coral growth just below. Because there is less light in deep water, the deepest part of the reef slope usually has less live coral and fewer coral species.

Fringing reefs grow close to shore and consist of an inner reef flat and an outer reef slope.

Large amounts of sediment and coral rubble tumble down the reef slope and settle at the base. As this material builds up, reef organisms may begin to grow on it, depending on the water depth and other factors. Thus, the reef can grow outward as well as upward. Beyond the base of the slope, the bottom is usually fairly flat and composed of sand or mud. On many Caribbean reefs, turtle grass (*Thalassia testudinum*) dominates the bottom beyond the slope.

Figure 14.16 The elkhorn coral (*Acropora palmata*) is a dominant coral on the reef slopes of fringing reefs in the Caribbean and Florida. Its broad branches rise parallel to the surface to collect light. This colony suffers from a disease known as white-band disease (see "Coral Reefs," p. 391).

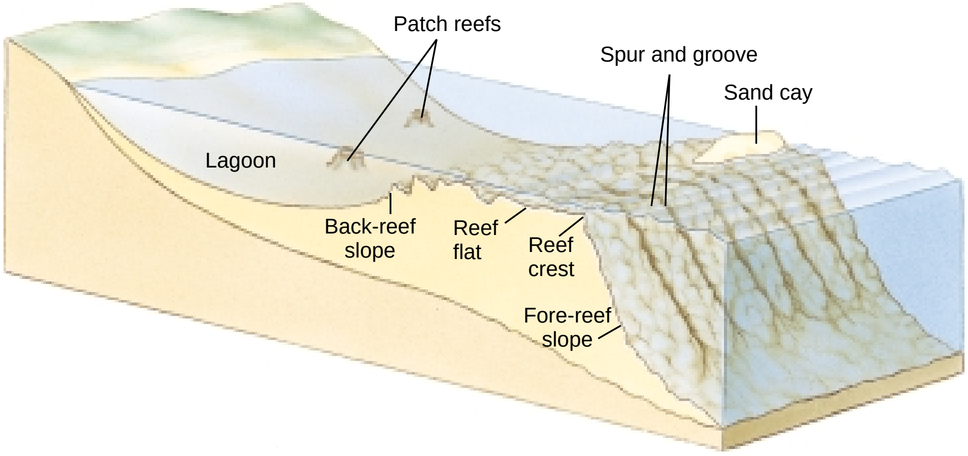


Figure 14.17 Typical structure of a barrier reef.

Barrier Reefs

The distinction between barrier reefs and fringing reefs is sometimes unclear because the two types grade into one another. Like fringing reefs, barrier reefs lie along the coast, but barrier reefs occur considerably farther from shore, occasionally as far as 100 km (60 mi) or more. Barrier reefs are separated from the shore—which may also have a fringing reef—by a relatively deep **lagoon** (Fig. 14.17). Largely protected from waves and currents, the lagoon usually has a soft sediment bottom. Seagrass beds often grow in shallow parts of the lagoon. Scattered coral formations variously known as **patch reefs, coral knolls,** or **pinnacles** depending on their size and shape may grow up nearly to the surface.

The barrier reef consists of a **back-reef slope,** a reef flat, and a **fore-reef slope,** which corresponds to the reef slope of a fringing reef and has a reef crest (Fig. 14.17). The back-reef slope may be gentle or as steep as the fore-reef slope. It is protected from waves by the rest of the reef, but waves wash large amounts of sediment from the reef down the slope. As a result, coral growth is often not as vigorous on the back-reef slope as on the fore-reef slope. This is not always true; some back-reef slopes, especially gentle ones, have luxuriant coral growth (Fig. 14.18).

The reef flat, like that on fringing reefs, is a shallow, nearly flat platform. Sand and coral rubble patches are interspersed with seagrass or seaweed beds, soft corals, and patches of dense coral cover. Waves and currents may pile up sand to form small sand islands called **sand cays** or, in the United States, **keys.**

The richest coral growth is usually at the outer reef crest. There may be a well-developed algal ridge if the reef is exposed to wave action, with coral growth most luxuriant just below the crest. Exposed fore-reef areas often have a series of finger-like projections alternating with sand channels (Figs. 14.17 and 14.19). There is still debate about what causes these formations, known as **spur-and-groove** formations or **buttresses.** The wind, waves, or both are definitely involved, because spur-and-groove formations develop primarily on reef slopes that are exposed to consistent strong winds. These formations are found on atolls and some fringing reefs as well as barrier reefs.

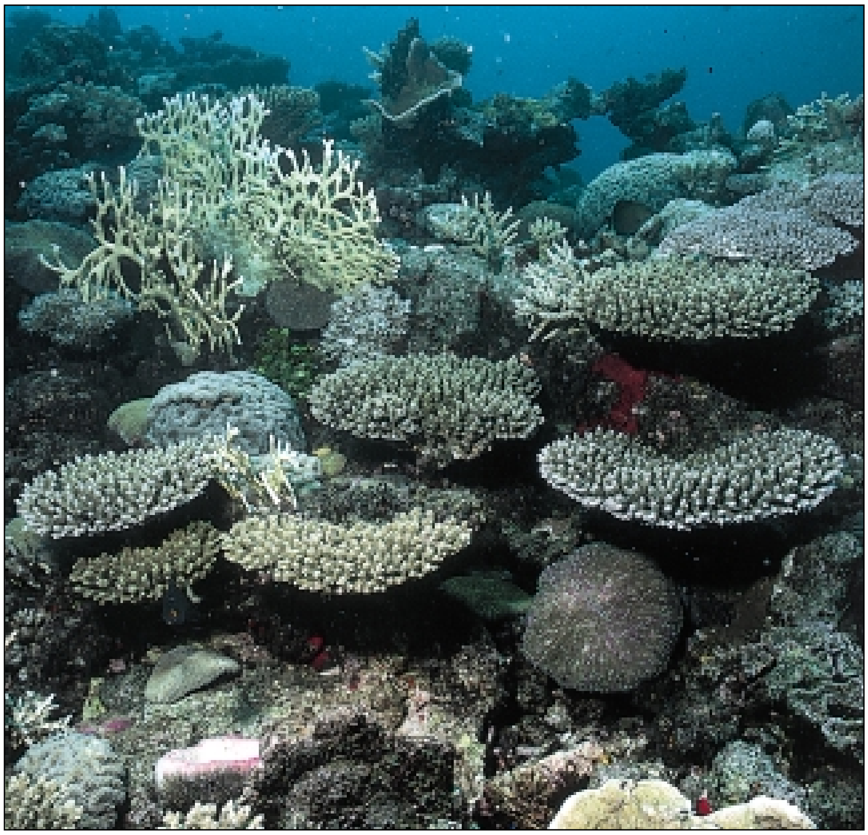


Figure 14.18 A rich back-reef slope on a Pacific barrier reef.

Figure 14.19 Spur-and-groove formations at Kure atoll in the northwestern Hawaiian Islands. The dark elevated ridges are the coral spurs; the light-colored grooves (arrows) channel sand down the reef slope. The northwestern Hawaiian Islands include 70% of the coral reef in United States waters and are one of the largest relatively pristine reef areas in the world.

Fore-reef slopes vary from relatively gentle to nearly vertical. The steepness depends on the action of wind and waves, the amount of sediment flowing down the slope, the depth and nature of the bottom at the reef base, and other factors. As with other types of reefs, the abundance and diversity of corals on the fore-reef slope generally decreases with depth. The growth form of the corals also changes down the slope. At the crest, under the pounding of the waves, the corals are mostly stout and compact; many are massive (Fig. 14.7). Below the crest there is great variety in form. Whether they form branches, columns, or whorls, corals in this zone often grow vertically upward. This may be an adaptation for competition. Corals that grow upward like skyscrapers rather than outward need less space to attach. They are also less likely to be shaded, and if they spread out at the top, can shade out other corals. Deeper on the reef slope, corals tend to grow in flat sheets, which probably helps them collect light (see Fig. 10.1).

The largest and most famous barrier reef is the Great Barrier Reef. It runs more than 2,000 km (1,200 mi) along the northeastern coast of Australia, varying in width between about 15 and 350 km (10 to 200 mi) and covering an area of over 225,000 km^2 (80,000 mi^2). Though not the longest reef in the world, it covers such a large area and is so complex and well developed that it is generally regarded as the largest reef structure. Actually, the Great Barrier Reef is not a single reef but a system of more than 2,500 smaller reefs, lagoons, channels, islands, and sand cays (Fig. 14.20).

