



CHAPTER 11

The Coral Reef Ecosystem

STUDENT LEARNING OUTCOMES

1. Analyze the conditions required for coral reef survival.
2. Explain the energy dynamics on coral reefs and the role photosynthesizers play in these dynamics.
3. Examine threats to coral reefs and potential solutions to their decline.
4. Discover the diversity of form, color, and habitat exhibited by coral reef fishes.
5. Compare and contrast the various mating systems of coral reef fishes.

CHAPTER OUTLINE

11.1 Coral Reefs

Coral Anatomy and Growth

Coral Distribution

Coral Ecology

Coral Reef Formation

Reproduction in Corals

Zonation on Coral Reefs

11.2 Coral Diversity and Catastrophic Mortality

RESEARCH in Progress: The Quest to Preserve Coral Reefs in Times of a Changing Climate

11.3 Coral Reef Fishes

Coral Reef Sharks and Rays

Case Study: The Lionfish Story: A Nonnative Invasion of the Sea Like Never Before

Coral Reef Teleosts

Study Guide

References

A healthy elkhorn coral (*Acropora palmata*) colony in St. Croix, U.S. Virgin Islands. This species has declined dramatically throughout its range and was the first coral species to be listed as a threatened species.

Courtesy of National Oceanic and Atmospheric Administration.

The tropical coral reef ecosystem is one of the most diverse and visually stunning ecosystems on Earth, with a species diversity that rivals that of rain forests. This diversity is immediately apparent when observing a coral reef underwater, with an amazing myriad of colors and unique body forms exhibited by the reef's inhabitants and a high number of life forms darting around the reef. Reef-building corals provide a three-dimensional living structure for other organisms to live near, on, or within. This structure is invaluable for the many inhabitants of the reef for survival, feeding, and reproduction, among other important life processes. The hard substrate that corals provide is in high demand and is a limited resource that is competed for. The evolutionary pathways of coral reef inhabitants have certainly included behavioral and physiological adaptations for obtaining space on the reef, and some of the behaviors exhibited by coral reef organisms are unique among the animal kingdom. In this chapter, we summarize the biology of coral reefs, a tropical ecosystem that provides, by virtue of its presence alone, millions of hectares of firm substrate and vertical structure on which countless plants and animals live, many of which are found nowhere else on Earth. The species that compose coral reefs are inherently interesting on their own, but the fact that they also create the physical structures for unique biological communities makes them especially fascinating and important subjects of study. We will also examine the biology and diversity of coral reef fishes and the health of coral reefs and their inhabitants worldwide, as coral reef mortality is a topic of grave concern.

11.1 Coral Reefs

For many people, thoughts of tropical islands conjure up images of a special type of marine ecosystem, coral reefs. Unlike the rocky substrate of intertidal communities, coral reefs are actually produced by some of the organisms that live on them. The entire reef, which may extend for hundreds of kilometers, is primarily composed of a veneer of tiny sea anemone-like creatures called *coral polyps*. These small colonial animals slowly produce the massive carbonate infrastructure of the reef itself, which a vast array of other organisms live on, around, and within.

Therein lies a wonderful biological paradox. Think of any common terrestrial ecosystem—a temperate forest, a tropical jungle, a Midwestern plain, or the field adjacent to your house. These areas are dominated by a great variety of plants (the producers) and contain just a handful of animal species, both herbivores and carnivores (the consumers). Conversely, a typical coral reef contains an impressive assemblage of consumers and just a few producers. The coral animals that create the reef feed by removing plankton from the water column, as do the many sponge species that decorate the reef and represent the second most important component of the benthic fauna on coral

reefs. Yet tropical seas are virtually devoid of plankton. That is why azure tropical waters are so transparent. A coral reef can be viewed as one giant animal that is inhabited by hundreds of other animals, such as sponges, snails and clams, squids and octopuses, sea anemones and jellyfish, shrimps and crabs, worms, and fish. This raises a number of questions: Where are the primary producers on a coral reef? Can an ecosystem violate the second law of thermodynamics by containing more consumers than producers? Why do planktivorous reef creatures, such as corals and sponges, not starve to death in the nearly plankton-free waters that surround them? In this section, we attempt to answer these fascinating biological riddles.

Coral Anatomy and Growth

Coral is a general term used to describe a variety of cnidarian species. Some grow as individual colonies; hence, not all corals produce reefs, and not all reefs are formed by corals; some reefs are formed by oysters, annelid worm tubes, red algae, or even cyanobacteria.

Reef-forming corals, the primary species that secrete the calcium carbonate (CaCO_3) matrix of coral reefs, are members of the class Anthozoa. All anthozoans are radially symmetrical, a morphology that is adaptive for sessile organisms, such as corals and sea anemones. Anthozoans are subdivided into two subclasses. The subclass Octocorallia, comprising soft corals, sea fans, sea whips, sea pansies, and sea pens, are characterized by the presence of polyps with eight pinnate, or feather-like, tentacles. Members of the subclass Hexacorallia have polyps possessing multiples of six smooth tentacles and include four orders of sea anemones (some exist as individuals, some in colonies, and others are tube dwellers) and three orders of corals (stony corals, false corals, and black corals). One group, the stony corals (order Scleractinia), is responsible for creating coral reefs. Stony corals and most of their cnidarian relatives are carnivores that use tentacles armed with cnidocytes that ring the mouth (Figure 11.1) to capture prey and push it into their gastrovascular cavity where it is digested.



Figure 11.1 Extended polyps of a coral colony. The numerous light-colored spots on the tentacles are batteries of cnidocytes.

Courtesy of George Schmahl, Flower Garden Banks National Marine Sanctuary, National Oceanic and Atmospheric Administration.

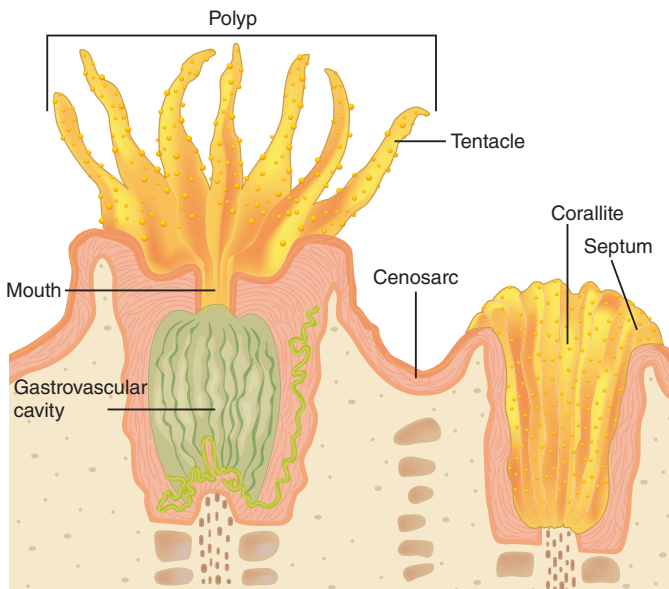


Figure 11.2 Cross section of a coral polyp and a calcareous corallite skeleton. The living coral tissue forms a thin interconnection, the cenosarc, over the surface of the reef.

Most corals are colonial, built of numerous basic structural units, or *polyps* (Figure 11.2), each usually just a few millimeters in diameter. Coral polyps sit in calcareous cups, or **corallites**, an exoskeleton secreted by their basal epithelium. Several wall-like **septa** radiate from the sides of each corallite, and a stalagmite-like **columella** extends upward from its floor. Periodically, the coral polyp grows upward by withdrawing itself up and secreting a new basal plate, a partition that provides a new elevated bottom in the corallite. In addition, the coral colony also increases in diameter by adding new asexually cloned polyps to its periphery. These new polyps secrete their own CaCO_3 corallites that share a wall with neighboring polyps. All polyps that comprise the colony are interconnected over the lips of their corallites via a thin sheet of tissue called a **cenosarc**; therefore, touching a living coral colony in any way can easily crush the cenosarc against its own CaCO_3 skeleton, thus compromising the colony by leaving it open

to infection. Coral reefs are living entities, and despite their stony appearance they are easily harmed by disturbances to the cenosarc.

The growth rate of corals is affected by light intensity (which is affected by water motion, depth, and turbidity), day length, water temperature, plankton concentrations, predation, and competition with other corals. Stony corals exhibit a large variety of growth forms that are typically described as encrusting, massive, branching, or foliaceous (Figure 11.3). In addition, many species are rather **polymorphic**, expressing different growth forms in response to differences in wave exposure or depth; therefore, growth may seem like a simple parameter to measure, but for corals it is not. Techniques for monitoring the growth of corals include measuring an increase in weight, diameter, surface area, branch length, number, or a combination of these factors. Individual coral colonies may grow continually for centuries or even longer. Some species exceed several meters in size. In general, species with lighter, more porous skeletons grow more rapidly than species with denser skeletons, and branching species grow more quickly than massive species. In general, an entire reef will grow upward as much as 1 mm a year and spread horizontally 8 mm a year.

The growth of an individual coral or an entire reef is not simply a function of the local rate of calcification for that species. The persistence of a coral colony or reef depends on a balance between the deposition and removal of CaCO_3 throughout the entire reef. In addition to calcium carbonate deposition by corals, several other types of organisms contribute their hard parts to the structure of coral reefs, including encrusting and segmented calcareous red and green algae; calcareous colonial hydrozoans; skeletons of crustaceans, bryozoans, and single-celled foraminiferans; mollusk shells; tests and spines of echinoderms; sponge spicules; and serpulid polychaete tubes. The loss or erosion of calcium carbonate is caused by grazers or scrapers, such as sea urchins and fish (Figure 11.4), and etchers, such as bacteria, fungi, and algae, that penetrate coral substrates. Infaunal organisms, such as sponges, bivalves, sipunculans, and polychaetes, also drill or bore into coral skeletons. From this encrusted, integrated base of living and dead

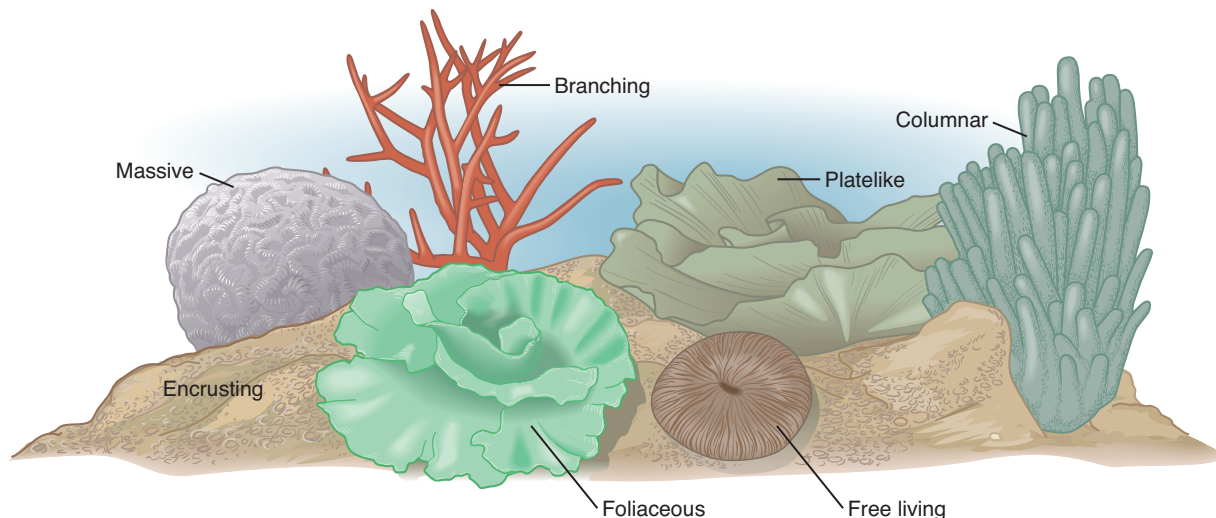


Figure 11.3 Corals exhibit a large variety of growth forms.



Figure 11.4 Parrotfish, major grazers of coral skeletal material and macroalgae, use their powerful jaws to produce large amounts of carbonate sand on the reef. These stoplight parrotfish are feeding on a star coral, *Orbicella faveolata*.

Courtesy of George Schmahl, Flower Garden Banks National Marine Sanctuary, National Oceanic and Atmospheric Administration.

skeletal remains, coral reef ecosystems have evolved as the most complex of all benthic associations.

DID YOU KNOW?



Although coral polyps are relatively tiny marine organisms, they combine to create the largest living structures on the entire Earth! Some reefs are so large that they are visible from space in satellite images. The Great Barrier Reef in Australia is the largest coral reef, stretching over a distance of 2,300 km (1,429 miles). It is made up of nearly 3,000 individual small reefs. The size and age of corals makes them truly remarkable organisms.

Coral Distribution

Like sea anemones, corals are ubiquitous. Non-reef-forming corals can be found in the deep sea (e.g., black corals) and in temperate zones (such as *Astrangia* on shipwrecks off New England), as well as in the tropics; however, there are several restrictions to the distribution of reef-forming corals, which are more abundant and diverse in the Indo-Pacific (about 700 species) than in the Atlantic Ocean (about 145 species; **Figure 11.5**). First, coral reefs generally are restricted to tropical and subtropical regions (usually below 30° latitude) where the annual sea-surface temperature averages at least 20°C. Second, coral reefs generally are better developed on the eastern margins of continents where shallow submarine platforms provide suitable habitat. Third, coral reefs generally thrive only in normal-salinity seawater; hence, reefs are rare on the eastern coast of South America because of the enormous outflow of freshwater from the Amazon River system. Fourth, reef-forming corals are usually found within 50 m of the surface in clear water on exposed surfaces.

These first two biogeographic restrictions suggest that reef-forming corals generally thrive only in warmer water, probably because only in warm waters can the high rates of CaCO_3 deposition needed for reef building be achieved. Hence, they are found in low latitudes and on eastern shorelines where coastal upwelling of cold water is less common and where the major ocean gyres direct warm tropical currents. These latitudinal limits of coral reef development also are often influenced by competition with macroalgae, with macroalgae being favored in higher latitudes because of increased nutrient concentrations, decreased water temperatures, and perhaps decreased grazing pressure.

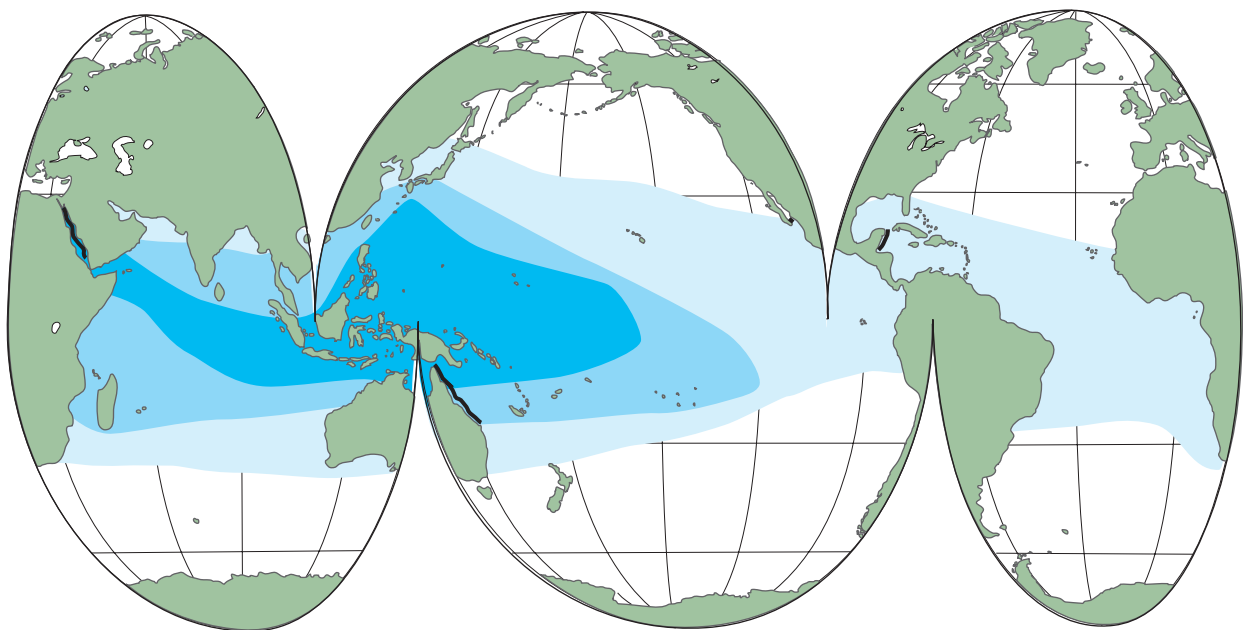


Figure 11.5 Distribution of reef-forming corals, by approximate number of genera: light blue, < 20 genera; medium blue, 20–40 genera; dark blue, > 40 genera. Heavy black lines indicate continental barrier reefs.

The third generalized limit to the global distribution of coral reefs suggests that coral animals cannot thrive in low-salinity seawater or in the sedimentation and high concentration of nutrients associated with rivers and freshwater runoff. The final biogeographic limitation—that coral reefs typically grow within 50 m of the surface in clear water on exposed surfaces—suggests that they need sunlight for their survival and growth. This limitation seems puzzling. Why would an animal (i.e., a coral colony) require sunlight, and why would their growth rates be affected by light intensity and day length, as described above? The answer to this question is also the answer to the apparent paradox posed at the beginning of this chapter.

Coral Ecology

Living intracellularly within the endodermal tissues of all reef-building, or **hermatypic**, corals are masses of symbiotic **zooxanthellae**, unicellular algae that, like all other photosynthetic organisms, require light. Solitary non-reef-building corals, such as *Astrangia* off the coast of New York, do not possess zooxanthellae and are termed **ahermatypic**. Zooxanthellae is a general term for a variety of photosynthetic dinoflagellates (genus *Symbiodinium*) that are mutualistic with several types of invertebrate species. To date, the many species of *Symbiodinium* cluster into eight genetic clades. Unlike the more typical dinoflagellates, zooxanthellae lose their flagella and cellulose cell walls. They occur in concentrations of up to 1 million cells/cm² of coral surface and often provide most of the color seen in corals. In fact, corals that grow in bright sunlight are often creamy white, whereas those in deep shade are nearly black. This difference is due to variations in the cellular concentrations of photosynthetic pigments of the zooxanthellae rather than differences in the densities of their cells.

Zooxanthellae and corals derive several benefits from each other. Thus, this relationship usually is considered a mutualistic

one. Corals provide the zooxanthellae with a stable, protected environment and an abundance of nutrients (CO₂ and nitrogenous and phosphate wastes from cellular respiration of the coral). In return, the host corals receive photosynthetic products (O₂ and energy-rich organic substances) from the symbiotic algae by stimulating or promoting their release with specific signal molecules that appear to alter the membrane permeability of the naked dinoflagellates. These zooxanthellae photosynthetically produce 10 to 100 times more carbon than is necessary for their own cellular needs, and almost all of this excess is transferred to the coral. Nearly all of the carbon that is transferred to the coral is respired and not used to build new coral tissue because it is low in nitrogen and phosphorus. This contribution by the zooxanthellae is sufficient to satisfy the daily energy needs of several species of corals. Soft corals are actually obligate symbionts, having lost the ability to capture and ingest plankton. The total contribution of symbiotic zooxanthellae to the energy budget of the reef is several times higher than phytoplankton production occurring in the waters above many reefs.

Hence, the answer to the mystery of how corals are able to construct enormous reefs in nutrient-poor waters is that they receive a significant supply of food from their algal associates, zooxanthellae. The coral animals also avoid the necessity of excreting some of their cellular wastes (which the algae absorb and use) and experience greater calcification rates than hermatypic corals that have been experimentally separated from their algal symbionts (Figure 11.6 a and b). Additional primary production on coral reefs is provided by several types of rather cryptic algae, cyanobacteria, and seagrasses. These include encrusting calcareous red algae, filamentous green algae that invade dead corals, a brown algal turf, photosynthetic symbionts in other reef invertebrates, macroalgae anchored in the sand, seagrass, and phytoplankton cells in the water column over the reef.

Despite the nutritional contribution of zooxanthellae, polyps of stony corals remain superbly equipped to prey on a

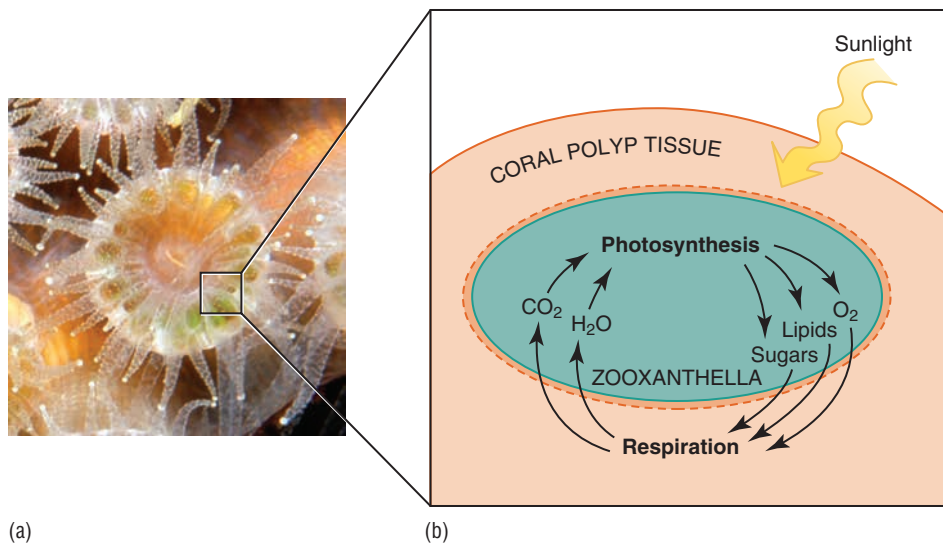


Figure 11.6 (a) Magnified view of coral polyps extending their tentacles to feed with algal symbionts visible. (b) Exchange of materials between zooxanthellae and their coral host.

(a) Courtesy of National Oceanic and Atmospheric Administration.

variety of external sources of food, and only soft corals depend solely on zooxanthellae. Corals with large polyps and tentacles, such as *Favia* or *Mussa*, feed exclusively on small fish and larger zooplankton, such as copepods, amphipods, and worms. Species with smaller polyps, such as *Porites* or *Siderastrea*, use ciliary currents to collect small plankton and detritus particles. Most coral polyps are capable of using **mesenterial filaments** to harvest particulate organic carbon from surrounding sediments. Corals also use their **mucus ciliary system** (analogous to the ciliated epithelium in the trachea of humans) to trap and ingest organic particles as small as suspended bacteria, bits of drifting fish slime, and even organic substances dissolved in passing seawater. Finally, the still controversial concept of **endo-upwelling** has been suggested as a possible source of additional dissolved nutrients, wherein geothermal heat deep within island reefs drives the upwelling of nutrient-rich water through the reef structure from depths of several hundred meters.

Corals are not the only animals on the reef that possess photosynthetic symbionts. Zooxanthellae also occur in other anthozoans, some medusae (such as the upside-down jellyfish, *Cassiopea*), sponges, and giant clams. In addition, it is well documented that sponges possess photosynthetic cyanobacteria. These photosynthetic symbionts are found in about 40% of sponge species from the Atlantic and Pacific Oceans, although their contribution to sponge ecology in the two oceans differs dramatically. On the Great Barrier Reef in the Pacific Ocean, 90% of the sponges on the outer reefs are **phototrophic** (they are flattened and obtain up to half of their energy from cyanobacteria), with 6 of 10 species studied producing three times as much oxygen as they consume. Very few of the sponges studied in the Caribbean Sea are phototrophic. This results in Caribbean sponges consuming 10 times more prey than their Pacific relatives. Perhaps this different reliance on energy from cyanobacteria is because primary productivity in the western Atlantic is higher than in the western Pacific.

Finally, nitrogen fixation, an activity that is light dependent, has recently been found to be associated with cyanobacteria living in the skeletons of various hermatypic corals. These nitrogen-fixing bacteria benefit from organic carbon excreted by the coral tissue. Corals also house other bacteria, archaea, and fungi, but little is known about the roles these microorganisms play. Perhaps these symbiotic associations are as important to corals as their mutualism with zooxanthellae, but more research is necessary.

The living richness of coral reefs stands in obvious contrast to the generally unproductive tropical oceans in which they live. The precise trophic relationships between producers and consumers on the reef are still largely unknown. Coral colonies seem to function as highly efficient trophic systems with their own photosynthetic, herbivorous, and carnivorous components. Crucial nutrients are rapidly recycled between the producer and consumer components of the coral colony. Because much of the nutrient cycling is accomplished within the coral tissues, little opportunity exists for the nutrients to escape from the coral production system. Coral colonies, therefore, are able to recycle their limited supply of nutrients rapidly between internal producer and consumer components and

keep productivity in coral reef communities relatively high (up to 5,000 gC/m² per year) compared with other regions of the ocean. Coral reefs are one example of an ecosystem adapted with high overall primary productivity despite low phytoplankton abundance.

Coral Reef Formation

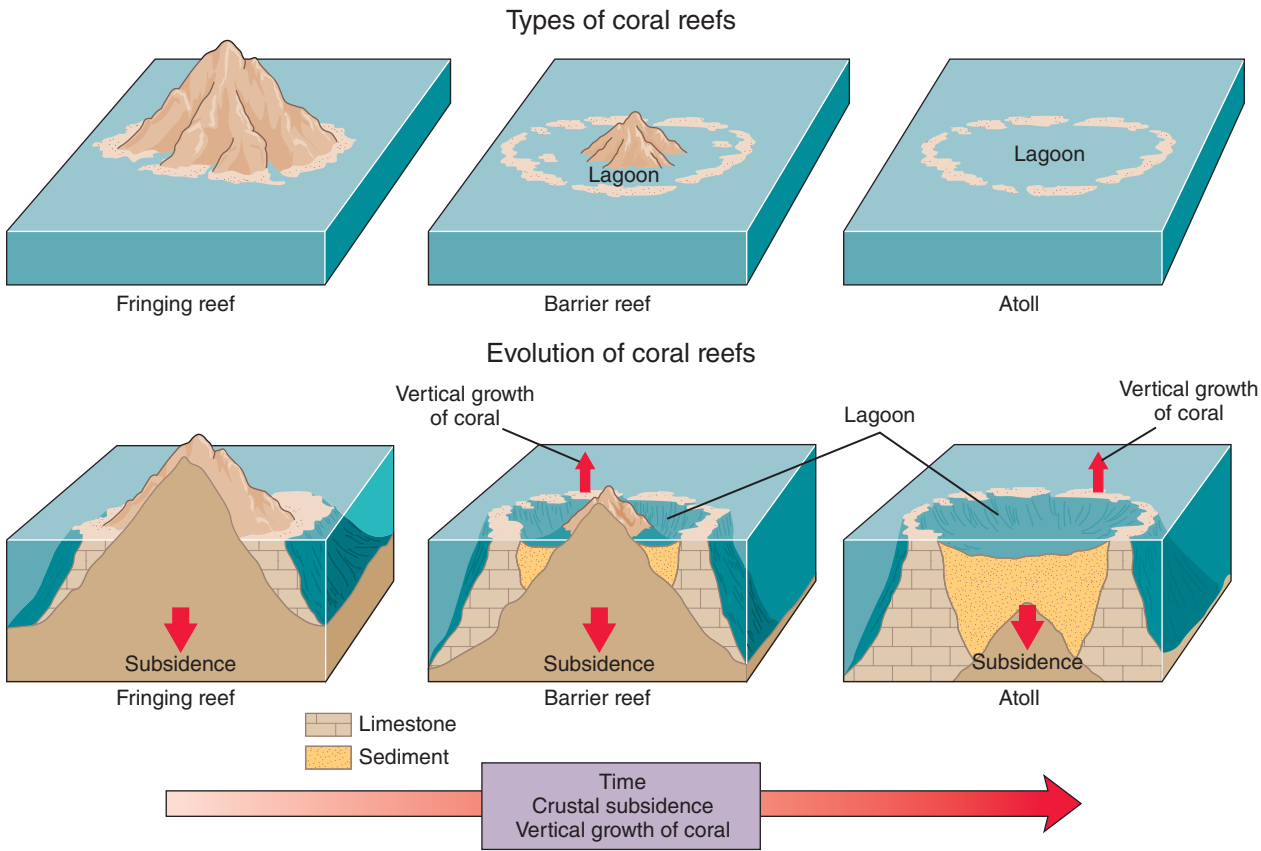
Coral reefs occur in two general types: shelf reefs, which grow on continental margins, and oceanic reefs, which surround islands. Oceanic reefs may be divided into three general subtypes: **fringing reefs**, **barrier reefs**, and **atolls**. Most shelf reefs are fringing reefs, which form borders along shorelines. Some of the Hawaiian reefs and other relatively young oceanic reefs are also of this type. The longest fringing reef known extends throughout the Red Sea, extending about 400 km. Barrier reefs are further offshore and are separated from the shoreline by a lagoon. The Great Barrier Reef of Australia is by far the largest single biological feature on Earth, bordering about 2,000 km of Australia's northeast coast. Smaller barrier reefs occur in the Caribbean Sea. Atolls are generally ring-shaped reefs from which a few low islands project above the sea surface (**Figure 11.7**). The largest atoll known is Kwajalein Atoll in the Marshall Islands, which has a lagoon 100 km long and 55 m deep.