The largest barrier reef in the Caribbean lies off the coast of Belize, Central America. Other major barrier reefs include the Florida Reef Tract and barrier reefs associated with the islands of New Caledonia, New Guinea, and Fiji in the Pacific. There are many other smaller barrier reefs, especially in the Pacific. Like the Great Barrier Reef, these usually are not single reefs but complex systems of smaller reefs.

Atolls

An atoll is a ring of reef, and often islands or sand cays, surrounding a central lagoon (Figs. 14.21 and 14.22). The vast majority of atolls occur in the **Indo-West Pacific region,** that is, the tropical Indian and western Pacific

Figure 14.20 The Great Barrier Reef is a complicated system of thousands of small reefs, sand cays, and lagoons. Shown here are four reefs that are part of the Great Barrier Reef Marine Park. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

Figure 14.21 Fulanga atoll, in the South Pacific nation of Fiji.

oceans. Atolls are rare in the Caribbean and the rest of the tropical Atlantic Ocean. Unlike fringing and barrier reefs, atolls can be found far from land, rising up from depths of thousands of meters or more. With practically no land around, there is no river-borne silt and very little freshwater runoff. Bathed in pure blue ocean water, atolls display spectacular coral growth and breathtaking water clarity. They are a diver's dream.

Atoll Structure Atolls range in size from small rings less than a mile across to systems well over 30 km (20 mi) in diameter. The two largest atolls are Suvadiva, in the Maldive Islands of the Indian Ocean, and Kwajalein, one of the Marshall Islands in the central Pacific. These atolls cover areas of more than 1,200 km^2 (700 mi^2). Atolls may include a dozen or more islands and be home to thousands of people.

An atoll's reef flat is much like the reef flat on a fringing or barrier reef: a flat, shallow area. The fore-reef and back-reef slopes can now be thought of as outer and inner slopes, respectively, since they extend all the way around the ring-shaped atoll.

Atoll reef crests are strongly influenced by wind and waves. Because most atolls lie in the zone of the **trade winds,** the wind usually comes from a consistent direction. Consequently, the wind affects various parts of the atoll in different ways. Encrusting coralline algae, which can endure the constant pounding of the waves, build a distinct algal ridge on the reef crest of the **windward** side of the atoll, the side that faces the prevailing wind. On the few Caribbean atolls, the coralline algae may be replaced by especially wave-resistant corals. The algal ridge is less prominent or absent on the **leeward,** or sheltered, side of the atoll. Spur-and-groove formations, too, are better developed on the windward side.

The fore-reef, or outer, slope is nearly vertical, though there is usually a series of ledges and overhangs. The rocky wall of the reef extends down to great depths, far beyond the limit of living corals themselves. The water may be hundreds, even thousands, of meters deep just a stone's throw from the reef.

The lagoon, on the other hand, is relatively shallow, usually about 60 m (195 ft) deep. The bottom of a lagoon is very uneven, with many depressions and coral pinnacles. Some pinnacles rise almost to the surface, where they may form "mini-atolls," small rings of coral within the lagoon.

Atolls are rings of reef, with steep outer slopes, that enclose a shallow lagoon.

How Atolls Form When atolls were discovered, scientists were at a loss to explain them. It was known that corals can grow only in shallow water, yet atolls grow right in the middle of the ocean, out of very deep water. Therefore, the atoll could not have grown up from the ocean floor. If the reefs grew on

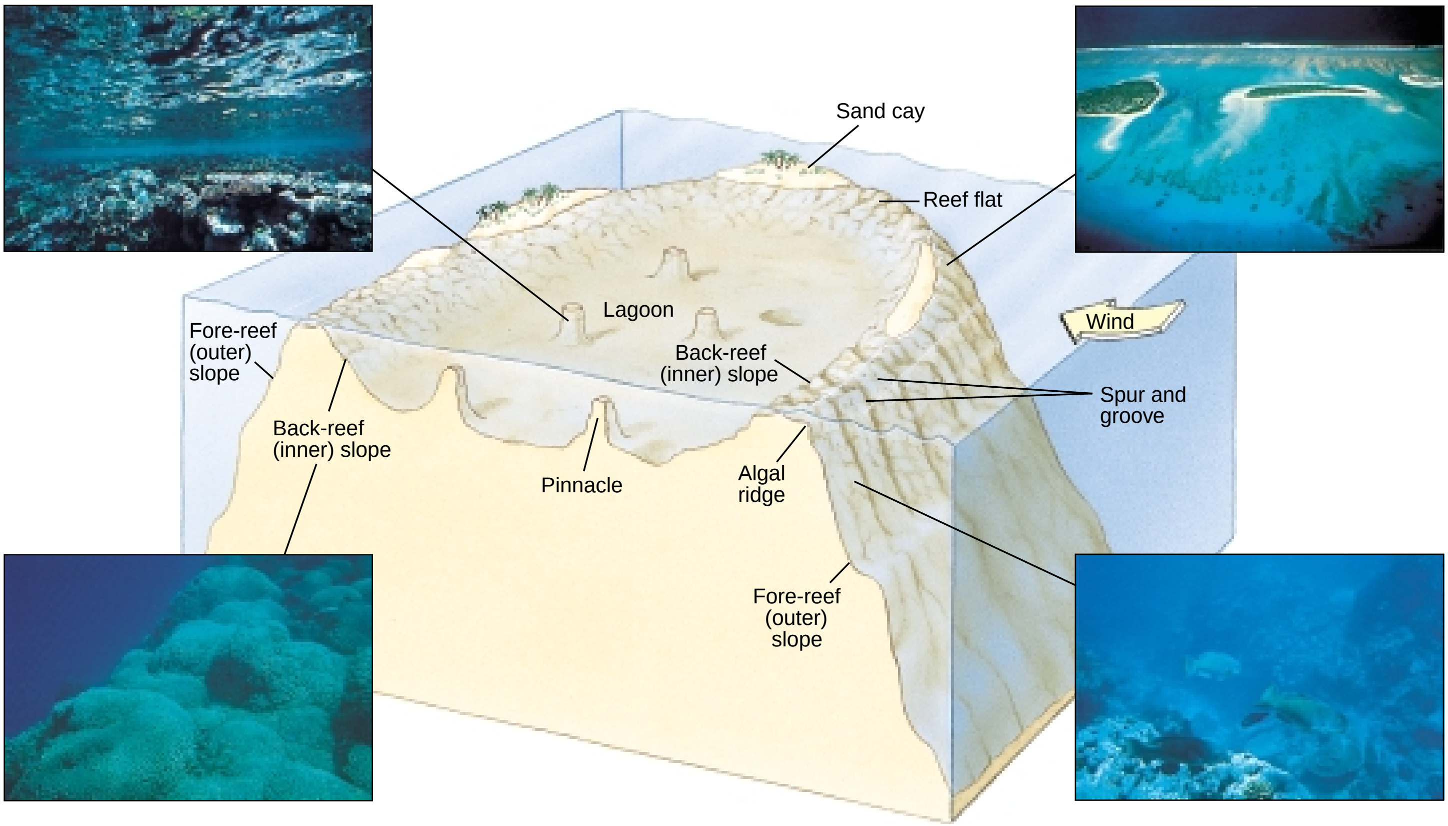


Figure 14.22 Typical structure of an atoll.

some kind of shallow structure that was already there, like a seamount, why is there no sign of it? The islands on atolls are simple sand cays that have been built by the accumulation of reef sediments and would not exist without the reef. They are *products* of the reef and could not provide the original foundation for reef growth. Finally, why do atolls always form rings?

The puzzle of atoll formation was solved by Charles Darwin in the mid-nineteenth century. Darwin is most famous, of course, for proposing the theory of evolution by natural selection, but his theory of atoll formation was another important contribution to science.

Darwin reasoned that atolls could be explained by reef growth on a subsiding island. The atoll gets its start when a deep-sea volcano erupts to build a volcanic island. Corals soon colonize the shores of the new island, and a fringing reef develops (Fig. 14.23*a*). As with most fringing reefs, coral growth is most vigorous at the outer edge of the reef. The inner reef is strongly affected by sediment and runoff from the island.