The famous evolutionary biologist Charles Darwin studied the morphology of coral reefs on several islands while serving as a naturalist aboard the H.M.S. *Beagle* during its voyage to circumnavigate the Earth from 1831 to 1836. His observations led him to propose that essentially all oceanic coral reefs were supported by volcanic mountains beneath their surfaces. Fringing reefs, barrier reefs, and atolls, he suggested, were sequential developmental stages in the life cycle of a single reef. Within the tropics, he argued, newly formed volcanic islands and submerged volcanoes that almost reach the sea surface are eventually populated by planktonic coral larvae from other nearby coral islands. The coral larvae settle and grow near the surface close to the shore, forming a fringing reef (**Figure 11.8**, left). The most rapid growth occurs on the outer sides of the reef where food and oxygen-rich waters are more abundant. Waves break loose pieces of the reef and move them down the slopes of the



Figure 11.7 A satellite view of several of the hundreds of atolls that make up the Maldives.

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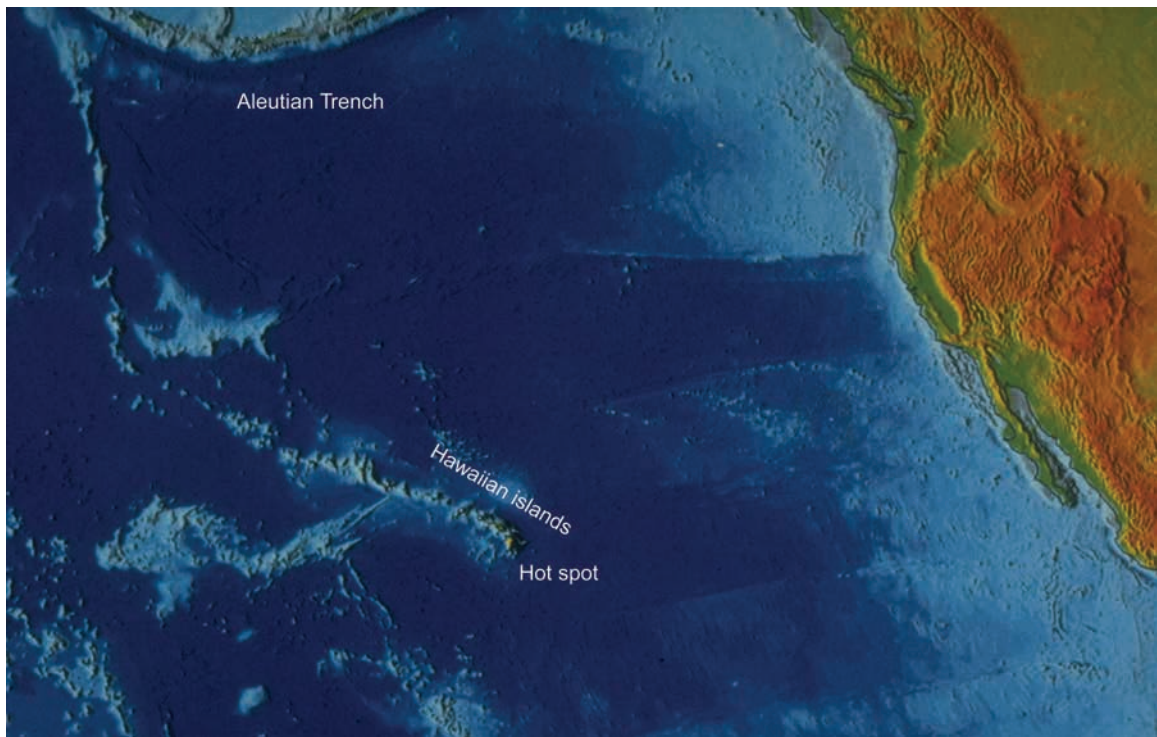


Figure 11.9 Chains of volcanoes along the Hawaiian Island–Emperor Seamount are carried, in a conveyor-belt fashion, north into deeper water by the movement of the Pacific Plate. Each volcano was formed over the “hot spot,” a continuous source of new molten material presently under Hawaii, and is carried to its eventual destruction in the Aleutian Trench.

Courtesy of NGDC/NESDIS/NOAA.

rose (about 1 cm/yr) until it reached its present level nearly 6,000 years ago. Many coral reefs did not grow upward quickly enough and perished. Those that did keep up with the rising sea are the living reefs we see today. Coral reefs in the Atlantic Ocean seem the most susceptible to glacier-induced changes in their morphology, and barrier reefs are most common in the Atlantic Ocean.

Coral reefs have also been subjected to the effects of global plate tectonics. The Hawaiian Islands and the reefs they support have been transported to the northwest by the movement of the Pacific Plate. Atolls at the northern end of the chain appear to have drowned as they reached the “Darwin Point,” a threshold beyond which coral atoll growth cannot keep pace with recent changes in sea level (Figure 11.9). At the Darwin Point, only about 20% of the necessary CaCO_3 production is contributed by corals.

Reproduction in Corals

Corals reproduce in a variety of ways, both asexually and sexually. Most corals bud off new polyps along their margins asexually as they increase in diameter. Sometimes these new polyps sever the cenosarc and initiate a new colony that is a clone of their neighbor. Branching species, such as *Acropora*, are frequently broken by storms or ship anchors into clonal colonies by fragmentation, the production of new colonies from portions broken off from established colonies. Fragmentation decreases the risk of mortality of the genotype and avoids the

risk of high mortality of larvae and juveniles during sexual reproduction. In addition, fragmentation by species with high growth rates often results in that species dominating certain reef zones (such as the buttress zone discussed below), as well as rapid recolonization after a disturbance. Researchers also have observed “polyp bailout” in the laboratory, when polyps crawl out of their corallites and drift away. It is not known whether these polyps remain viable or whether this occurs naturally on coral reefs, or rather is an artifact of a laboratory setting.

Corals also reproduce sexually, either by brooding fertilized eggs internally or by spawning millions of gametes into the water column for external fertilization. In brooding species, the eggs remain in the gastrovascular cavities of the adults where they are fertilized by motile sperm cells. The developing zygotes and resultant larvae are brooded before they are released to settle nearby. Some evidence suggests that coral species with small polyps have low numbers of eggs combined with internal fertilization and brooding, whereas large-cupped species spawn huge quantities of eggs that are fertilized externally. In addition, the strategy of sexual reproduction used (brooding larvae vs. spawning gametes) is highly correlated with taxonomic affiliation at the family level. Members of the families Agariciidae, Dendrophylliidae, and Pocilloporidae commonly brood, whereas broadcast spawning is predominant in the Acroporidae, Caryophyllidae, Faviidae, and Rhizangidae. Family Poritidae includes both brooders and broadcasters.



(a)



(b)

Figure 11.10 Spawning corals. (a) Female brain coral, *Diploria*, releasing egg packets; (b) male star coral, *Montastraea*, releasing sperm.

(a) Courtesy of Emma Hickerson, Flower Garden Bank National Marine Sanctuary, National Oceanic and Atmospheric Administration; (b) Courtesy of Flower Garden Bank National Marine Sanctuary, National Oceanic and Atmospheric Administration.

Of nearly 200 species of corals studied on the Great Barrier Reef, 131 were hermaphroditic spawners, 37 were dioecious spawners, 11 were hermaphroditic brooders, and 7 were dioecious brooders. Hence, spawning by hermaphrodites seems to be the most common method of sexual reproduction among corals. Spawning is usually accomplished during a highly synchronous event known as *mass spawning*. On the Great Barrier Reef of Australia, mass spawning by corals is a spectacular sight. More than 100 of the 340 species of corals found there synchronously spawn on only one night each year, just a few days after the late spring full moon (**Figure 11.10**). A similar episode of mass spawning has been documented in the Gulf of Mexico in the evening 8 days after the full August moon. Mass spawning by corals seems to be induced by specific dark periods, and it can be delayed by experimentally extended light periods. Mass spawning also seems to be broadly influenced by temperature. Such highly seasonal spawning is surprising in the tropics, an area wherein reproduction throughout the year is said to be the norm because of relatively constant climatic conditions.



Figure 11.11 Micrograph of a planula larva of the coral *Pocillopora*.

© Valerie Hodgson/Visuals Unlimited.

A few days after spawning, the fertilized eggs develop into ciliated **planula** larvae (**Figure 11.11**). These larvae, each already containing a supply of zooxanthellae, initially are positively phototactic; that is, they swim toward brighter light. This ensures that they remain near the sea surface where maximal dispersal by surface currents is likely. Then, after a specific time interval, they become negatively phototactic and attempt to settle on the seafloor. They thrive only if they encounter their preferred water and bottom conditions. From these planula larvae, new coral colonies develop and mature in about 7 to 10 years. Research has indicated that the larvae of *Pocillopora damicornis*, the commonly named cauliflower coral of the Indian and Pacific Oceans, are capable of reversible metamorphosis. In this species, the planula larva settles and begins to metamorphose into a juvenile. It forms a CaCO_3 exoskeleton, a mouth, and tentacles; however, if it is stressed within the first 3 days of settling, it will sever its attachments to its carbonate exoskeleton, revert back into a planula larva, and reenter the water column to search for an alternate settlement site. During their planktonic phase, coral larvae are capable of settling at new volcanic islands some distance from their island of origin. When they do, the form of the reef they eventually create depends on existing environmental conditions and the prior developmental history of reefs in the area.

It is unclear why some corals spawn synchronously and why this event occurs just several nights after the full moon. One advantage to mass spawning is that the chance of fertilization will increase greatly for one species. It is unclear, however, why mass spawnings are multispecies events, in that simultaneous spawning by many species may increase the risk of gamete loss via hybridization. Perhaps such an epidemic spawning event overwhelms (and satiates) active predators and filter feeders in the area, increasing the likelihood of gamete survival; however, these species also risk big losses by spawning on just a few nights each year. A sudden rain storm resulting in a drop in salinity of surface waters during a mass spawning event around Magnetic Island in November 1981 destroyed the entire reproductive effort of those corals for that year. Another hypothesis is that when environmental conditions necessary for

development of gametes exist, all coral species in an area spawn to take advantage of these conditions. Some conditions that appear to be of importance for coral spawning are water temperature, day length, tidal height, and salinity. Mass spawning is not a universal behavior of reef corals; in the northern Red Sea, none of the major species of corals reproduces at the same time as any of the other major species.

The early life phases of all marine organisms are sensitive time periods, with survival rates very low for most species, especially those that use broadcast spawning methods. The first challenge is fertilization, involving clouds of sperm and eggs being released into the water with hopes that some sperm will find eggs of the same species. After fertilization takes place the zygote must remain in the water column in favorable water conditions for rapid growth. The larvae are subject to ocean water movements with little control over where they reside in the water column. Fish and other predators feed on newly fertilized eggs and larvae, further decreasing the chances of survival. If a larva lives long enough to reach settlement age, it must find a suitable area to settle to on the seafloor. If suitable habitat is available at the right time for settlement, timing that involves multiple factors, settlement will take place and the juvenile coral will grow rapidly. Recent work on *Acropora palmata*, a federally listed threatened species, indicates that all of the early life stages of this coral species are negatively impacted by decreased pH. Decreased pH from ocean acidification is occurring today and is predicted to become more extreme over time as more CO₂ enters the oceans. If early stages of corals are negatively impacted by ocean acidification, there may come a time when new adults will be rare.

Interestingly, calcareous green algae found in the Caribbean coral reef ecosystem also exhibit mass spawning. Nine Caribbean species in 5 genera participate in a predawn episode, with a total of 17 species of green algae exhibiting highly synchronous reproductive patterns. Unlike the coral phenomenon described previously, closely related algal species broadcast their gametes at different times, and the environmental or biological triggers of these events remain unknown. In all cases, gametes from both sexes remain motile for 40 to 60 minutes after release but sink quickly after combining to form a zygote.

Zonation on Coral Reefs

Environmental conditions that favor some coral reef inhabitants over others in a particular habitat depend a great deal on wave force, water depth, temperature, salinity, and a host of biological factors. These conditions vary greatly across a reef and provide for both horizontal and vertical zonation of the coral and algal species that form the reef. **Figure 11.12**, a cross section of an idealized Indo-Pacific atoll, includes the major features and zones of the reef.

The living base of a coral reef begins as deep as 150 m below sea level. Between 150 and 50 m on outer reef slopes, a few small, fragile species, such as *Leptoseris*, exist despite the low level of sunlight that penetrates to these depths. Above 50 m and extending up to the base of vigorous wave action (at a depth of approximately 20 m) is a transition zone between

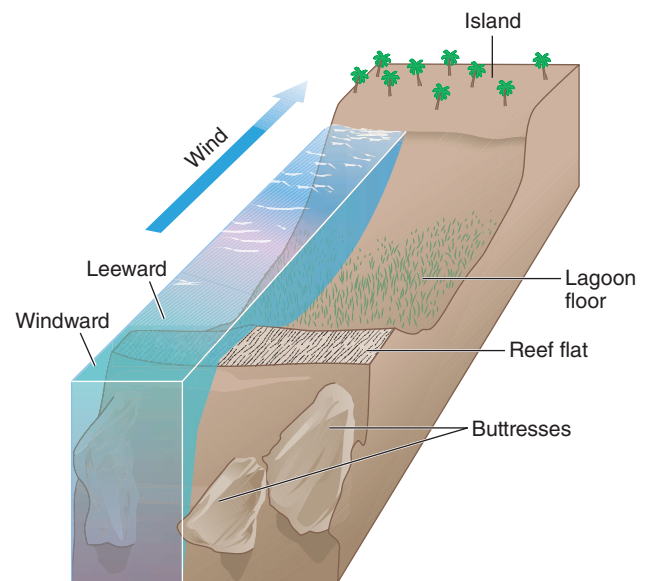


Figure 11.12 Cross-sectional zonation of an atoll.

deep- and shallow-water associations. In this zone, the corals and algae receive adequate sunlight, yet are sufficiently deep to avoid the adverse effects of surface waves. Several of the delicately branched species commonly found in the protected lagoon waters also occur in this relatively calm transition zone.

From a depth of about 20 m to just below the low-tide line is a rugged zone of spurs, or buttresses, radiating out from the reef. Interspersed between the buttresses are grooves that slope down the reef face. This windward profile of alternating buttresses and grooves is useful in dissipating some of the energy of waves that crash into the face of the reef, but damage to the reef and its inhabitants is inevitable. The grooves drain debris and sediment produced by wave impacts off the reef and into deeper water. Continual heavy surf makes it difficult to conduct detailed studies of the buttress zone, but it is known to be dominated by several species of encrusting coralline algae and by rapidly growing branching coral species (such as *Acropora*) that repair damage quickly and thrive when fragmented. Small fish seem to be in every hole and crevice on the reef, and many of the larger fishes of the reef—sharks, jacks, and barracudas—patrol the buttresses in search of food.

Most coral reefs are swept by the broad reaches of the trade winds. The waves generated by these winds crash as thundering breakers on the windward sides of reefs. Windward reefs are usually characterized by a low, jagged algal ridge that suffers the full fury of incoming waves. In this high-energy habitat, a few species of calcareous red algae, especially *Porolithon*, *Hydrolythion*, *Goniolithon*, and *Lithothamnion*, flourish and produce the ridge, creating new reef material as rapidly as the waves erode it. A few snails, limpets, and urchins (**Figure 11.13**) can also be found wedged into surface irregularities. Slicing across the algal ridge are surge channels that flush bits and fragments of reef material off the reef and down the seaward slope.

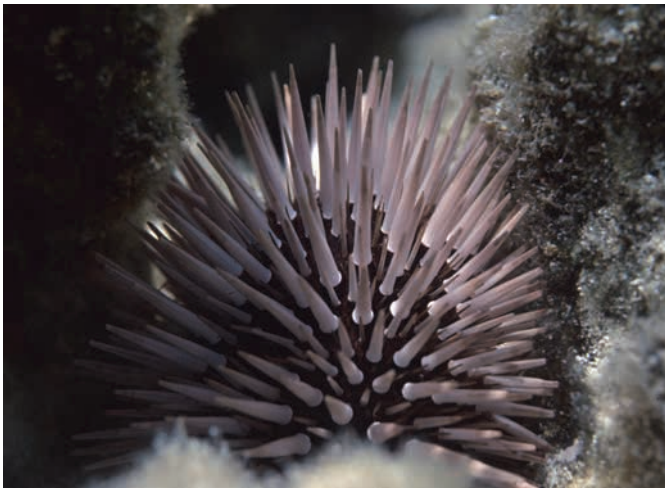


Figure 11.13 A sea urchin.

Courtesy of Dr. Dwayne Meadows, National Oceanic and Atmospheric Administration.

Extending behind the algal ridge to the island (or, if the island is absent, to the lagoon) is a reef flat, a nearly level surface barely covered by water at low tide in the Atlantic (Indo-Pacific reef flats are intertidal). The reef flat may be narrow or very wide, may consist of several subzones, and may have an immense variety of coral species and growth forms. In places where the water deepens to a meter or so, small raised microatolls occur. Microatolls are produced by a half dozen different genera of corals and, with other coral growth forms, provide the framework for the richest and most varied habitat on the reef. Burrowing sea urchins are common, and calcareous green algae and several species of large foraminiferans thrive and add their skeletons to the sand-sized deposits on the reef flat. The sand, in turn, provides shelter for other urchins, sea cucumbers, and burrowing worms and mollusks.

One of the most spectacular animals of the reef flat is the giant clam, *Tridacna*. The largest species of this genus occasionally exceeds a meter in length and weighs more than 100 kg. Some tridacnids sit exposed atop the reef platform; others rock slowly to work themselves into the growing coral structure beneath (**Figure 11.14**). Like corals and many other invertebrates, tridacnid clams house dense concentrations of zooxanthellae in specialized tissues, particularly the enlarged mantle that lines the edges of its shell. When the shell is open, the pigmented mantle tissues with their zooxanthellae are fully exposed to the energy of the tropical sun.

Tridacnid clams were long thought to “farm” their zooxanthellae in blood sinuses within the mantle and then transport them to the digestive glands, where they were then digested by single-celled amoebocytes. However, using elaborate staining and electron microscope techniques, scientists have demonstrated that the digestive amoebocytes of *Tridacna* selectively destroy only the old or degenerate zooxanthellae. Healthy zooxanthellae are maintained to provide photosynthetic products to their hosts in dissolved rather than cellular form. This selective capability of amoebocyte cells is a wonderful example of an advanced adaptation for survival in a sedentary marine organism.



Figure 11.14 A giant clam, *Tridacna*, amid mixed corals. Note the blue mantle tissue that is brightly colored due to the presence of innumerable mutualistic zooxanthellae.

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The tranquil waters of the lagoon protect two general life zones: the lagoon reef and the lagoon floor. The lagoon reef is a leeward reef. It forms the shallow margin of the lagoon proper and is usually free of severe wave action. It lacks the challenging algal ridge characteristic of the windward reef and in its place has a more luxuriant stand of corals (**Figure 11.15**). Other algae, some specialized to burrow into coral, and uncountable species of crustaceans, echinoderms, mollusks, anemones, gorgonians, and representatives of many other animal phyla flourish in the lagoon reef. In this gentle, protected environment, single coral colonies of *Porites* and *Acropora* may achieve gigantic proportions. Branching bush- and treelike forms extend several meters from their bases. The plating, branching, and overtopping structures common in the protected lagoon are most likely



(a)

Figure 11.15 Variation in coral growth forms: (a) table coral, *Acropora*: (Continued)

(a) © Andy Lim/Shutterstock, Inc.



(b)



(c)

Figure 11.15 (continued) (b) brain coral, *Diploria*; and (c) staghorn coral, *Acropora*.
 (b) © Lawrence Cruciana/Shutterstock, Inc.; (c) © Andy Lim/Shutterstock, Inc.

structural adaptations evolved in response to competition for particles of food and sunlight, two resources vital to the survival of reef-forming corals.

11.2 Coral Diversity and Catastrophic Mortality

The great diversity of species on coral reefs is legendary and rivals that of tropical rain forests. The classic explanation for this high diversity was that the uniform and predictable

conditions on tropical coral reefs promoted high diversity by enabling species to become increasingly specialized relatively quickly. Recently this view has been challenged by an opposing argument that suggests that the high diversity of coral reefs is a nonequilibrium state in which diversity can persist only if it is disturbed. Like some rocky intertidal communities, coral reefs are subject to severe disturbances (e.g., hurricanes) often enough that equilibrium, or a climax stage, may never be reached, and high diversity is maintained by frequent catastrophic mortality. According to this view, some of the catastrophic mortality of corals and coral reef species that has been observed in the past 25 years can be viewed as natural perturbations of these communities rather than abnormal events. One common natural cause of catastrophic coral mortality is storm waves from hurricanes and typhoons. At Heron Island on the Great Barrier Reef, for example, the highest number of species of corals occurs on the crests and outer slopes that are constantly exposed to damaging waves. In fact, it has been reported that the most significant factor determining the spatial and temporal organization of Hawaiian coral reef communities is physical disturbance from waves. Nevertheless, there is still some cause for concern about coral loss, especially when new corals do not appear to be replacing those lost. The recent rate of loss of coral reefs worldwide may be higher than ever before, and it is likely that at least some of the loss is due to anthropogenic sources of pollution, disturbance, and changes to ocean chemistry due to ocean acidification. When coupled with natural causes of reef mortality, these human-induced mortality events may exceed a reef's ability to recover.

Coral reefs fringe about one sixth of the world's coastlines and are estimated to house about 25% of known marine species. Sadly, over half of those reefs are now threatened by human activities, with the Caribbean region being hardest hit. Moreover, the forecast for future mortality is even more dire. In 1994, the Global Coral Reef Monitoring Network (part of the International Coral Reef Initiative), a consortium of hundreds of coral reef scientists and managers from nearly 100 countries, published a *Call to Action* document concerning global coral reef health. Several updates have been made to this document that is now called the *Continuing Call to Action*, and in the latest edition published in 2013 it was confirmed that the world has effectively lost 19% of coral cover since 1950 and that over 60% of the world's reefs are under immediate and direct threat. The *Continuing Call to Action* document is an attempt to reach out to governments, individuals, or anyone with any influence on the health of our world ocean to keep the issue of coral reef health at the forefront of conservation efforts. The negative impacts humans are having on coral reefs worldwide are ongoing, will not be remedied quickly, and some may be irreversible.

In response to the declining trends in coral reefs in waters of the United States or U.S. territories, the National Marine Fisheries Service has approved requests to add numerous species to the threatened species list. As of 2016, 22 species have been listed, 7 from the Caribbean and 15 from the Indo-Pacific. Of the 22 total, 10 are in the genus *Acropora*, discussed throughout this chapter. Petitions to list other species have been submitted and rejected, and more are certainly being crafted as this

RESEARCH in Progress

The Quest to Preserve Coral Reefs in Times of a Changing Climate

It has been estimated that more than 50% of the world's coral reefs have perished in the last century. With climate change, ocean acidification, and other anthropogenic threats imminent, some scientists predict that coral reefs will be gone within 50 years. This prediction is grim, as coral reefs support countless other life forms in their vast ecosystem, including commercially important or rare fish and invertebrate species. From an economic standpoint, coral reefs support many economies worldwide as tourist attractions for diving, glass-bottom boats, fishing, and other ecotourism pursuits. A world ocean without corals would be an entirely different place than we experience today.

The threat of the great demise of coral reefs worldwide has inspired research on corals to investigate their basic life history characteristics and tolerance to stressors such as increased temperature and acidity. Surprisingly little research has been conducted on corals and their algal symbionts with respect to environmental stressors, which is the basic information necessary to predict the effects of environmental changes on corals. Most corals worldwide are limited by temperature due to their algal symbionts. Although temperature tolerances vary, for many corals temperatures above 32°C (90°F) can lead to coral bleaching events. Water temperature predictions are made through satellite monitoring and mapped to indicate potential coral bleaching events around the world based on our limited knowledge of coral heat tolerances (Figure A).

The prediction for climate change is an increase in water temperature worldwide by 2°F to 4°F (1°C) over the next century, potentially leading to many bleaching events.

Corals already living at the high end of their heat tolerance were once predicted to perish as climates warm several degrees, but research conducted by scientists at Stanford University suggests that some corals are currently capable of tolerating remarkably high temperatures, and some may actually be able to adapt to warmer temperatures if allowed time to acclimate. Some populations of *Acropora hyacinthus* (Figure B) in American Samoa live in waters with little mixing, leading to extremely high temperatures (35°C [95°F]). These temperatures are hotter than scientists believed corals should be able to survive in. Other nearby populations of the same species live in well-mixed waters with temperatures in what is considered the normal range for corals. Upon observing these corals surviving and thriving in very warm water, the following research questions were explored: (1) how is *Acropora hyacinthus* capable of surviving in 35°C (95°F) water? and (2) can *Acropora hyacinthus* currently living in cooler water adapt to warmer conditions, and if so, do they require an acclimation period?

To answer the question of how *Acropora hyacinthus* is adapting to warmer waters, researchers looked at the genes of corals. Genetic test results indicated that the corals living in high temperatures appear to be able to express genes that produce particular proteins that aid in resisting physiological damage from increased temperatures. Corals found residing in warmer water possess these genes and use them for protection and to thrive in water temperatures that should kill their algal symbionts and cause physiological stress to the corals. It was also discovered that the *Acropora hyacinthus* living in moderate temperatures possess the same genes, but do not express them while living in moderate temperatures. Other corals have been documented actually switching out

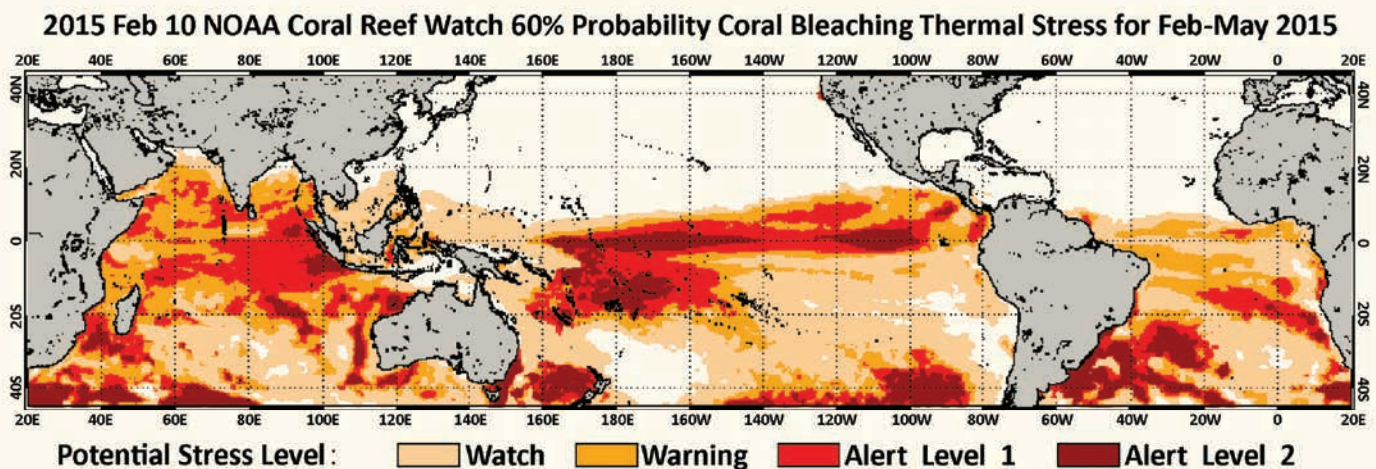


Figure A Water temperature predictions for the entire ocean provide useful information to potentially predict coral bleaching events.

Courtesy of National Oceanic and Atmospheric Administration ReefWatch.



Figure B A healthy *Acropora hyacinthus* in the Maldives.
Courtesy of MDC Seamarc Maldives.

their algal symbionts for new ones that are more heat resistant when water temperatures rise.

Researchers set out to answer the question of the ability of *Acropora hyacinthus* populations living in moderate temperatures to adapt to much warmer waters by transplanting corals in their natural habitat from a cooler area to a warmer area. Corals transplanted from cooler waters to warmer ones bleached quickly. The same experiment was conducted in the winter, allowing transplanted corals to acclimate before temperatures rose significantly, and these transplanted corals survived. To verify these results, laboratory experiments were conducted in a more controlled setting. Corals that were allowed acclimation time, sometimes as little as 2 weeks, survived. These results confirmed the field experiment results and suggest that corals may be able to adapt to warmer waters relatively quickly, likely by turning on the genes that provide instructions for proteins that help protect the corals and their symbionts.

These study results are promising and indicate that some coral species may be more resilient than scientists initially thought. Although this is just one study, it sheds light on the adaptive mechanisms that corals possess for surviving in a changing environment. Corals have been in existence for millions of years and have survived wide swings in environmental conditions, so their

ability to adapt is not surprising in some ways. The problem that still exists is that many anthropogenic environmental changes are taking place much more quickly than natural environmental fluctuations do. Whether corals can adapt and change quickly enough to keep up with increased temperature, acidity, and nutrients is still unknown, but the information gained from studies like this one are paramount to understanding the possibilities and to potentially intervening to save coral reefs worldwide.

Critical Thinking Questions

1. Is it surprising to you that some corals can resist physiological damage when water temperatures are extremely high? Explain your answer.
2. How can having an understanding of the potential adaptive capabilities of corals to changing climates help humans to preserve corals?

For Further Reading

- Palumbi, S. R., D. J. Barshis, N. Traylor-Knowles, and R. A. Bay. 2014. Mechanisms of reef coral resistance to future climate change. *Science* 344:895–898.
- Seneca, F. O., and S. R. Palumbi. 2014. The role of transcriptome resilience in resistance of corals to bleaching. *Molecular Ecology* 24:1467–1484.

book is written. Protecting corals from collection, pollution, and other harm due to humans will no doubt be instrumental in protecting and reviving this crucial ecosystem.

DID YOU KNOW?



Over half a billion people are impacted by the health of coral reefs worldwide, and around 30 million are totally dependent upon them. Coral reefs supply food, jobs in various industries, protection from storms, and many other services to humans. It is estimated that these services contribute nearly \$30 billion to the world economy annually. Healthy reefs are a great benefit to humans and the inhabitants of reefs.