Surprisingly, Darwin's explanation of atoll formation was pretty much ignored for a century while scientists proposed various other hypotheses, none of which held up. Finally scientists found conclusive evidence that Darwin was right. Unlike other hypotheses for atoll formation, Darwin's hypothesis predicted that, below the thick calcium carbonate cap formed by the reef, there should be volcanic rock—the original island. In the 1950s the United States Geological Survey drilled several deep holes on Enewetak atoll in the Marshall Islands. These cores revealed exactly what Darwin predicted: volcanic rock far beneath the calcium carbonate of the reef. The thickness of the carbonate cap is impressive. The volcanic island underlying Enewetak is covered by more than 1,400 m (4,600 ft) of calcium carbonate!

Scientists now believe almost unanimously that Darwin's hypothesis of atoll formation is correct. There are, of course, a few details to be added to the picture, in particular the effects of changes in sea level (see "Climate and Changes in Sea Level," p. 32). When sea level is low, atolls may be left above the surface. The corals die and the reef is eroded by the wind and rain. If sea level rises rapidly, the atoll may be drowned, unable to grow in deep water. In either case, corals recolonize the atoll when the sea level returns to "normal."

The Ecology of Coral Reefs

Coral reefs may be impressive to geologists, but to the biologist they are simply awesome. They are easily the richest and most complex of all marine ecosystems. Literally thousands of species may live on a reef. How do all these different species live? How do they affect each other? What is their role in the reef ecosystem? These and countless other questions fascinate coral reef biologists.

Our ability to answer the questions, however, is surprisingly limited. This is partly because reefs are so complicated. Just keeping track of all the different organisms is hard

The **trade winds,** the steadiest winds on earth, blow from latitudes of about 30° toward the Equator.

• *Chapter 3, p. 53; Figure 3.20*

Subsidence The slow sinking into the *mantle* of a part of the earth's crust that contains a landmass.

• *Chapter 11, p. 226*

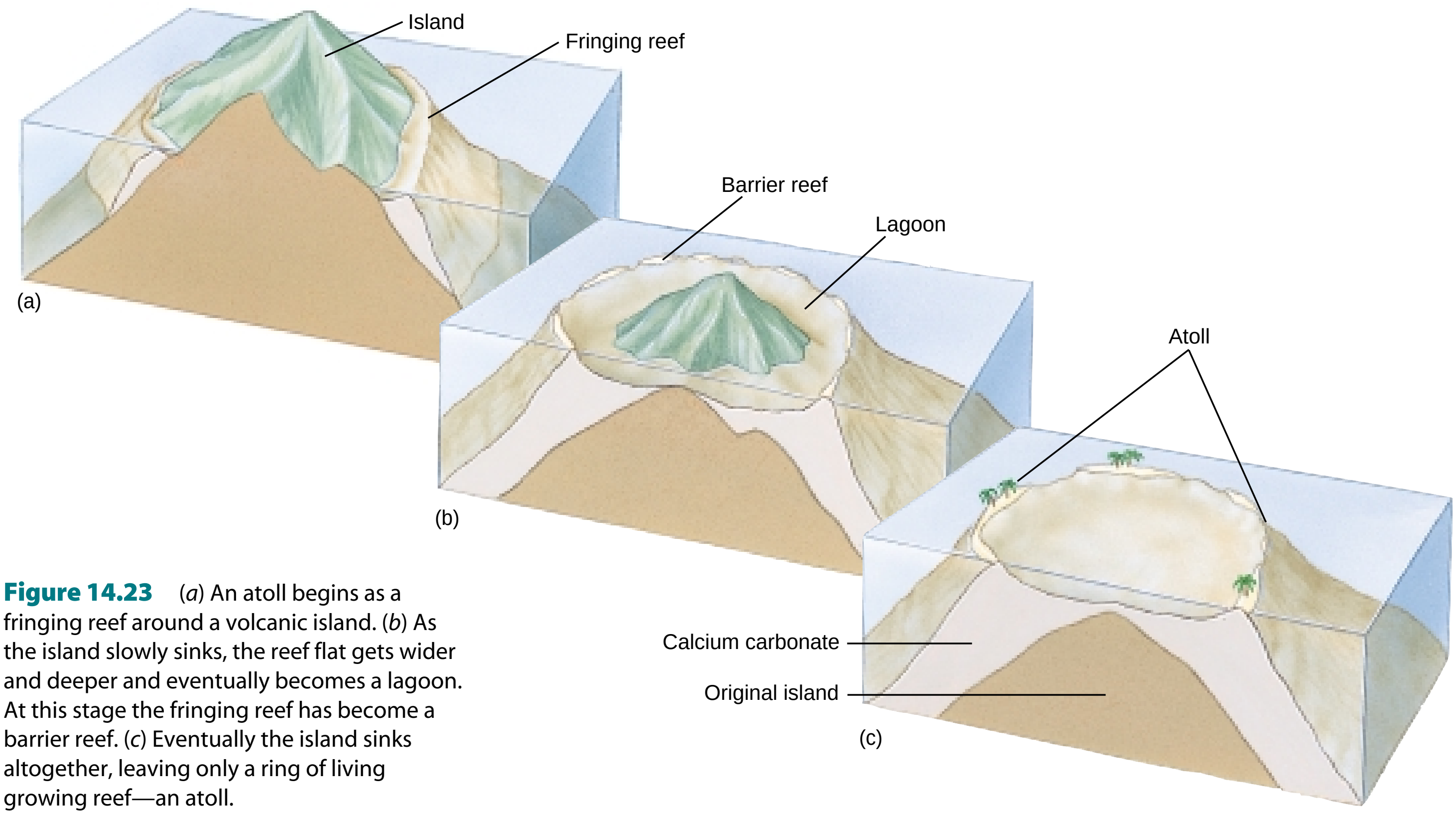


Figure 14.23 (*a*) An atoll begins as a fringing reef around a volcanic island. (*b*) As the island slowly sinks, the reef flat gets wider and deeper and eventually becomes a lagoon. At this stage the fringing reef has become a barrier reef. (*c*) Eventually the island sinks altogether, leaving only a ring of living growing reef—an atoll.

enough; the task of figuring out what they all *do* is mind-boggling. Furthermore, until the last half century or so most marine biologists lived and worked in the temperate regions of the Northern Hemisphere, far from the nearest reef. As a result, relatively few biologists studied reefs. Tremendous progress has been made in recent years, but there is still much to learn. The rest of this chapter summarizes what *is* known about the ecology of coral reefs and points out some of the important questions that remain.

The Trophic Structure of Coral Reefs

The tropical waters where coral reefs are found are usually poor in nutrients (see "Patterns of Production," p. 329) and therefore have very little phytoplankton or **primary production.** In these barren waters, coral reefs are oases of abundant life. How can such rich communities grow when the surrounding sea is so unproductive?

A good part of the answer lies in the mutualistic relationship between corals and their zooxanthellae. We have already learned what the zooxanthellae do for the coral: They provide food and help make the calcium carbonate skeleton. In return the zooxanthellae get not only a protected place to live, but also a steady supply of carbon dioxide and nutrients such as **nitrogen** and **phosphorus.** Most of the coral's nitrogen and phosphorus waste products are not released into the water. Instead, they are taken up and used as nutrients by the zooxanthellae. Using sunlight, the zooxanthellae incorporate the nutrients into organic compounds, which are passed on to the coral. When the coral breaks down the organic matter, the nutrients are released and the whole process begins again **(Fig. 14.24).** The nutrients are **recycled,** used over and

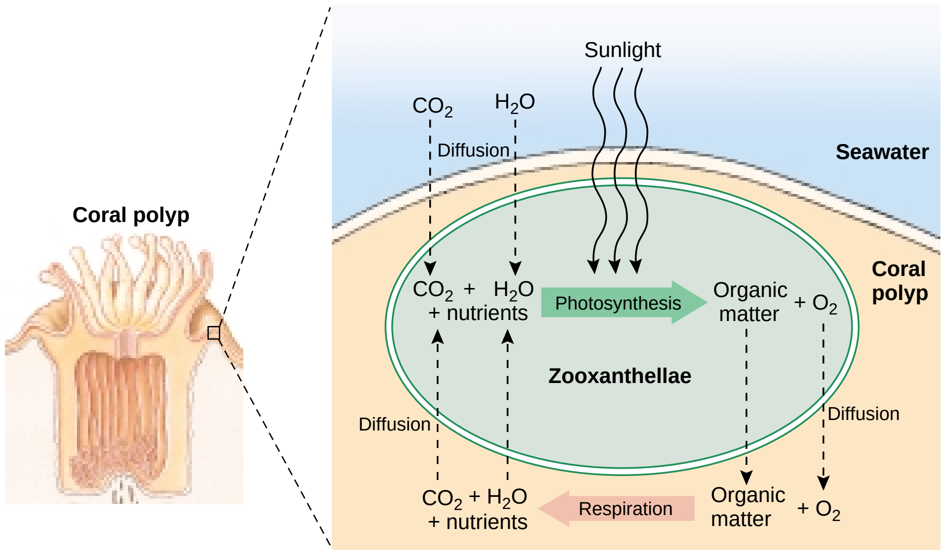


Figure 14.24 Carbon dioxide and nutrients are continually recycled between a coral polyp and its zooxanthellae.

over, so that far fewer nutrients are needed than would otherwise be the case.

Nutrient recycling occurs not just between corals and their zooxanthellae, but among all the members of the coral reef community. Sponges, sea squirts, giant clams, and other reef invertebrates have symbiotic algae or bacteria and recycle nutrients just as corals do. Recycling also takes place outside the bodies of reef organisms. When fishes graze on seaweeds, for example, they excrete nitrogen, phosphorus, and other nutrients as waste. These nutrients are quickly taken up by other algae. Many corals provide shelter to schools of small fish (see Fig. 8.20). The fish leave the coral at night to feed and return during the day. The waste products of the fish can be an important source of nutrients and help the coral grow faster. In this way nutrients are cycled from whatever the fish feed on to the coral. Nutrients pass through the community again and again in this cycle of feeding and excretion.

Coral reef communities use nutrients very efficiently as a result of recycling. The recycling is not perfect, however, and some nutrients are lost, carried away by the currents. Thus, the reef still needs a supply of new nutrients. Recycling alone is not enough to account for the high productivity of reefs.

The reef is able to provide some of its own nutrients. Coral reefs have among the highest rates of **nitrogen fixation** of any natural community. The main nitrogen fixers are cyanobacteria, especially a free-living one called *Calothrix* and another group that lives symbiotically in sponges. There is evidence that corals, too, have symbionts that fix nitrogen, providing nutrients for the zooxanthellae. Just what the symbionts are is not known. Because of this nitrogen fixation, nitrogen probably does not limit most coral reef communities, though not all reef biologists agree about this.

Ocean currents bring in additional nitrogen and, more importantly, phosphorus and other nutrients that are not produced on the reef. Corals, bacteria, algae, and other organisms absorb nutrients directly from the water. Even though the water is nutrient-poor, if enough water washes over the reef the nutrients add up. In business terms, this is a low-margin, high-volume proposition. More importantly, the water carries zooplankton, a rich nutrient source. When zooplankton are captured by the "wall of mouths," the nutrients in the zooplankton are passed on to the reef community. In fact, many biologists think that corals eat zooplankton not so much to feed themselves as to get nutrients for their zooxanthellae. Animals like seabirds, dolphins, and large fishes that spend part of their time around reefs but venture out into the open ocean to feed also transfer nutrients from oceanic waters to the reef community.

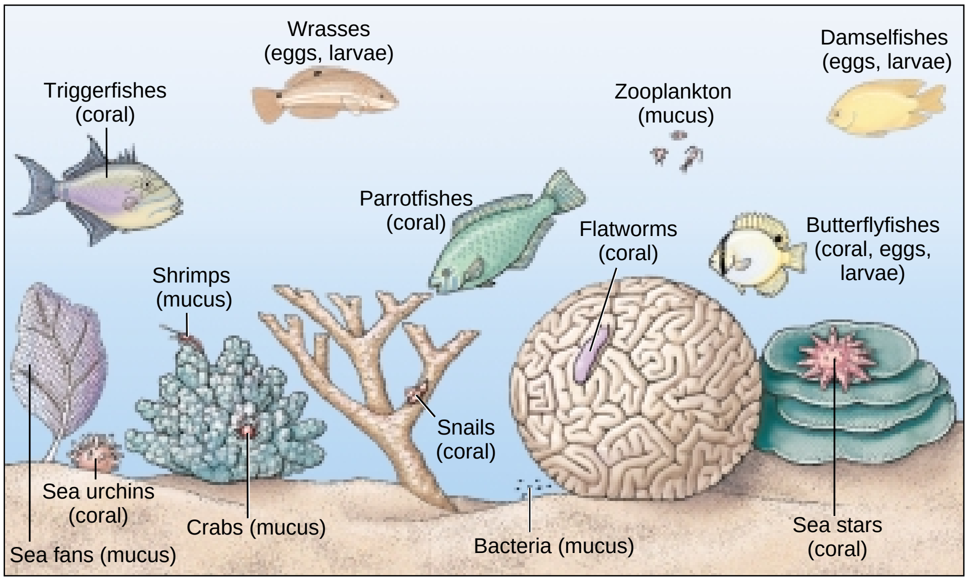


Figure 14.25 A number of animals eat coral directly, and many others feed on the mucus that corals produce or on coral eggs and larvae. The primary production of coral zooxanthellae is thus passed on to coral feeders, and then to the animals that eat them.

Coral reefs are very productive even though the surrounding ocean water lacks nutrients because nutrients are recycled extensively, nitrogen is fixed on the reef, and the zooplankton and nutrients that occur in the water are used efficiently.

The production and efficient use of nutrients by coral reef communities result in high primary productivity. This is reflected in the overall richness of the community. Scientists aren't sure, however, just how much primary production there is on coral reefs, or which particular organisms are the most important producers. There is no doubt that zooxanthellae are very important, but because they live inside corals, it is hard to measure exactly how much organic matter they produce. For a time it was thought that very few animals eat coral, since there is so little live tissue on a coral colony. It was therefore believed that, even though zooxanthellae produce a lot of organic matter, most of it was consumed by the coral and not much passed on to the rest of the community. As biologists looked closer, however, they found more and more animals that eat corals or their products (Fig. 14.25). Primary production by coral zooxanthellae therefore may be important not only to corals but to the community at large. Exactly how much production corals and their zooxanthellae contribute is still unknown.

Seaweeds are also important primary producers on the reef (Fig. 14.26), especially the small, fleshy or filamentous types that are called **turf algae** because they often grow in

Primary Production The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs, that is, the production of food.

• *Chapter 4, p. 70*

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.