The main human activities that are implicated as causes for this unprecedented reef mortality include agricultural activities, deforestation, and coastal development, all of which introduce sediments, excessive nutrients, and assorted pollutants into coastal areas. A coating of sediment on a coral colony can smother it, clogging its feeding structures and increasing the colony's energy expenditure by causing its mucociliary system to work overtime to rid its surface of sediment particles. Sediments also decrease the photosynthetic output of zooxanthellae by shading them and reducing their light absorption.

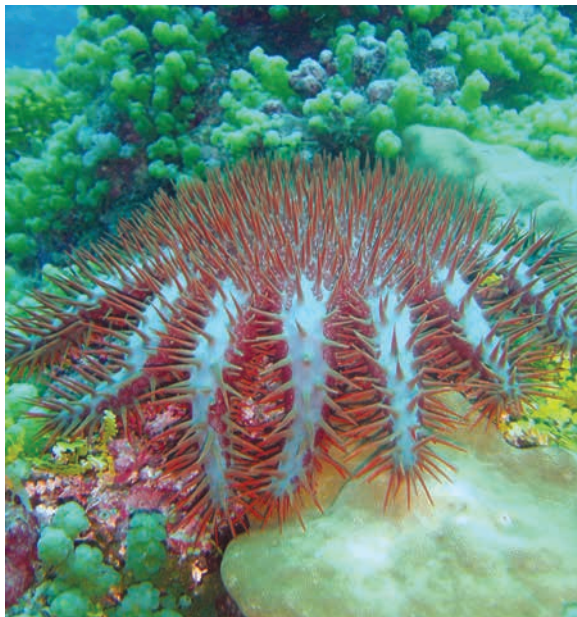
Elevated nutrient levels occur when runoff from agricultural areas injects excess quantities of fertilizers in the waters that bathe coral reefs. Sewage runoff also supplies unnaturally high concentrations of nutrients to coastal areas. These increased concentrations of nitrogen and phosphorus enhance algal growth and enable macroalgae to dominate corals in their competition for space on the reef. They also result in phytoplankton blooms that cloud the water and further handicap zooxanthellae. These two common anthropogenic causes of coral mortality, increased sedimentation and eutrophication, are thought to be responsible for the devastation of corals in the Florida Keys, in parts of Hawaii, and elsewhere that has occurred in recent decades.

Other reef herbivores seem to be equally important in helping corals maintain their dominance over rapidly growing seaweeds. A waterborne pathogen killed large numbers of a ubiquitous, long-spined, black sea urchin (*Diadema antillarum*) in the Caribbean Sea in 1983. It is estimated that 93% of the urchins in an area of 5 million square kilometers perished during what Knowlton called “the most extensive and severe mass mortality ever reported for a marine organism.” The urchin mass mortality event is now rivaled by the sea star mass mortality seen in 2014 on rocky shorelines of the Pacific Coast. The rapid extermination of this urchin, an important grazer of algae, enabled algal populations to overgrow corals in their competition for space on reefs. Some Caribbean reefs still have not recovered and remain green, fuzzy remnants of their former beauty. Although the cause of this epidemic remains undetermined, some speculate that the Panama Canal enabled a virulent Pacific pathogen to make its way into the Caribbean Sea to cause these urchin deaths. If this is the case, humans are once again to blame for the resultant coral mortality.

Moreover, many reefs are badly overfished, and this removal of the majority of herbivorous teleosts from a reef by overfishing also enables macroalgae to overgrow corals quickly. Yet this is not the only impact that overfishing has on reefs. The methods used for removing desirable teleosts, either for food or for aquarium display, also result in reef destruction. Because the structural complexity of coral reefs provides countless homes and hiding places for reef fishes, traditional low-impact fishing methods (such as hook and line and netting) are inefficient ways to capture reef teleosts. Thus, fishers and shell collectors on reefs often turn to much more destructive methods, including dynamite, crowbars, and poisons, to obtain their catch. Dynamite and crowbars destroy the physical structure of the reef, and poisons (cyanide is used most commonly) can stun fish that then become available for the live fish trade (popular among Asian restaurants and aquarium hobbyists). It is estimated that the use of cyanide results in the unintentional deaths of about 50% of the fish exposed on the reef and the subsequent deaths of about 40% of captured fish during transport. This \$1.2 billion industry centered in Southeast Asia, although lucrative, is very damaging and incredibly wasteful. It is estimated that only about 4% of Philippine reefs and less than 7% of Indonesian reefs remain unaffected by cyanide use.

Overfishing can also lead to outbreaks of coral predators, with massive mortality of corals being the obvious consequence. Over the past 50 years, several outbreaks of the coral-eating crown-of-thorns sea star, *Acanthaster planci* (Figure 11.16a), have occurred in the western Pacific Ocean. In some places, coral mortality adjacent to aggregations of the sea stars approached 100%. During the first outbreak in the 1960s, ecologists speculated that these sudden occurrences of large populations of this damaging sea star were the result of human activities, specifically the disappearance of its major predator, the Pacific triton, *Charonia tritonus* (Figure 11.16b). A large and beautiful snail, the Pacific triton had been nearly exterminated by shell collectors, but now populations appear to be recovering. Others suspect that the population increases are due to natural causes, such as unusually frequent storms.

Research has shown that more recent *Acanthaster* outbreaks occurred about 3 years after periods of unusually abundant rainfall. Perhaps abnormally high rainfall causes nutrient runoff, which leads to plankton blooms that feed *Acanthaster* larvae, resulting in subsequent increases in their successful settlement. Others suggest that outbreaks of *Acanthaster* are a recent phenomenon that is caused by the overfishing of prawns, which are major predators of juvenile *Acanthaster*. Although still poorly understood, outbreaks of *Acanthaster* and resultant reef mortality may have been augmented by the overfishing of tritons and prawns by humans. Humans with good intentions to remove *Acanthaster* from reefs actually made the problem worse. Some locals were collecting the sea stars, chopping them up into pieces and dumping the pieces back into the ocean. Little did they know that *Acanthaster* are capable of regeneration, so some of the pieces of sea star regrew arms and survived; thus, one sea star became several in some cases. Luckily, *Acanthaster* does not appear to be as good at regeneration as some sea star species capable of regenerating an entire body from a relatively small fragment.



(a)



(b)

Figure 11.16 (a) The predatory sea star, *Acanthaster*, and (b) its major predator, the endangered Pacific triton, *Charonia*.

(a) Courtesy of David Burdick/NOAA; (b) Courtesy of AIMS/NOAA.

Previously unknown coral diseases also have begun plaguing coral reefs on a global scale. A fourfold increase in whitepox disease was documented at 160 reef sites that were monitored in Florida since 1996. Data show that 37% of all coral species in Florida have died since the study began, and 85% of elkhorn coral have expired. Elkhorn coral, sometimes described as “the sequoia of the reef,” is a beautiful, orange, 3-m-tall branching species that so dominates Caribbean reefs that the seaward-facing *Palmata* zone is named in recognition of its ubiquitous occurrence (its scientific name is *Acropora palmata*). *Serratia marcescens*, a bacterium common in human feces and sewage, is the cause of whitepox disease, the affliction causing the death of elkhorn coral in Florida. The disappearance of this majestic species is perhaps the greatest aesthetic loss suffered to date.

Of the many new diseases currently plaguing corals, most are named by the appearance of the affected coral tissue (as in whitepox); black band disease, white band disease, brown band disease, red band disease, yellow band disease, yellow blotch



Figure 11.17 Black band disease overgrowing a coral head.

Courtesy of Paige Gill, Florida Keys National Marine Sanctuary, National Oceanic and Atmospheric Administration.

disease, black necrosing disease, white plague, and bleaching are most common. **Black band disease**, first reported in the 1970s in Belize and Bermuda, is now causing high mortalities in susceptible corals worldwide. This disease is characterized by a band of blackened necrotic tissue that advances several millimeters per day around coral colonies (**Figure 11.17**). Black band disease is caused by *Phormidium corallyticum*, a sulfate-reducing cyanobacterium that invades corals, attacks their zooxanthellae, feeds on dying coral tissues, and grows as a densely interwoven mat that separates the cenosarc from the coral's skeleton. This tissue damage eventually results in death because of the invasion of a consortium of opportunistic pathogens, such as *Beggiatoa* and *Desulfovibrio*. This consortium of bacteria, several of which are known only from humans (and their sewage), creates a sulfide-rich environment that prevents photosynthesis by zooxanthellae. Black band disease is the only coral disease that can be successfully treated. The infected tissue can be removed and the area covered with putty to prevent the disease from spreading.

White band disease was first reported in the late 1970s in Caribbean species of *Acropora* (elkhorn and staghorn corals are the most well-known members of this genus). By 1989, 95% of the elkhorn coral in St. Croix had succumbed to this disease, which also appears to involve a suite of pathogenic agents. **White plague** (or just *plague*) is a disease that resembles white band disease, only it moves and kills much more quickly. It first appeared in the Florida Keys in the 1980s. Although this disease, like most tissue-sloughing coral ailments, is poorly understood, the 1995 plague in Florida seems to have been caused by *Sphingomonas*, a common bacterium that causes infections, septicemia, and peritonitis in humans. Once again, sewage transport of this pathogen is suspected.

It is possible for all of these negative impacts on coral reefs to be managed on a local scale. Unfortunately, coral death is also caused by global-scale environmental changes. For example, a team of scientists from the U.S. Geological Survey believe that none of the many hypotheses offered to explain coral deaths around the world is adequate to explain the vast distribution of coral diseases, nor coral's inability to recover after a die-off. They suggest that the hundreds of millions of tons of dust carried by

winds to the Americas from Africa and Asia each year may transport viable pathogens, nutrients, trace metals, and other organic contaminants that could contribute to reef deaths worldwide. Another global issue is **ocean acidification**. Carbon dioxide entering the atmosphere worldwide affects water chemistry of the world ocean. Corals are susceptible to ocean acidification during all life stages, as early life stages appear to be sensitive to slight changes in pH, and adult forms rely on a steady supply of CaCO_3 for reef formation. The changes in ocean chemistry due to ocean acidification are just one more set of challenges for coral survival.

Perhaps the most well-studied cause of episodic coral mortalities is **bleaching**, a recently characterized phenomenon first observed in the mid-1980s. Bleaching occurs when physiologically stressed, pathogen-free corals expel their mutualistic zooxanthellae (**Figure 11.18**). This results in a whitening of the colony (due to the CaCO_3 skeleton of the coral being visible through its now pigment-free *cenosarc*), and perhaps its death. Bleaching events have been correlated with increased sea-surface temperatures, such as those that occur in the tropical eastern Pacific

Ocean during the El Niño–Southern Oscillation (ENSO). For example, nearly all the living coral in the Galapagos Islands bleached and died after the severe 1982–1983 ENSO episode. Some species completely disappeared during this event in the eastern Atlantic. Researchers reported that the even more intense ENSO event of 1997–1998 resulted in the deaths of fully one sixth of our planet's coral via bleaching. This event enabled the bacterium *Vibrio shiloi* to invade Mediterranean corals, and the Maldives were so badly impacted that virtually none of their corals survived. Some are now concerned that the 1,200 atolls that constitute the Maldives nation (see **Figure 11.7**) are no longer protected from erosion, which may lead to the complete disappearance of this archipelago over time.

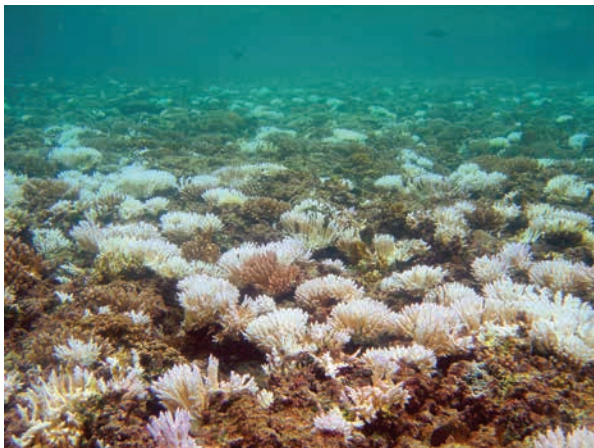
The first Caribbean bleaching event occurred in 1987–1988 and affected all species living down to 30 m depth (only *Madracis* and *Acropora* seem minimally affected). A second event occurred in 1990. Unlike Pacific episodes that are usually attributed to increased water temperatures, both of the mass bleaching events in the Caribbean Sea were not readily explained by temperature alone. Recent studies suggest that decreased temperatures, increased levels of ultraviolet radiation, increased sediment loads, changes in salinity, or toxic chemicals may also play roles in Caribbean bleaching episodes during periods of calm clear water that occur during ENSO events.

However, the actual cause and mechanism of coral bleaching remain unknown. Do corals evict malfunctioning algae, thus hurting themselves in the process, or do the zooxanthellae voluntarily leave stressed coral polyps? Some have even suggested that latent viral infections are induced by the above coral stressors.

Incontrovertible evidence links greenhouse gases, climate change, and coral bleaching. Projected increases in atmospheric CO_2 and global temperatures during the next 50 years will rapidly exceed the conditions under which coral reefs have thrived for 500,000 years. Researchers have found that coral species with unusual algal symbionts are able to achieve increased thermal tolerance, so perhaps adaptive shifts between corals and new zooxanthellae clades will confer increased resistance to future climate change.

11.3 Coral Reef Fishes

Associated with the reef and lagoon but with the mobility to escape the limitations of a benthic existence are thousands of species of reef fishes (**Figure 11.19**). These fishes find protection on the reef; prey on the plants, algae, and animals living there; and sometimes nibble at the reef itself. These assemblages of shallow-water coral reef fishes are easily observed by divers and have been intensively studied for decades. Less well known are the fish of the deeper portions of coral reef communities (below 100 m). Submersible-based studies recently demonstrated that as one works down the reef face into deep water the same general assemblages are present, but individual numbers and species diversity both diminish. Coral reef fishes are extremely diverse in their form, coloration, and behaviors. Here we explore some representatives of the major groups of these organisms.



(a)



(b)

Figure 11.18 (a) Widespread bleaching on a Pacific coral reef, and (b) Coral bleaching on an individual brain coral becoming overgrown by algae.

(a) Courtesy of David Burdick/NOAA; (b) Courtesy of National Oceanic and Atmospheric Administration.