• *Chapter 5, p. 90; Table 5.1*

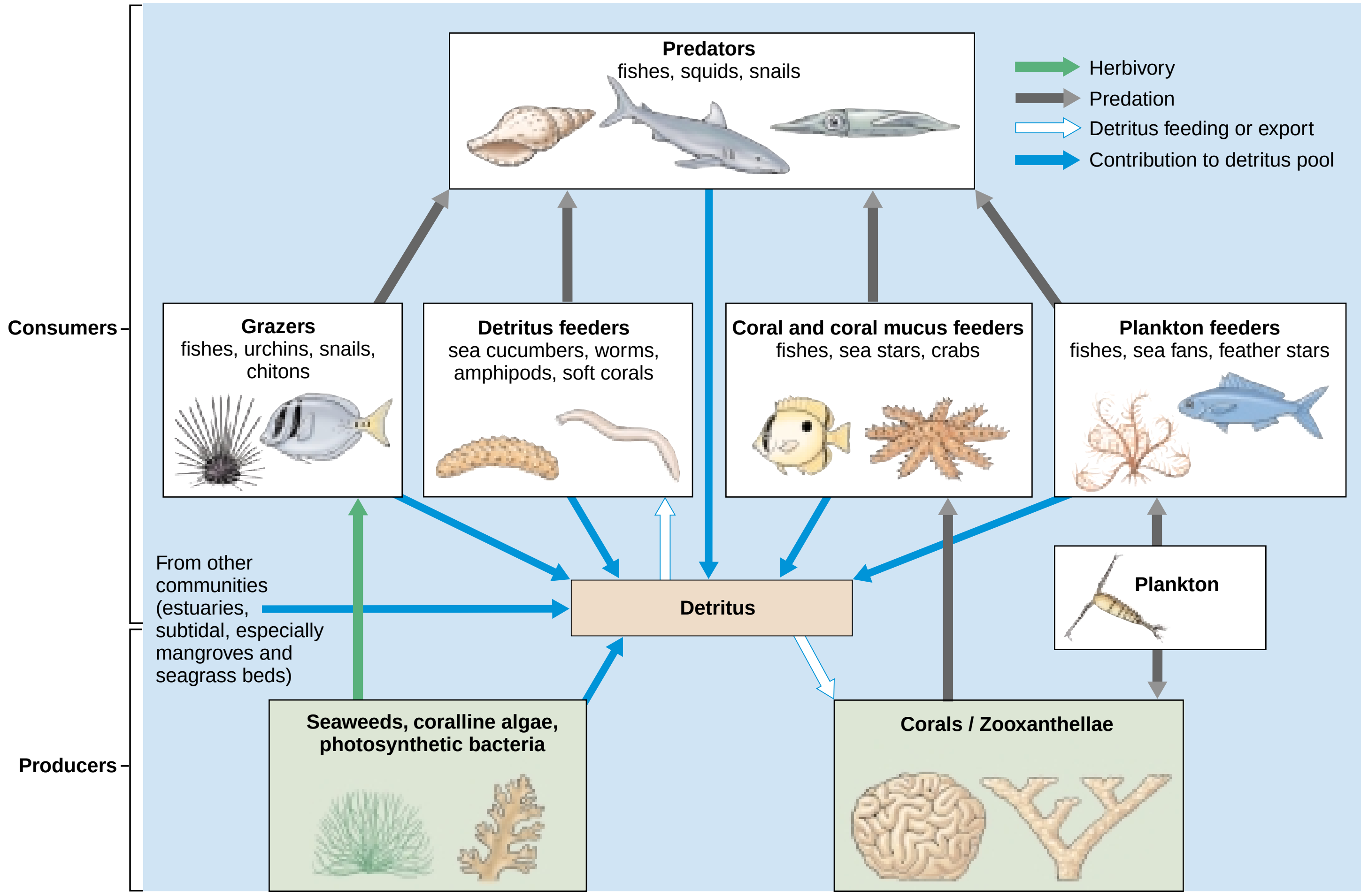


Figure 14.26 A generalized coral reef food web. Coral reefs are extremely diverse, and most components include many organisms in addition to those listed here.

a short, thick turf on the reef flat. A great many fishes, sea urchins, snails, and other animals graze on these seaweeds. The turf algae may perform more photosynthesis on the reef than the zooxanthellae, but biologists are not sure.

Zooxanthellae and turf algae are probably the most important primary producers on coral reefs.

Cyanobacteria, some other bacteria, and coralline algae are also primary producers on coral reefs. They probably account for less primary production than do zooxanthellae and turf algae.

Coral Reef Communities

With so many species on coral reefs, the interactions among them are exceedingly complex. What is known about these interactions is fascinating; what remains to be learned will be even more so.

Competition Space is at a premium on coral reefs, as it is in the rocky intertidal (see "The Battle for Space," p. 232). Corals, seaweeds, and many others need a hard place on which to anchor themselves. Corals and seaweeds need not just space but space in the sunlight. The reef is crowded, and most of the available space is taken. As a result the sessile organisms, those that stay in one place, must compete for space.

Sessile coral reef organisms must compete for space. Corals and seaweeds compete for light as well.

Corals compete for space in different ways. The fast-growing ones tend to grow upward and then branch out, cutting their neighbors off from the light. Other corals take a more direct approach and actually attack their neighbors (Fig. 14.27). Some use their mesenterial filaments for this. When they contact another coral, they extrude the filaments and digest away the tissue of the other coral. Still other corals develop special long tentacles, called **sweeper tentacles,** that are loaded with nematocysts and sting neighboring colonies. Corals differ in their aggressive abilities. The most aggressive corals tend to be slow-growing, massive types, whereas the less aggressive forms are usually fast-growing, upright, and branching. Both strategies have their advantages, and both kinds of corals thrive on the reef.

The two main ways in which corals compete for space are by overgrowing their neighbors and by directly attacking them.

Figure 14.27 When different species of coral come in contact, they attack each other. The pink band separating the brown (*Porites lutea*) and blue (*Mycedium elephantotus*) corals is a dead zone where the blue coral has killed the brown one in the process of overgrowing it. The width of the pink band corresponds to the length of the blue coral's tentacles. To the upper left of the brown coral is a soft coral (*Sarcophyton*), which may be attacking the brown coral by releasing poison. The brown coral seems to be stuck between a rock and a soft place!

Figure 14.28 Soft corals can form dense patches on coral reefs, as on this reef in Papua New Guinea.

Corals compete for space and light not only with each other, but also with seaweeds and sessile invertebrates. Like corals, encrusting algae have to produce a calcium carbonate skeleton and therefore grow relatively slowly. They tend to be found in places where corals don't do well because of sedimentation, wave action, or predation.

Under the right conditions seaweeds, except for encrusting forms, can grow much faster than either corals or encrusting algae. Even with the nitrogen fixation and nutrient cycling that occur on reefs, seaweeds are probably somewhat nutrient-limited most of the time. Hence they grow fairly slowly. The reef also has an abundance of hungry grazers that eat the seaweeds. The combination of nutrient limitation and grazing keeps the seaweeds in check. If the nutrient levels increase or the grazers are removed, seaweeds may rapidly take over, overgrowing and choking out corals and other organisms.

Soft corals are also important competitors for space on reefs (Fig. 14.28), and in some places they make up almost half the living tissue. Like most seaweeds, soft corals lack a calcium carbonate skeleton and are able to grow faster than hard corals. Some soft corals contain sharp little calcium carbonate needles, or **spicules**, that discourage predation. Many of them also contain chemicals that are toxic or taste bad to predators. Because of these defense mechanisms, only a few specialized predators eat soft corals. The defensive chemicals can also be released into the water, where they kill hard corals that come too close (Fig. 14.27). Another competitive advantage enjoyed by some soft corals is that they are not completely sessile. Though they stay in one place most of the time, they can move about slowly. This helps them invade and occupy available space on the reef.

Soft corals are important competitors for space on reefs. They grow rapidly, are resistant to predators, and can occasionally move about.

With all these competitive weapons at their disposal, why don't soft corals take over? Not much is known about how soft corals compete with reef-building corals and other reef organisms or what determines the winner. Many soft corals appear to have shorter lives than reef-building corals although some may live for decades. They are also more easily torn away by storm waves. They have symbiotic zooxanthellae like reef-building corals, but are much less efficient photosynthesizers. They also seem to depend on very favorable physical conditions. It is not known how these factors interact to determine when and where soft corals compete successfully for space on the reef.

Like soft corals, sponges often have spicules and nasty chemicals that protect them from predators. They can be important users of space on reefs, much more so in the Caribbean than in the Pacific and Indian oceans. Part of the reason for this seems to be that there are fewer species of coral in the Caribbean than in the Indo-West Pacific. This is a result of geological history. During the most recent series of ice ages, the sea surface was cooler. Corals survived in the heart of the Indo-West Pacific region, around Indonesia and New Guinea, but many coral species became extinct in other parts of the ocean. When the ice age ended, corals spread out again across the Pacific, recolonizing areas where they had died out. The Caribbean, however, was not recolonized because the Isthmus of Panamá blocked their dispersal. It is thought that the Caribbean contains only those coral species that managed to survive the ice ages there.

Figure 14.29 Diving on a coral reef is like taking a swim in a tropical fish aquarium—brightly colored fishes seem to be everywhere. The competitive relationships among the various species of fishes are poorly understood.

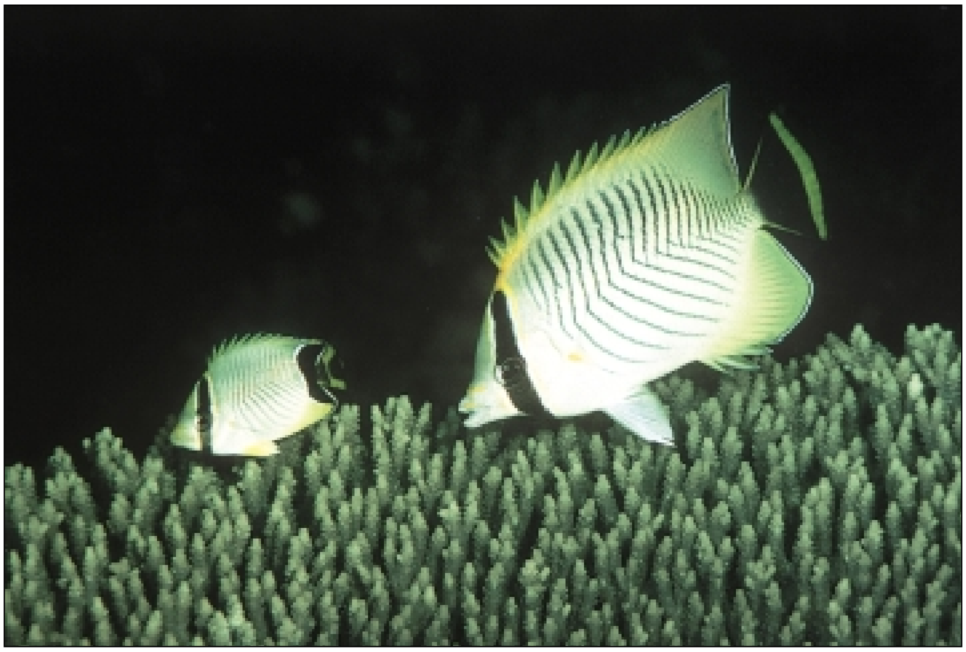


Figure 14.30 The chevron butterflyfish (*Chaetodon trifascialis*) is one of many reef animals that feed on corals without killing the entire coral colony. Its mouth is adapted for nipping off individual coral polyps (also see Fig. 8.28).

Coral reef fishes are another group in which competition may be important. Along with corals, fishes are probably the most conspicuous and abundant animals on the reef (Fig. 14.29). Many of these fishes share similar diets; for example, many species eat coral, many graze on algae, and many are carnivores. Different species of fishes of the same feeding type at least potentially compete with each other.

There is much debate about how competition affects coral reef fishes. One hypothesis is that competition is relatively unimportant, and that the abundances of individual species are determined mainly by how many of their larvae settle out from the plankton. With favorable currents and other conditions, many larvae will be available to settle out and the species becomes abundant. If the supply of larvae is low, for example if currents carry the larvae away from the reef, the species becomes rare. This is called a **pre-settlement** hypothesis because it holds that the nature of reef fish communities is determined by the availability of different species' larvae before the larvae settle.

An alternative, **post-settlement,** hypothesis is that for most species there are plenty of larvae available to settle out on the reef. The species that survive and become abundant are those that compete successfully for space, food, and other resources after the larvae settle, that is, as juveniles and adults. This hypothesis holds that so many different fish species can live on the reef because each does something a little different from other species, thereby avoiding competition and the risk of **competitive exclusion.** In other words, each species has its own particular **ecological niche.** According to this view, the structure of the fish community on a reef is determined by the range of resources available on that reef, and the fish communities of reefs vary because different reefs offer different resources.

It is still not clear whether the supply of larvae for settlement or post-settlement competition is more important in structuring reef fish communities. Their relative importance probably varies from species to species and from reef to reef, and other factors such as predation and natural disturbances are also significant.

There are two competing schools of thought about what controls the structure of reef fish communities. One holds that reef fish abundances are determined by how many larvae are available to settle out from the plankton. The other asserts that there is an ample supply of larvae for most species, and that reef fish communities are structured by competition among juveniles and adults after the larvae settle out.

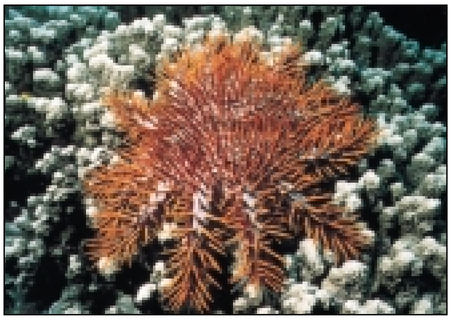


Figure 14.31 The crown-of-thorns sea star (*Acanthaster planci*) is an important and controversial coral predator.

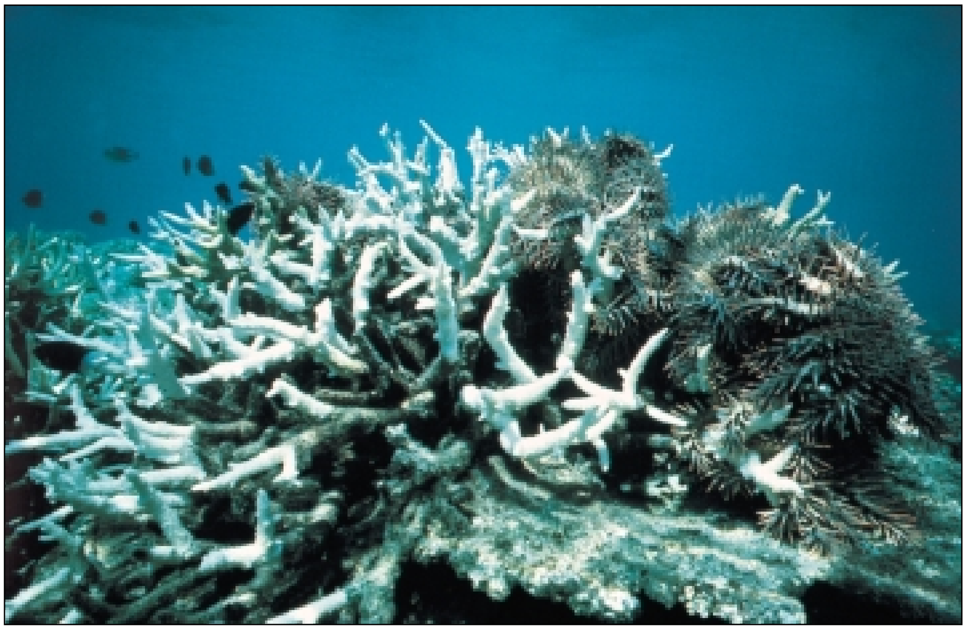


Figure 14.32 An outbreak of crown-of-thorns sea stars (*Acanthaster planci*) in Australia. The white branches of this colony of staghorn coral (*Acropora*) show the bare calcium carbonate skeleton left behind after being fed upon by several sea stars. Photograph courtesy of the Great Barrier Reef Marine Park Authority.

Predation on Corals As in other communities, predation and grazing are important in structuring coral reef communities. A variety of animals eat corals, but instead of killing the coral and eating it entirely, most coral predators eat individual polyps or bite off pieces here and there (Fig. 14.30). The coral colony as a whole survives and can grow back the portion that was eaten. In this respect, coral predation is similar to grazing by herbivores.

Coral predation affects both the number and type of corals that live on a reef, as well as how fast the reef as a whole grows. In Kane‘ohe Bay, for example, a butterflyfish (*Chaetodon unimaculatus*) slows the growth of a particular coral (*Montipora verrucosa*) that it likes to eat. When the coral is protected from the fish by a cage, it grows much faster. If it were not for the fish, this fast-growing coral would probably dominate other corals in the bay. Coral-eating snails (*Coralliophila, Drupella*) have similar effects on some reefs.

The Crown-of-Thorns Sea Star Another example of the effect of coral predators is the **crown-of-thorns sea star** (*Acanthaster planci;* Fig. 14.31). The crown-of-thorns feeds by pushing its stomach out through the mouth, covering all or part of the coral colony with the stomach, and digesting away the live coral tissue. The crown-of-thorns has distinct preferences for certain types of coral and avoids others—some corals must taste bad. Other corals harbor symbiotic crabs (see the photo on p. 113), shrimps, and fishes that discourage the sea stars by pinching and biting their **tube feet.**

The crown-of-thorns has had a major impact on some reefs. Beginning in the late 1950s, people began to notice large numbers, sometimes thousands, of the sea star on reefs scattered across the Pacific (Fig. 14.32). The sea stars in these large aggregations move in a mass across the reef, consuming almost every coral in their path. Reefs recover in 10 to 15 years, though it may take longer for slow-growing coral species to grow back.