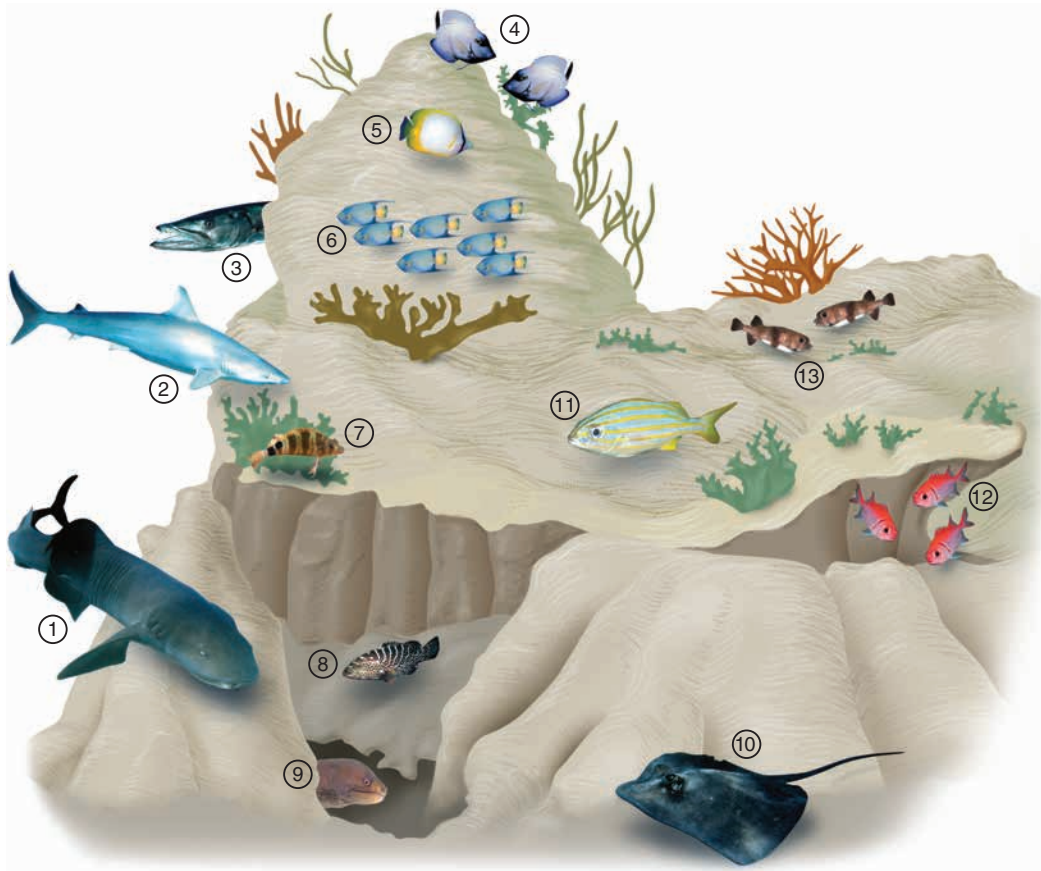


Figure 11.19 Some common reef fishes on a tropical Caribbean reef: (1) nurse shark (*Ginglymostoma*), (2) reef shark (*Carcharhinus*), (3) barracuda (*Sphyraena*), (4) surgeonfish (*Acanthurus*), (5) butterflyfish (*Chaetodon*), (6) angelfish (*Pomacanthus*), (7) hawkfish (*Amblycirrhitus*), (8) grouper (*Mycteroperca*), (9) moray eel (*Gymnothorax*), (10) stingray (*Dasyatis*), (11) grunt (*Haemulon*), (12) soldierfish (*Myripristis*), (13) porcupinefish (*Diodon*).

Coral Reef Sharks and Rays

Sharks are often described as large, voracious predators. Yet about 80% of known species are less than 2 m in length, half of all shark species are less than 60 cm long, and some species barely attain a length of 30 cm. Many of these smaller sharks are found only on coral reefs.

Without question, nurse sharks, carpet sharks, wobbegongs, and bamboosharks in the order Orectolobiformes dominate coral reefs. Some carcharhinid sharks, such as reef sharks, blacktips and whitetips, lemons, bulls, and tigers, also frequent coral reefs. All of these reef-dwelling sharks contradict the myth that sharks must constantly swim to breathe by coasting to a stop and resting on the seafloor for many hours at a time. Thanks to their inshore existence, they have developed the ability to flex their muscular gill slits and create the necessary flow of water over their gills even while stationary.

Most sharks that inhabit coral reefs also fail to fit the standard view of sharks as apex predators. Some consume large invertebrates, such as conchs, sea urchins, and clams from the seafloor. Caribbean nurse sharks suck sleeping wrasses from the sand under which they sleep. Many cryptic species are ambush predators, launching themselves from the reef when a prey species swims nearby. The numerous dermal flaps on the jaw margin of wobbegongs may function as lures to “bait”

prey near their mouths (**Figure 11.20**). Nurse sharks and some rays perch on extended pectoral fins, perhaps in an attempt to attract prey to the cavelike space that they create just under their chins. Some reef sharks are masters when it comes to extracting prey from reef crevices or using their snouts to flip coral rubble to reveal hidden crustaceans or annelids, and filter-feeding whale sharks and manta rays routinely visit reefs to consume the reproductive products of spawning corals and fish. The importance of sharks and other apex predators on reefs is highlighted when their numbers decline; apex predators help to maintain greater biodiversity in the ecosystem, and when their numbers decline, shifts in community structure occur. On coral reefs the shift is often toward algal-dominated reefs.



Figure 11.20 Dermal flaps around the mouth of a wobbegong, a benthic reef shark.
Courtesy of John Morrissey.

Case Study

The Lionfish Story: A Nonnative Invasion of the Sea Like Never Before

A recent invasion has taken place in the western Atlantic along the East Coast of the United States, the Caribbean, the Gulf of Mexico, and spanning the coasts of Central and South America. It is an alien invasion, but not of the extraterrestrial kind. Two very similar lionfish species, the devil firefish (*Pterois miles*) and the red lionfish (*Pterois volitans*), are reproducing rapidly with no end in sight, and these species are not native to the Atlantic Ocean. Lionfish are scorpionfish from the Indo-Pacific and are popular aquarium fish due to their beautiful and elaborate fins and coloration (Figure A). Unfortunately, and for unknown reasons, some aquarists release their lionfish into the ocean in areas that are not their natural homes, and populations of invasive lionfish are now thriving. The presence of these nonnative species is disrupting the natural flow of the food web and leading to fierce competition with native fish species.

Lionfish have modified dorsal and anal fins with elongated poisonous spines, making them virtually inedible by natural predators. Not only do the lionfish lack predators in their new home, but they are voracious carnivores, and they are not picky eaters. Gut content studies have revealed that lionfish choose to eat a large variety of juvenile or small adult fish and crustaceans, many of them commercially important species. In Belize, nearly half the stomach gut content of lionfish studied was a critically endangered wrasse species. Lionfish food preferences also overlap with native snappers and groupers; thus, they are directly competing with these commercially important, and in some cases low-abundance, fish species for food. In areas of heavy infestation it is estimated that lionfish have reduced their fish prey abundance by approximately 90%, which is unsustainable.

In response to the dramatic increases in abundance of nonnative lionfish, scientists set out to find out as much as possible about these invasive species so that efforts to eradicate them can be effective and efficient. They discovered that lionfish are sexually



Figure A A lionfish displaying long spines on the dorsal and anal fins glides over the seafloor. Courtesy of National Oceanic and Atmospheric Administration.

mature around the young age of 1 year and reproduce throughout the year every few days, which is why nonnative populations have exploded so quickly. They also estimate that lionfish can live around 15 years, which is a relatively long life span for a teleost fish, leading to a large reproductive potential for each individual fish. They appear to adapt well to all habitats, from the shoreline out to approximately 183 m (600 ft.). It was thought that lionfish required warm waters, but the presence of individuals along the central East Coast of the United States in waters barely above 13°C (56°F) has scientists questioning the presumed temperature requirements (Figure B). The rough abundance estimate as of 2015 is in the millions in the Gulf of Mexico region alone, and those numbers are predicted to keep climbing.

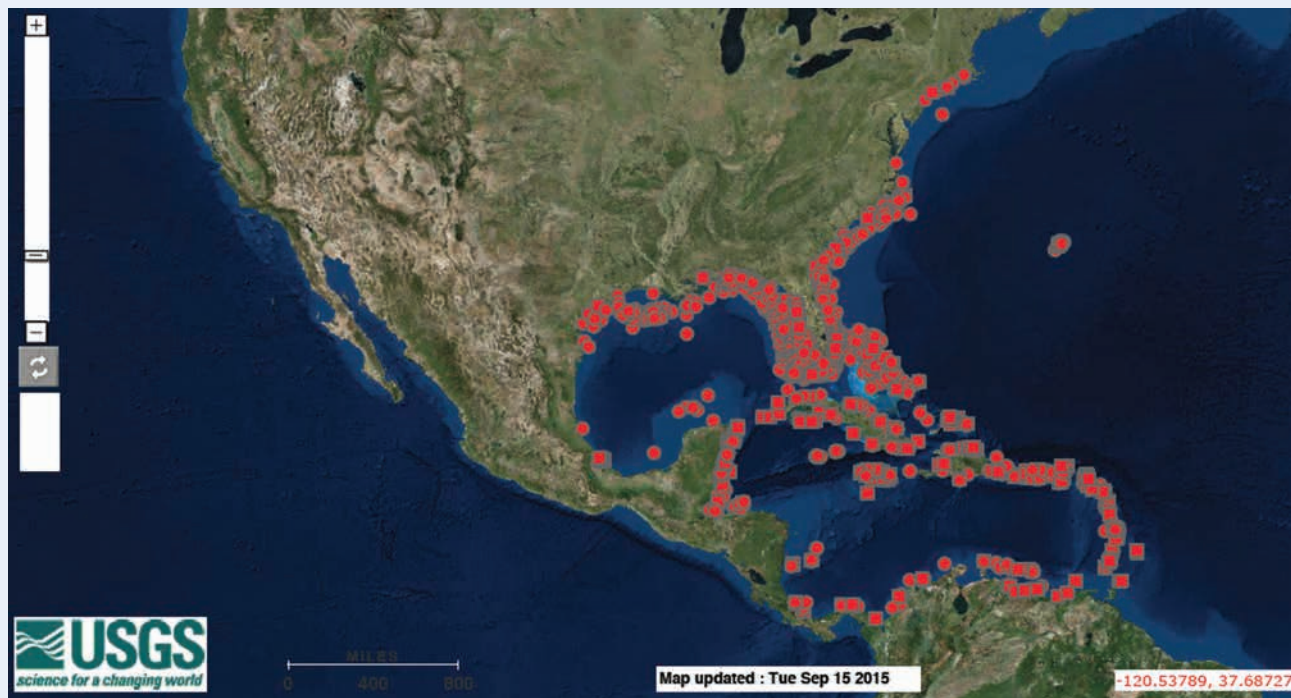


Figure B Distribution of documented established lionfish populations according to the U.S. Geological Survey as of September 2015. Undocumented invasions and those outside of the United States or its territories are not displayed on this map.

Courtesy of United States Geological Survey.

Case Study (Continued)



Figure C A research diver counting and observing lionfish.

Courtesy of National Oceanic and Atmospheric Administration.

It is clear that the lionfish introduction has created a remarkable problem in the Atlantic, Caribbean, and Gulf Coast regions. The question now is what can be done about it, if anything. Some scientists have predicted that lionfish are already too numerous to eradicate. Others suggest that great efforts should be made to remove as many as possible as quickly as possible. Although the invasive lionfish currently have no natural predators, it is possible that over time some larger fish or sharks may acquire a taste for them and figure out a way to eat them, despite their spiny fins. If humans make a valiant effort to remove lionfish and one or several predators start to consume them, the hope is that their impacts on the communities they reside in may be reduced. Fishers are highly encouraged to capture lionfish, and the most effective fishing methods are spearfishing and hand netting. These fishing methods are limiting in that they must occur at depths where humans can safely dive, and capturing large numbers of lionfish is challenging (**Figure C**). Communities of concerned citizens and scientists around Florida and the Caribbean have responded by organizing lionfish tournaments and competitions to encourage fishing. Another angle is to encourage the use of lionfish as food for humans. They are considered a delicacy in some parts

of the world, and their flesh is mild and flavorful. These are two species that fishers are encouraged to overfish! In all likelihood, these efforts will not be enough to wipe out lionfish populations, so innovative ways to remove these fish will be necessary for success. Scientists and citizens are working hard on these innovations as you read this case study, and one can only hope that they are successful.

Critical Thinking Questions

1. Do you think it is possible to eradicate nonnative lionfish? Why or why not? If you do think it is possible, propose a novel way to remove them from the Atlantic.
2. Consider the extreme appearance of lionfish, with their long, sharp spines. What selective pressures can you identify that may have driven lionfish species toward such extreme body designs?

Coral Reef Teleosts

Several groups of derived bony fishes are common to coral reefs worldwide (**Figure 11.21**). These include grunts, snappers, cardinalfish, moray eels, porcupinefish, butterflyfish, squirrelfish, groupers, triggerfish, gobies, blennies, wrasses, parrotfish, surgeonfish, and seahorses. Many of these fish are thought to be major importers of important limiting nutrients to local reef systems by foraging on pelagic prey during the day and then defecating at night while resting on the reef. Others feed in surrounding seagrass meadows at night and defecate on the reef while resting during the day. The results of this off-reef predation are converted through detritus food chains to dissolved nutrients usable by plants, phytoplankton, and the coral-based zooxanthellae.

Recent research on parrotfish has revealed an additional and crucial role of this group of fish to coral reef health. Caribbean coral reefs have declined dramatically in the past 50 years, and although there are several likely causes (as discussed earlier), one fact is clear: reefs with healthy populations of herbivorous parrotfish have healthier corals. Parrotfish graze heavily on the normally limited amount of macroalgae that grow on the reef. If these grazers are removed, macroalgae overgrow the reef and block the sun from reaching the symbiotic algae living within the corals. A direct result of macroalgae growth is death of corals and a conversion from healthy reef to what is termed **pavement**, the leftover dead coral skeleton with macroalgae growth on top. Some scientists claim that in the Caribbean immediately preserving the amount of grazers is more important than global warming and all of the other threats to coral reefs combined. These same scientists claim that Caribbean coral reefs will be gone in 20 years if populations of herbivores are not restored. Healthy reefs are more resilient and may be able to adapt to larger, gradual environmental changes or sudden and brief disturbances such as hurricanes, but unhealthy reefs have very little chance for survival with additional environmental stress, whether it is human-made or naturally occurring.



Figure 11.21 Numerous species of teleost fishes are associated with coral reefs. This photo was taken at the Pearl and Hermes Atoll, part of the northwestern Hawaiian Islands. Courtesy of National Oceanic and Atmospheric Administration.



Figure 11.22 Two remoras with modified dorsal fins attached to a manta ray. Courtesy of National Oceanic and Atmospheric Administration.

Symbiotic Relationships

Excellent examples of all the types of symbiosis can be found in many of the abundant animal groups of the coral reef. Our discussions are limited to some of the better-known symbiotic relationships involving coral reef fishes. These relationships span the entire spectrum of symbiosis, from very casual commensal associations to highly evolved parasitic relationships.

Remoras (**Figure 11.22**) associate with sharks, billfish, parrotfish, sea turtles, and even the occasional dolphin in a mutualistic symbiosis. The remora's first dorsal fin is modified as a sucking disc and is used to attach itself to its host. From its attached position, it feeds on scraps from the host and often cleans the host of external parasites. Thus, the remora gains food, a free ride, and protection via proximity, whereas the host rids itself of many ectoparasites. A similar association in the open ocean exists between sharks and pilotfish (*Naucrates*). The pilotfish swim below and in front of their hosts and scavenge bits of food from the shark's meal. It has been speculated that pilotfish may attract prey species to the shark.