The first response to the problem was panic. Coral reefs are valuable resources: They support fisheries, tourism, and recreation and protect coastlines from erosion. With the crown-of-thorns apparently threatening reefs, people decided to take action and control the sea star. The first attempt backfired. With limited knowledge of the animal's biology, some people cut the sea stars into pieces and dumped them back in the sea. Because sea stars can regenerate, the pieces grew into new sea stars! More sophisticated methods, such as poisoning the sea stars, were tried, but these methods were time consuming and expensive, did not work that well, and sometimes did more harm than good. Fortunately, the outbreaks mysteriously went away by themselves. Did the sea stars starve? Did they move away? No one knows. Crown-of-thorns outbreaks are still appearing, and disappearing, without explanation.

The debate over what causes these outbreaks has been controversial and sometimes emotional. At first it seemed obvious that the outbreaks must be unnatural, with humans to blame. After all, the plagues had never occurred before. Or had they? People had only begun using scuba a short time before the sea star plagues were noticed. Even if the plagues had been occurring for a long time, there were

Competitive Exclusion The elimination of one species by another as a result of competition.

• *Chapter 10, p. 210*

Ecological Niche The combination of what a species eats, where it lives, how it behaves, and all the other aspects of its lifestyle.

• *Chapter 10, p. 211*

Tube Feet Water-filled tubes possessed only by echinoderms, many of which end in a sucker and can be extended and contracted to grip things and to move around.

• *Chapter 7, p. 136*

no scientists around to see them. Geologists found fossil evidence of crown-of-thorns outbreaks dating back thousands of years, and in some places there are old stories and other historical evidence for past outbreaks. The outbreaks, then, may be a natural part of the reef ecosystem. A leading hypothesis is that in unusually wet years river runoff naturally brings more nutrients into the sea than normal. According to this hypothesis, the extra nutrients increase the growth of phytoplankton that are food for sea star larvae. It may also be that periodic population explosions are a natural part of the sea star's biology.

The evidence for past outbreaks of the crown-of-thorns, however, is hotly disputed. Some scientists are convinced that the plagues result from some human activity that has altered the ecological balance of reefs. Even if outbreaks did occur in the past, they seem to be happening more often. If occasional peaks in nutrient inputs cause natural outbreaks, nutrients from fertilizers, sewage, and other human sources may be making them worse. Another hypothesis is that fishers have caught too many fishes that eat young sea stars, allowing more to survive to adulthood. Some biologists have suggested that plagues occur because shell collectors have removed the triton shell, a large snail that preys on adult crown-of-thorns. Others argue that even without shell collectors the triton shell has always been naturally rare and unlikely to control sea star populations. They also point out that crown-of-thorns outbreaks continue to occur in areas where collecting triton shells has been banned for years.

The mystery of what causes crown-of-thorns plagues remains unsolved. The question has practical implications for the management and protection of reefs. If the plagues are caused by humans and threaten reefs, then we should probably try to do something to stop them. On the other hand, the "plagues" may be a natural, potentially important, part of the ecosystem. We might do more harm than good by interfering in a system we don't understand. The managers of the Great Barrier Reef have taken a middle road. They have developed an effective method to kill sea stars by injecting them with a poison. They use the poison, however, only if a crown-of-thorns outbreak is threatening a particularly valuable part of the reef, for example, a popular dive spot or a scientific research site. Otherwise, they allow the outbreak to run its course.

The crown-of-thorns sea star has undergone population explosions on many Pacific reefs. There is still debate about what causes the outbreaks and what should be done about them.

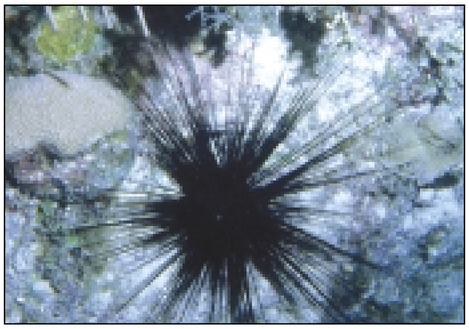


Figure 14.33 The long-spined black sea urchin (*Diadema antillarum*) is one of the most important grazers on Caribbean reefs. Closely related species are found on reefs in other parts of the world.

Grazing Grazing on algae by herbivores is at least as important in coral reef ecosystems as is predation on corals. Many fishes, especially surgeonfishes (*Acanthurus*), parrotfishes (*Scarus, Sparisoma*), and damselfishes (*Pomacentrus, Dascyllus*) graze intensively on reefs. Among the invertebrates, sea urchins (*Diadema, Echinometra*) are especially important. Many **microherbivores,** small invertebrates like snails, **chitons,** crustaceans, and polychaete worms, also eat algae.

Many seaweeds grow rapidly and have the potential to outcompete and overgrow corals. Under natural conditions they are kept in check by grazers, and to some extent by nutrient limitation. Caging experiments (see "Transplantation, Removal, and Caging Experiments," p. 236) have been used to demonstrate the importance of grazers. For example, seaweeds are abundant on sand flats next to many Caribbean reefs but relatively scarce on the reef itself. To test the hypothesis that reef fishes were responsible for this, biologists transplanted seaweeds from the sand flat to the reef. If left unprotected, they were soon eaten by fishes. When protected by cages, they grew even faster than on the sand flat! The seaweeds are perfectly capable of living on the reef, therefore, but are rare there because they get eaten. Caging experiments on the Great Barrier Reef have had similar results.

If grazers are removed, seaweeds can flourish and take over space from corals and other organisms. In many parts of the Caribbean, for example, grazing reef fishes have become less common because of fishing. When this happened another important grazer, a sea urchin (*Diadema antillarum;* Fig. 14.33), became more common. The urchin apparently benefited from the reduced competition. For years, the urchin seems to have picked up the slack for the fishes, and seaweed populations remained more or less stable. In 1983, however, a disease wiped out populations of the urchin over much of the Caribbean. Seaweeds, released from grazing pressure, became much more abundant on many reefs, at the expense of corals. In Jamaica they took over many reefs almost completely, and the formerly rich coral reefs are now more seaweed bed than coral reef.

Many reef scientists fear that such changes are becoming more and more common as fishing pressure on reefs escalates because of increasing populations and demand for tasty reef fish. There is often a double whammy. Coastal development often leads not only to more intensive fishing, but also to greater release of nutrients from sewage and agricultural fertilizer. Thus, seaweed growth may be artificially enhanced by eutrophication at the same time that the grazers that keep the seaweeds under control are removed. This is one of the main global threats to coral reefs.

Grazers help prevent fast-growing seaweeds from overgrowing other sessile organisms on the reef.

In addition to controlling how *much* algae there is, grazers affect which particular *types* of seaweed live on the reef and where. Coralline algae, for example, are abundant because the calcium carbonate in their tissues discourages grazers. Other seaweeds produce

"Must Have Been Something I Ate"

Ahhhhh! You're relaxing on a warm tropical night after a delicious fish dinner. The palm trees sway, a warm tropical breeze blows—and suddenly your bowels begin to churn. Before long your lips burn and tingle, and your hands and feet feel like pins and needles. You go into the kitchen for a drink, but the cool water feels warm. The cool floor and the cold compress you put on your forehead are also warm to the touch: The sensations of hot and cold are reversed. As you stagger to the bathroom, your arms and legs are heavy and weak. Now feeling really sick, you mumble, "Must have been something I ate."

You're right. What you have is a case of **ciguatera**—tropical fish poisoning. Maybe it will comfort you to know that you're not alone. Tens, perhaps hundreds of thousands, of people get ciguatera every year. And relax, you probably won't die, though you might be a little sick (if you're unlucky, *very* sick) for months or even years. Don't count on a cure, though there are various folk remedies that might help a little. The intravenous administration of an inexpensive sugar called mannitol also helps sometimes.

So what *is* ciguatera, anyway? The disease has been known for hundreds of years. The name comes from the Spanish word for a Caribbean snail: You can also get ciguatera from eating molluscs, and perhaps sea urchins, though fish dinners are the most common cause. Ciguatera is most common in the top predatory fishes on the reef, like jacks, barracudas, and groupers, but it can also be caused by eating herbivorous fishes like parrotfishes and surgeonfishes. A given kind of fish may be perfectly safe in most places, but poisonous in particular spots. To make matters even more confusing, ciguatera may disappear from one area and pop up in another. All of which makes things difficult for lovers of fresh reef fish.