It is common for smaller defenseless fish to live on or near better-defended species of reef invertebrates. For example, shrimpfish often hover vertically in a head-down position among the long, sharp spines of sea urchins in a commensal symbiosis (**Figure 11.23**). The shrimpfish acquire protection from the sea urchin without affecting it. Brightly colored clownfish and anemonefish find equally effective shelter by nesting among the stinging tentacles of several species of sea anemones (**Figure 11.24**). This relationship, somewhat more complex than those just described, is also probably a mutualistic one. In return for the protection they obtain, clownfish assume the role of "bait" and lure other fish within reach of the anemone. They occasionally collect morsels of food and, in at least one observed instance, catch other fish and feed them to the host anemone. Clownfish, however, are not immune to the venomous cnidocytes of all sea anemones. Although some clownfish are innately protected from some anemone species (i.e., their protection results from their normal development rather than from contact with chemical, visual, or mechanical stimuli from an anemone), researchers have demonstrated that some clownfish must acclimate to some anemone species. Moreover, they



Figure 11.23 An urchin clingfish, *Diademichthys*, nestled between urchin spines in Indonesia.

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also reported that other clownfish are unable to acclimate to certain species of anemones.

The increased popularity of skin diving and scuba diving has led to many more observations of coral reef fishes, and as a result has revealed some remarkable cleaning associations involving a surprising number of animals. Cleaning symbiosis is a form of mutualism; one partner picks external parasites and damaged tissue from the other. The first partner gets the parasites to eat; the other partner has an irritation removed.

The behavioral and structural adaptations of cleaners are well developed in a half dozen species of shrimps (**Figure 11.25**) and several groups of small fishes. Tropical cleaning fishes include juvenile butterflyfish, angelfish, and damselfish, but only some neon gobies in the Atlantic (*Elacatinus*) and cleaner wrasses in the Pacific (*Labroides*) are cleaning specialists throughout their lives (**Figure 11.26**). All tropical cleaning fish are brightly marked, are equipped with pointed, pincer-like snouts and beaks, and occupy a cleaning station around an obvious rock outcrop or coral head. Most are solitary; a few species, however, live in pairs or larger breeding groups.



Figure 11.24 A clownfish, *Amphiprion*, nestled within the protective tentacles of its host anemone.

© Russell Swain/Shutterstock, Inc.

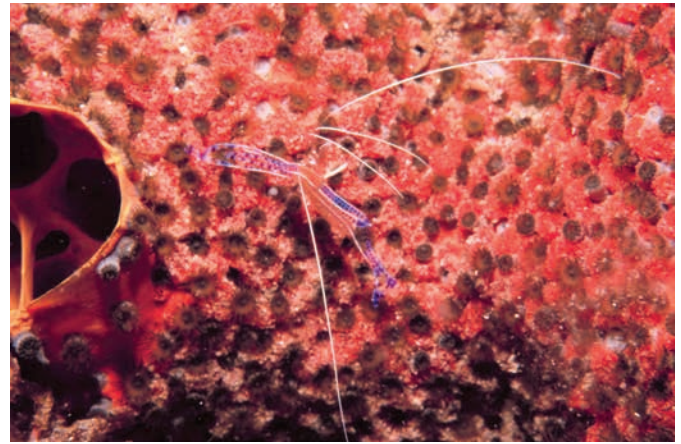


Figure 11.25 A nearly transparent cleaner shrimp, *Periclimenes*, on a Caribbean sponge.

Courtesy of Dr. Anthony R. Picciolo, NOAA/NODC.

Host fish approach cleaning stations, frequently queuing up and jockeying for position near the cleaner. Often, they assume unnatural and awkward poses similar to courtship displays. As the cleaner fish moves toward the host, it inspects the host's fins, skin, mouth, and gill chambers and then picks away parasites, slime, and infected tissue.

In the Bahamas, one study tested the cleaner's role in subduing parasites and the infections of other reef fishes. Two weeks after all known cleaner fish were removed from two small reefs, the areas were vacated by nearly all but territorial fish species. Those species that remained had an overall ratty appearance and showed signs of increased parasitism, frayed fins, and ulcerated skin. It was concluded that symbiotic cleaners were essential in maintaining healthy fish populations in this particular study area.

Others conducted similar studies on a Hawaiian reef. In this situation, the small cleaner wrasse, *Labroides phthirophagus* (the major cleaner on the reef), was excluded from the study site for more than 6 months. During that time, no increase in the level of parasite infestation was observed. This result suggests



Figure 11.26 Neon gobies, *Elacatinus*, clean the head of a large green moray, *Gymnothorax*.

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that for some cleaner–host associations the role of the cleaner is not crucial. The cleaner may be dependent on the host for food, but the host's need for the cleaner seems to be variable.

The fine line separating mutualistic cleaning of external parasites and actual parasitism of the host fish is occasionally crossed by cleaner fish. In addition to unwanted parasites and diseased tissue, some cleaners take a little extra healthy tissue or scales or graze on the skin mucus secreted by the host. Thus, the total range of associations displayed by cleaning fish encompasses mutualism, commensalism, and parasitism.

Because parasitism is such a widespread way of life in the sea, few fish avoid contact with parasites throughout their lives. The groups notorious for creating parasitic problems in humans—viruses, bacteria, flatworms, roundworms, and leeches—also plague marine fish. Despite the bewildering array of parasites that infest fish, very few fish become full-time parasites themselves. A remarkable exception is pearlfish. They find refuge in the intestinal tracts of sea cucumbers, the stomachs of certain sea stars, the body cavities of sea squirts, and the shells of clams. After this association is established, some pearlfish assume a parasitic existence, feeding on and seriously damaging the host's respiratory structures and gonads. When seeking a host sea cucumber, pearlfish detect a chemical substance from the cucumber and then orient themselves toward the respiratory current coming from the cucumber's cloaca. Sea cucumbers draw in and expel water through their cloacae for gas exchange. The fish enters the digestive tract tail first via the cloaca. The hosts are not willing participants in this relationship. They sometimes eject their digestive and respiratory organs in an attempt to rid themselves of the symbiont. In fact, sea cucumbers of the genus *Actinopyga* have evolved five teeth on their cloacal margin, perhaps as a pearlfish-exclusion mechanism.

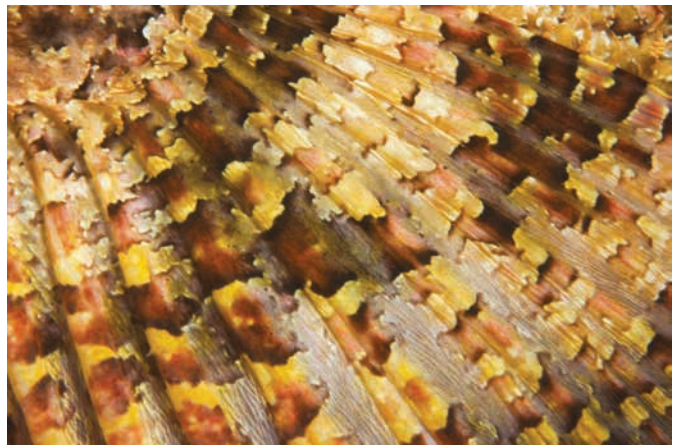
Coloration

Against the colorful background of their coral environment, reef fishes have evolved equally brilliant hues and color patterns. The colors are derived from skin or internal pigments and from iridescent surface features (like those of a bird's feathers) with optical properties that produce color effects. Most fish form accurate visual color images of what they see, but like humans, they are susceptible to misleading visual images and camouflage.

Our interpretation of the adaptive significance of color in fish falls into three general categories: concealment, disguise, and advertisement. Some seemingly conspicuous fish resemble their coral environment so well that they are nearly invisible when in their natural setting. Extensive color changes often supplement their basic camouflage when they are moving to different surroundings. These rapid color changes are accomplished by expanding and contracting the colored granules of pigmented cells (**chromatophores**) in the skin and are governed by the direct action of light on the skin, by hormones, and by nerves connected to each chromatophore. As the chromatophore pigments disperse, the color changes become more obvious (**Figure 11.27**). When the granules are contracted, the pigment retreats to the center of the cell, and little of it is visible. Other cells, called **iridocytes**, contain reflecting crystals of



(a)



(b)

Figure 11.27 A well-camouflaged scorpionfish, *Scorpaena* (a), with magnified chromatophores from a section of skin (b). The multicolored pigments of some are expanded and diffused; others are densely concentrated in small spots.

(a) © Frank Boellmann/Shutterstock, Inc.; (b) © Rene Frederic/age fotostock.

guanine. Impressive to the observer, iridocytes can produce an entire spectrum of colors within a few seconds.

Several distinctive fish conceal themselves with color displays reminiscent of disruptive coloration, or *dazzle camouflage*. Bold contrasting lines, blotches, and bands tend to disrupt the fish's image and draw attention away from recognizable features such as eyes. Eyes are common targets for attack by predators, and thus a disguised eye is a protected eye. One common strategy masks the eye with a dark band across the black, staring pupil so that it appears to be continuous with some other part of the body (**Figure 11.28**). To carry the deception even further, masks hiding the real eyes are sometimes accompanied by fake eyespots on other parts of the body or fins. Eyespots, intended as visual attention-getters, are usually set off by concentric rings to form a bull's eye. As a result, predatory attacks are more likely to be directed away from the eyes and head and drawn to less vital parts of the body that may not lead to death upon attack.

The flashy color patterns of cleaning fish serve different functions. If the fish are to attract any business, they must be conspicuous. Thus, they advertise themselves and their location



(a)



(b)

Figure 11.28 Disruptive coloration patterns of two species of butterflyfish, *Chaetodon*.

(a) © cbpix/Shutterstock, Inc.; (b) © Lawrence Cruciana/Shutterstock, Inc.

with bright, startling color combinations. These bold advertisement displays are also useful for sexual recognition. One or both sexes of certain species assume bright color patterns during the breeding period. The colors play a prominent role in the courtship displays, which lead to spawning. During this period, the positive value gained from sexual displays must offset the adverse impact of attracting hungry predators. Between breeding periods, these fish usually assume a drab, less conspicuous appearance.

Advertisement displays are also used to warn potential predators that their prey carry sharp or venomous spines, poisonous flesh, or other features that would be painful or dangerous if eaten. Predatory fish recognize the color patterns of unpalatable fish and learn to avoid them. This type of bright coloration to indicate harm and deter predators is seen throughout the animal kingdom.

Occasionally, a species capitalizes on the advertisement displays of another fish by closely mimicking its appearance. The cleaner wrasse (*Labroides*, the upper fish in **Figure 11.29**) is nearly immune to predation because of the cleaning role it performs for its potential predators. Over much of its range, *Labroides* live close to a small blenny (*Aspidontus*). The blenny so closely resembles *Labroides* in size, shape, and coloration (lower fish in **Figure 11.29**) that it fools many of the predatory fish that approach the wrasse's cleaning station. Not content to share the *Labroides* immunity to predation, the blenny also uses its disguise to prey on fish that mistakenly approach it for cleaning. This ability to disguise and thereby be protected is known as **mimicry**.



(a)



(b)

Figure 11.29 A cleaner wrasse, *Labroides dimidiatus* (a), and its mimic, the bluestriped fangblenny, *Plagiotremus rhinorhynchos* (b).

(a) © vkilikov/Shutterstock; (b) © RGB Ventures/SuperStock/Alamy Stock Photo.

Only in the clear waters of the tropics and subtropics does color play such a significant role in the lives of shallow-water animals. In the more productive and turbid waters of temperate and colder latitudes, light does not penetrate as deeply nor is the range of colors available. In coastal waters and kelp beds, monotony and drabness of appearance, not brilliance, are the keys to camouflage. In the deep ocean, color is even less important. Without light to illuminate their pigments, it matters little whether deep-water organisms appear red, blue, black, or chartreuse when viewed at the surface. In the abyss, they would all assume the uniform blackness of their surroundings were it not for bioluminescence.

Spawning and Recruitment

Coral reef teleosts are a very diverse lot, yet most share a common life-history strategy: most adult reef teleosts are benthic fishes that spawn in the water column. Only about 20% to 30% of reef species (damselfish, gobies, and triggerfish) deposit 1-mm-long benthic eggs that stick to the substrate until they hatch after 1 to 4 days (longer in some species). Of these, damselfish are the most conspicuous, and the courtship and mating rituals of some damselfish are well known (Figure 11.30). For example, bicolor damselfish, *Stegastes partitus*, mate between full and new moons. The male builds a nest and then attempts to persuade females to deposit their eggs in his nest by performing a series of dips in the water column. Females typically choose the male that performs the most dips in a given time. Presumably, the female uses his dance to assess his health and fitness. Because the male must guard her eggs for 3 to 4 days (Figure 11.31), the female uses the rate of dipping during courtship to determine which male in her vicinity has the most energy stored as fat, which is energy that will be very useful while he guards her eggs relentlessly before their hatching.



Figure 11.30 Two bicolor damselfish mate inside a discarded PVC pipe on a Caribbean reef.

Courtesy of Dr. Michael P. Robinson, University of Miami.



Figure 11.31 A sergeant major (*Abudefduf*) guards its purple egg mass in the Caribbean Sea.

© David Fleetham/Alamy Images.

The majority of reef teleosts are pelagic spawners. In some cases, many species, 30 or more at any given time, will assemble around the same coral promontory to broadcast as many as 50,000 eggs/female and over 1,000,000 sperm/male into the water column (Figure 11.32) during the course of an hour or so. The coral pinnacle that is selected is not obviously different from neighboring outgrowths, but the fish seem to understand the difference. In fact, if one removes all female bluehead wrasses from a reef, the new set of replacement females that arrives will pick many (maybe completely) new spawning sites, and these sites will become the new “traditional” sites on that reef. This is one of the few examples of “culture” in fish. Wrasses are known to travel 1.5 km to a spawning site (a distance equal to 15,000 body lengths, or the equivalent of a 55-km round-trip for a human), and Nassau groupers, *Epinephelus striatus*, may travel up to 240 km to spawn.

After fertilization, these pelagic eggs drift away from the reef and disperse for a period of time that ranges from 1 day to a year or more. This time period, known as the **pelagic larval duration**, influences dispersal greatly and is of intense interest because of its influence on the potential efficacy of national marine sanctuaries.

In 1972, a century after the United States established the first national park at Yellowstone, legislation was passed to create the National Marine Sanctuary Program (NMSPP). The intent of this legislation was to provide similar protection to selected coastal habitats as provided for land areas designated as national parks. The designation of an area as a marine sanctuary says to all that, like our national parks, this is a safe refuge where people can observe organisms in their natural environment, but tread lightly. Three decades later, only 13 marine sanctuaries and 1 marine national monument have been designated (Figure 11.33). In addition, the National Estuarine Research Reserve System has designated 28 national estuarine research reserves. A recent designation of additional protected areas has led to the umbrella term of *marine protected areas* (MPAs)



Figure 11.32 Dog snappers, *Lutjanus jocu*, return to the reef after a spawning run in the water column off Belize.