Ciguatera is caused by toxic dinoflagellates that live on the reef. Herbivorous fishes eat the dinoflagellates, and the poison is passed on to the predatory fishes that eat them. As blooms of the dinoflagellates arise and die out, ciguatera comes and goes in the area. Predatory fishes range over larger areas and eat many fish, which may all contain small amounts of the toxin. Thus, they are most likely to cause ciguatera. Herbivorous fishes probably carry the toxin only when they feed in an area with a bloom.

The big problem is trying to tell when a fish carries the poison. You could just avoid reef fish altogether, but if you are in the tropics that means missing out on a lot of tasty meals. One way to tell if a fish is carrying ciguatera is to feed a bit to a cat: Cats are highly sensitive to ciguatera. If any mongooses are handy, they're good tasters too. Of course, this isn't exactly kind to the animals, who usually die if the fish carries ciguatera. Chemical tests for ciguatera poison are available but are not yet in widespread use. Furthermore, there are actually several different dinoflagellate toxins that can cause ciguatera and it is difficult to test for them all. We aren't even sure we know what they all are. For now at least, the best strategy is to avoid eating fish species known to carry a high risk of ciguatera. Otherwise, it's go hungry or take your chances.

noxious chemicals that are poisonous or taste bad; these seaweeds also tend to be abundant. Seaweeds that lack such defenses are most heavily grazed and thus tend to be rare. Even so, they generally grow rapidly and are an important food source.

Damselfishes provide some interesting examples of the effects of grazing on reefs. Many damselfishes graze on seaweeds inside territories that they vigorously defend, chasing away other fishes that happen to venture inside. Many such damselfishes actually "farm" their territories. They weed out unpalatable algae, pulling them up and carrying them outside the territory. What is left in the territory is a dense mat of tasty seaweeds, usually fine, filamentous types. Protected by the damselfish, these algae grow very rapidly and outcompete corals and coralline algae. Outside the territory, parrotfishes and surgeonfishes gobble up the algae, clearing space for other organisms. Thus, the community inside the territory is very different from that outside. One interesting point is that cyanobacteria, which are nitrogen fixers, are much more common inside damselfish territories than outside. Thus, damselfishes may indirectly have an important role in the nutrient balance of the reef.

Living Together Among the vast number of species that live on coral reefs, many have evolved special symbiotic relationships. There are far too many cases of symbiosis on the reef to describe here. In fact, coral reefs probably have more different symbiotic relationships than any habitat on earth. The few examples discussed here will give you some idea of how fascinating these relationships are.

Symbiotic relationships are very important in coral reef communities. Coral reefs probably have more examples of symbiosis than any other biological community.

We have already seen how mutualism between corals and their zooxanthellae is the essential feature of reef formation. Many other

Chitons Molluscs whose shells consist of eight overlapping plates on their upper, or dorsal, surface.

• *Chapter 7, p. 129*

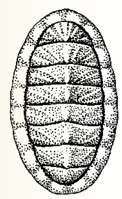


Figure 14.34 The giant clam (*Tridacna gigas*) does not deserve its reputation as a killer: Stories of people getting trapped in them and drowning are myths. Symbiotic zooxanthellae give the upper surface its blue and green colors, and provide food that allows the clam to get so big. The clam also filter feeds. The hole visible on the clam's fleshy upper surface is one of the siphons through which it pumps water to feed and obtain oxygen. Giant clams do not occur in the Caribbean.

organisms also have photosynthetic symbionts. Sea anemones, snails, and giant clams (*Tridacna*) all harbor zooxanthellae. The "deal" between the two partners is the same as in corals: The zooxanthellae get nutrients and a safe place to live, and the host gets food. Giant clams grow so large (Fig. 14.34) because their zooxanthellae provide a constant food supply.

There are primary producers other than zooxanthellae that live inside reef animals. As mentioned previously, some sponges have cyanobacteria that fix nitrogen in addition to performing photosynthesis. Certain sea squirts house a photosynthetic bacterium called *Prochloron*. *Prochloron* is especially interesting because it may be similar to the

Figure 14.35 An orange-fin anemonefish (*Amphiprion chrysopterus*) and its sea anemone host.

symbiotic organisms that eventually became the chloroplasts of plants (see "From Snack to Servant: How Complex Cells Arose," p. 75).

Another important example of mutualism on the reef is the relationship between corals and the crabs, shrimps, and fishes that help protect them from the crown-of-thorns sea star and other predators. Most corals host a number of **facultative** and **obligate symbionts,** especially crustaceans. Some of the obligate symbionts are parasites and harm the coral, some are commensals and apparently have no effect on the coral, and some are mutualists that benefit the coral. It is often hard to tell which is which, because for most symbionts the nature of the relationship between coral and symbiont is not well understood. Those who study such organisms frequently revise their ideas as more information is obtained. The crabs that protect their coral from predators, for instance, were once thought to be parasites.

Anemonefishes (*Amphiprion;* Fig. 14.35) have an interesting relationship with several kinds of sea anemones. The anemones inhabited by anemonefishes have a powerful sting and are capable of killing the fish. The fish have a protective mucus, however, that keeps the anemone from stinging. It is not known whether the mucus is produced by the fish themselves, by the anemone, or by both. When anemonefishes are newly introduced to an anemone, they typically rub against and nip the anemone's tentacles. They may be coating themselves with the anemone's mucus. To understand why this is an advantage, you have to remember that anemones have no eyes and no brain, but lots of tentacles. If the anemone simply stung everything it touched, it would end up stinging itself every time the tentacles bumped into each other. The anemone recognizes itself by the "taste" of its own mucus. When one tentacle touches another, the anemone detects the mucus coating on the tentacles and refrains from stinging. Anemonefishes may be taking advantage of this. On the other hand, there is evidence that the fishes' own mucus protects them against the anemone, and in some cases the fish can enter an anemone unharmed without having ever contacted it before.

Anemonefishes are protected by the anemone's stinging tentacles and brood their eggs under the anemone. In at least some cases the relationship is mutually beneficial because the anemonefish drive away other fishes that eat anemones. Anemonefishes kept in aquaria will sometimes feed their host, but this behavior does not seem to be important in nature. It is also possible that the fishes benefit their host in ways that are not yet understood.

Facultative Symbiont A symbiont that is not completely dependent on its partner and can live outside the symbiosis.
Obligate Symbiont One that depends on its partner and does not occur outside the symbiosis.

• *Chapter 10, p. 212*

Interactive Exploration

Check out the Online Learning Center at **www.mhhe.com/marinebiology** and click on the cover of *Marine Biology* for interactive versions of the following activities.

Do-It-Yourself Summary

The Online Learning Center provides a fill-in-the-blank summary that allows you to review and check your understanding of this chapter's subject material.

Key Terms

All key terms from this chapter can be viewed by term, or by definition, when studied as flashcards in the Online Learning Center.

Critical Thinking

1. What factors might account for the fact that the vast majority of atolls occur in the Indian and Pacific oceans and that atolls are rare in the Atlantic?
2. Scientists predict that the ocean will get warmer and the sea level will rise as a result of an intensified greenhouse effect (see "Living in a Greenhouse: Our Warming Earth," p. 394). How might this affect coral reefs?
3. There are only a few reefs off the northeast coast of Brazil (see map in Fig. 14.10), even though it lies in the tropics. How would you explain this?

For Further Reading

Some of the recommended readings listed here may be available online. These are indicated by this symbol and will contain live links when you visit this page in the Online Learning Center.

GENERAL INTEREST

Benchley, P., 2002. Cuba reefs. *National Geographic,* vol. 201, no. 2, February, pp. 44–67. The reefs and coral keys of Cuba are home to spectacular gardens of sponges, fishes, and other organisms.

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Wilkinson, C. (Editor), 2002. *Status of Coral Reefs of the World: 2002.* Australian Institute of Marine Science, Townsville, 378 pp.

See It in Motion

Within this chapter, this icon represents an underwater videoclip that helps illustrate a specific topic being discussed. These videoclips can be viewed within the Online Learning Center for this chapter.

Marine Biology on the Net

To further investigate the material discussed in this chapter, visit the Online Learning Center and explore selected web links to related topics.

- Coral reefs
- Class Anthozoa
- Color bleaching
- Mangroves
- Community ecology
- Competition
- Parasitism, predation, and herbivory
- Biodiversity
- Food webs

Quiz Yourself

Take the online quiz for this chapter to test your knowledge.