© Doug Perrine/Seapics.com.

for all marine areas that are protected for conservation. Over 400 MPAs with varying degrees of protection have been established in the United States and U.S. territories; some MPAs are fully protected no-take reserves, others allow fishing of particular species, and some are simply recognized as special areas and allow fishing for all species (except those protected by the Endangered Species Act).

The national system of MPAs should be viewed as a crucial part of new management practices in which whole communities, and not just individual species, are offered some degree of protection from habitat degradation. Nevertheless, because of the interactions between and inexplicable changes of the pelagic larval durations of reef invertebrates and teleosts and surface currents, one can never be certain that protection of a spawning population on one reef will ensure augmented recruitment of juveniles into that sanctuary. It seems just as likely that efforts at one location will result in huge benefits in terms of larval recruitment somewhere down current. Therefore, a great deal of research effort is also being directed to the study of **settlement**, or the passage from the pelagic existence of a larva to the benthic life of a reef-dwelling fish or invertebrate. Hypothetical recruitment factors that are being investigated include active mechanisms, such as larvae being attracted to reef sounds (such as waves breaking on the reef crest or the snapping of shrimp) or reef smells (in a mechanism analogous to the homing behavior of salmon), as well as passive mechanisms that may enable the settlement of postlarval juveniles (such as retention in gyres around some Hawaiian islands or the Florida Keys).

It is estimated that only about 1% of the eggs spawned survive to produce an individual that will settle on a reef, but successful settlement does not mean that the intense mortality is over. About 90% of those teleost larvae that settle on a reef are eaten during their first night. If a larva is lucky enough to



Figure 11.33 Locations of U.S. National Marine Sanctuaries.

survive its first night on the reef, it then must metamorphose into a benthic juvenile within a day or two. Only 50% of those that begin metamorphosis survive to complete the transformation. After they acquire the morphology, appearance, and behavior of a juvenile, mortality decreases greatly.

DID YOU KNOW?



Many fish are not done with their journey to a new home once they settle to the seafloor. Some species settle to one habitat as juveniles, then when they are a certain size move to an adult habitat. Others transition between multiple habitats during one or more of their life phases. Coral reefs are often the adult habitat, with juvenile habitats at nearby seagrass beds or mangroves. The ocean is a dynamic place to live, so it is no surprise that fish, highly mobile organisms, are adapted to change homes when necessary.

Sexual Systems in Reef Fishes

Reef teleosts display a great variety of sexual systems, from relatively straightforward **gonochorism**, with separate males and females (as seen in grunts, snappers, and most damselfish), to complex systems involving **hermaphroditic** individuals that play the roles of both genders during their adult lives. Simultaneous hermaphrodites function as males and females at the same time, whereas sequential hermaphrodites are born as one gender and then change sex during their life.

The best-known simultaneous, or synchronous, hermaphrodite on the reef is the hamlet (a relative of groupers in family Serranidae). All hamlets are monogamous, forming faithful pairs that often last throughout the breeding season, and perform synchronous mating rituals that involve choosing a sex for each event. During courtship, one member of the pair will “act male” and will release sperm during a stereotypical “clasp” in the water column above the reef (Figure 11.34). Its mate will play the female role and release eggs. Immediately after spawning, the couple will reverse roles and recourt, with the first individual now acting female and releasing eggs and the second fish acting male and releasing sperm. They then repeat this ritual 2 to 15 times, trading roles repeatedly, until they are both spent and unable to court with another fish.

Sequential hermaphrodites come in two varieties, those that begin their adult life as a male (**protandry**) and those that begin their adult life as a female (**protogyny**). Both types change sex as they age. The best-known protandrous hermaphrodites on the reef are clownfish (see Figure 11.24), which all begin their adult lives as a male. In each clownfish community (often a single sea anemone), a pecking order exists wherein the largest individual is an adult female, the second largest is an adult male, and the remaining individuals are all undifferentiated juveniles. If the alpha female is removed via death or predation, oppression on the large male is released, and he becomes a female. Soon after, the individual that formerly was third in line differentiates and matures into an adult male.

Beginning adult life as a female is much more common among reef fishes, and wrasses and parrotfish in the family Labridae are perhaps the best-known protogynous hermaphrodites.



Figure 11.34 Clasp-hamlets above a reef.

© WaterFrame/Alamy Images.

The bucktooth parrotfish, *Sparisoma radians*, of Caribbean coral reefs has a particularly interesting sexual system that involves several phases of male and female fish that look and act quite different, but are all the same species. All *S. radians* begin life as females, so all males have changed sex at some point from an initial-phase female to a male. The most conspicuous phase is the large phase of the terminal-phase male, with bold and bright coloration, a turquoise stripe that connects from the mouth to the eye and distinct black markings on the body (Figure 11.35). Females are comparatively drab in color with no eye stripe, and this coloration is considered the initial phase. Some small males



Figure 11.35 A late-phase male bucktooth parrotfish, *Sparisoma radians*. The distinctive turquoise mouth to eye stripe and black markings indicate a fully transformed male.

Courtesy of Kirk Kilfoyle, Nova Southeastern University.

change only their behavior and physiology, but retain the look of an initial-phase female.

Spawning in *S. radians* occurs daily in the afternoon. Terminal-phase males are territorial and defend a **harem** of females that they spawn with in the same location each day. Courtship behavior begins a few minutes before spawning, as the male swims over to and brushes up against a female. Eventually the two fish join together in a vertical spiraling movement toward the surface where sperm and eggs are released. It is during this time that drab-colored initial-phase males take advantage of their cryptic coloration to blend into the environment and sneak up to release sperm into the spawning event. The spawning ritual is very costly in that leaving the safety of the reef or seagrass makes them extremely vulnerable to predation. It can be presumed that releasing gametes into the water column allows for better dispersal of gametes and soon after, fertilized eggs.

The various phases of *S. radians* are quite unique among fish and somewhat of a mystery to scientists. Living in the seagrass bordering the reef are small versions of males and females. These small individuals are not necessarily younger than the large-phase individuals, just smaller, and genetic tests reveal that they are the same species as the larger individuals.

The small-phase fish spawn with one another, and small initial- and terminal-phase males sometimes sneak in to spawn with larger females, too. Another unique feature of this species is the mechanism of sex change. In most sequentially hermaphroditic harem fish, the largest female changes sex when the male is removed by predation. In most cases for *S. radians*, it is the second largest female that changes sex and takes over as the terminal-phase male. Sex change begins with morphological changes (color change) and is followed by behavioral and eventually physiological changes (**Figure 11.36**). About 20 days after the first signs of sex change, the newly transformed male looks, acts, and spawns as a male.

The tropical cleaner fish *Labroides* (also in the family Labridae; see Figure 11.29) is also protogynous. This inhabitant of the Great Barrier Reef of Australia occurs in small social groups of about 10 individuals. Each group consists of one dominant male and several females existing in a hierarchical harem. This type of social and breeding organization is termed **polygyny**. Only the dominant, most aggressive individual functions as the male and, by himself, contributes half the genetic information to be passed on to the next generation. In the event the dominant male of a *Labroides* population dies or is removed, the most dominant of the remaining females immediately assumes



Figure 11.36 A newly transformed male bucktooth parrotfish, *Sparisoma radians*. The turquoise mouth to eye stripe indicates that sex change from female to male has begun, but the gray coloring and lack of black on the body indicate that sex change is not yet complete.

Courtesy of Kirk Kilfoyle, Nova Southeastern University.

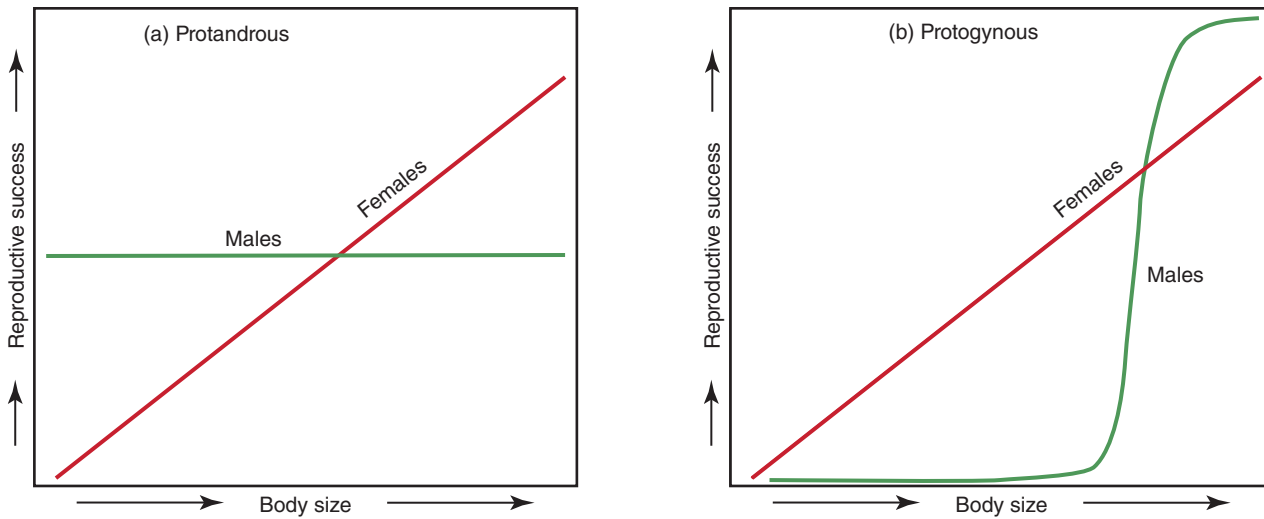


Figure 11.37 Relative reproductive success experienced by males and females of (a) protandrous fishes (e.g., clownfish) and (b) protogynous fishes (e.g., wrasses).

the behavioral role of the male. Within 2 weeks, the dominant individual's color patterns change, and the sex transformation to a male is complete. In this manner, males are produced only as they are needed, and then only from the most dominant of the remaining members of the population.

Before ending our discussion of hermaphroditic reef fishes, it is helpful to consider the benefits of such a sexual system. Why should an individual change its sex during its life, and under what circumstances should a reef fish begin life as a male (as opposed to a female)? Biologists hypothesize that changing sex is advantageous when reproductive success is closely tied to body size, and when being one sex (as opposed to the other) results in increased reproductive success at a given body size (this is known as the *size-advantage model*). **Figure 11.37a** shows the relative reproductive success of male and female clownfish from the time they are small adults to sometime later when they are older and larger. Body size does not influence the reproductive success of male clownfish. It remains the same as they grow because they produce countless sperm cells at all body sizes and they do not compete with other males for access to females; they simply mate with the adult female inhabiting their sea anemone. Yet female reproductive success among clownfish is greatly influenced by body size because eggs are very large and expensive to produce. Therefore, young (small) females do not produce nearly as many eggs as larger (older) females. Hence, it is advantageous for clownfish to be male while young (and small) and then change into females once older (and larger). Via this sex-changing strategy, they achieve maximal reproductive success at all sizes.

Figure 11.37b presents the relative reproductive success achieved by protogynous fishes, such as the bucktooth parrotfish described above. Female parrotfish and wrasses are very similar to female clownfish in that they only produce a large number of eggs when they possess a large body. Unlike male clownfish, small (young) male parrotfish experience very limited reproductive success because they are too small to compete for access to females and their eggs. Hence, their reproductive success is very low and unpredictable while young and small and then suddenly sky rockets after they become large enough to gain access to eggs in the water column. Hence, unlike the situation experienced by clownfish, it is better for a parrotfish to begin life as a small female (because small males do not reproduce much at all) and later change into a male after becoming large and competitive.

But the size-advantage model does not explain all changes of sex. The coral goby, *Paragobiodon echinocephalus*, changes sex both ways. Coral gobies are small, black fish with orange heads that live on the branching coral *Stylophora pistillata*. On each coral colony, only the two largest fish (one male and one female of similar sizes) breed monogamously. The reproductive success of the pair is positively correlated with size in both sexes; larger males are more successful at guarding benthic eggs, and larger females can produce more eggs. Hence, the size-advantage model does not explain the factors that induce sex change in this species. Instead, change in social rank determines the direction of sex change. When a coral goby loses its mate, it prefers to change sex in either direction to form a mating bond with the nearest adult goby, as opposed to traveling a great distance to locate a heterosexual mate.

STUDY GUIDE

TOPICS FOR DISCUSSION AND REVIEW

1. Summarize the physical and biological limitations to coral reef distribution, and then explain why coral reefs do not form at all latitudes and depths.
2. Tally the pros and cons experienced by each member of the symbiotic relationship between corals and zooxanthellae, and demonstrate that this relationship is mutualistic.
3. Why is hermaphroditic spawning the most common method of sexual reproduction in reef-building corals?
4. What can be done to slow or end the global destruction of coral reefs that we are experiencing currently?
5. What is a marine protected area (MPA)? A marine reserve? Are all MPAs “no take” reserves? How do MPAs benefit neighboring areas?
6. Describe the relationship between clownfish and sea anemones, listing the benefits and disadvantages experienced by each.
7. Generate a list of all potential cues that postlarval reef fishes could use to locate the coral reef on which they eventually settle.
8. Describe the main difference between protogynous hermaphroditism and protandrous hermaphroditism in coral reef fishes, and explain the advantages of each mating system.
9. What sex change feature is so different about the parrotfish, *Sparisoma radians*, compared to other hermaphroditic fishes?

KEY TERMS

ahermatypic 302	harem 325
atoll 303	hermaphroditic 324
barrier reef 303	hermatypic 302
black band disease 313	iridocyte 320
bleaching 314	mesenterial filament 303
cenosarc 300	mimicry 321
chromatophore 320	mucusciliary system 303
columella 300	ocean acidification 314
corallite 300	pavement 318
endo-upwelling 303	pelagic larval duration 322
fringing reef 303	phototrophic 303
gonochorism 324	planula 306
guyot 304	

polygyny 325
polymorphic 300
protandry 324
protogyny 324
septa 300

settlement 323
white band disease 313
white plague 313
zooxanthellae 302

KEY GENERA

Abudedefduf	Leptoseris
Acanthaster	Lithothamnion
Acanthurus	Lutjanus
Acropora	Madracis
Actinopyga	Montastraea
Amblycirrhitus	Mussa
Amphiprion	Mycteroperca
Aspidontus	Myripristis
Astrangia	Naucrates
Beggiatoa	Orbicella
Carcharhinus	Paragobiodon
Cassiopea	Periclimenes
Chaetodon	Phormidium
Charonia	Plagiotremus
Dasyatis	Pocillopora
Diademichthys	Pomacanthus
Desulfovibrio	Porites
Diadema	Porolithon
Diodon	Scorpaena
Diploria	Serratia
Elacatinus	Siderastrea
Favia	Sparisoma
Ginglymostoma	Sphingomonas
Goniolithon	Sphyraena
Gymnothorax	Stylophora
Haemulon	Symbiodinium
Hydrolithon	Tridacna
Labroides	Vibrio

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