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Primer

Coral reefs

Nancy Knowlton

Coral reefs, renowned for their diversity and beauty, are often called the 'rainforests of the sea'. They form best in warm, clear, well-lit waters (Figure 1) where they fringe shorelines, form offshore barriers and ring volcanoes, becoming atolls once the volcanoes themselves sink below the surface — a process first outlined by Darwin. Some of the structures coral reefs form can even be seen from space, although in total they occupy just 600,000 km^2, or about 0.1% of the surface of the planet. There are also deep-water coral reefs, but they will not be considered further here.

Today most reefs are primarily built by members of the order Scleractinia, skeleton-forming relatives of sea anemones whose fossil record dates back to the Triassic. The taxonomic relationships of scleractinian corals have been in turmoil for a number of years — many traditional groupings are not supported by modern molecular analyses — and species boundaries are also often difficult to define. Other important reef builders today include fire corals, blue corals and coralline algae. In the geological past, reefs have been formed by many kinds of organisms, including microbes, sponges and clams.

Although all corals, like other members of the phylum Cnidaria, can capture prey using their stinging cells, the ability of some corals to grow at rates sufficient to form reefs is due to their nutritional symbiosis with single-celled algae — a group of dinoflagellates that are broadly referred to as zooxanthellae. Zooxanthellae provide their coral hosts with the products of photosynthesis, and in turn the corals provide nutrients to the zooxanthellae. For many years it was thought that all zooxanthellae belonged to a single species, but it is now recognized that zooxanthellae represent a highly diverse collection of symbionts that differ in their light and host preferences and in their life histories.

Most coral reef biodiversity lies not with the corals themselves (~1000 species) but rather with the many other organisms that live on reefs. Their numbers are highly uncertain, with estimates ranging from about one million to about 9 million species, and we know little about the extent to which

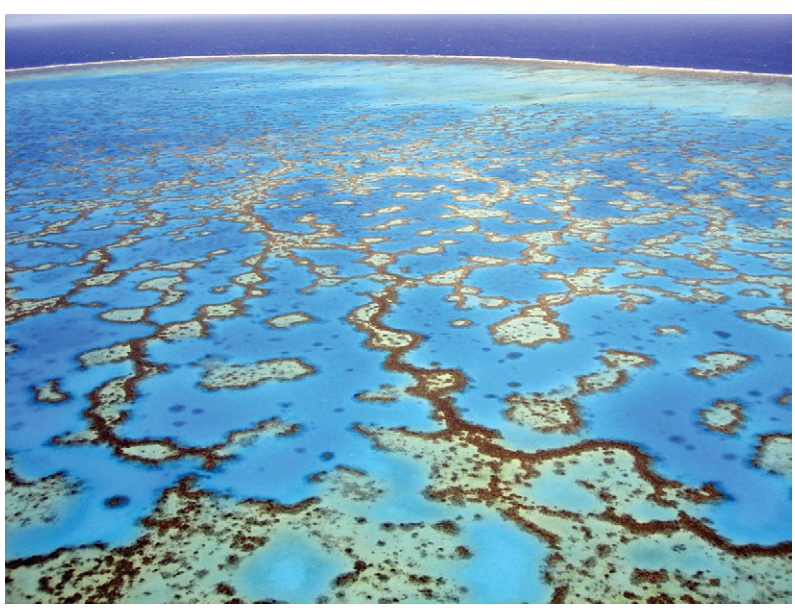

Figure 1. Aerial view of the coral reefs of Heron Island, Great Barrier Reef, Australia. Photo courtesy of Ove Hoegh-Guldberg.

these organisms are obligate reef dwellers. The center of coral reef diversity is in the Indo-west Pacific, the so-called 'coral triangle', while the Caribbean represents the second most diverse coral reef region. The reasons for the reef biodiversity patterns we observe today remain hotly debated. Because the diversity is so enormous, it is difficult to characterize. A single labor-intensive study of a 15,000 ha region in the Philippines documented over 5,000 species of mollusks, most of them tiny and observed just once. Genetic barcoding can help cope with the documentation of reef diversity, but the task remains daunting.

Not surprisingly, food webs on reefs are extraordinarily complex. Fishes play many important ecological roles: Some are herbivores, while others prey on other fish, bottom-dwelling invertebrates or plankton. At the bottom of the food web, both animals — because of their symbionts — and seaweeds are important primary producers. Other invertebrates are filter feeders (e.g., sponges, ascidians), herbivores, carnivores, and deposit feeders (e.g., sea cucumbers). Bioeroders, both fish and invertebrate, constantly eat away at the physical structure of reefs. Coral reefs can also be linked ecologically to other adjacent ecosystems, particularly seagrass beds and mangroves.

The ecology of some parts of coral reefs is very poorly understood. For example, reefs are riddled with a multitude of caves and crevices that are lined with filter feeders which can only be seen in their natural state with fiber-optic tools. Deep reefs are also difficult to study because they are out of the range of divers using standard SCUBA, and as a consequence each new study brings to light many new species. The roles of reef microbes, whose diversity dwarfs that of other groups, are just now being unraveled thanks to modern genomic techniques.

Much of the massive size and structural complexity of reefs is the product of a very simple process — the asexual budding of polyps to form coral colonies; only a few reef building corals are not colonial. Colony morphologies include mounds, plates, crusts, columns and a variety of branching forms (Figure 2). As in plants, close relatives (e.g., members of the same genus) can have very different forms, which are often associated with different life histories; for example, asexual propagation via fragmentation is most prolific in branching species. As clonal organisms, they are also capable of sustaining partial mortality and subsequently regenerating — for this reason, small colonies are not necessarily young. Some colonies lay down clearly readable annual bands, like tree rings, and may live for hundreds of years; such skeletons provide important sources of information for reconstructing paleoclimates.

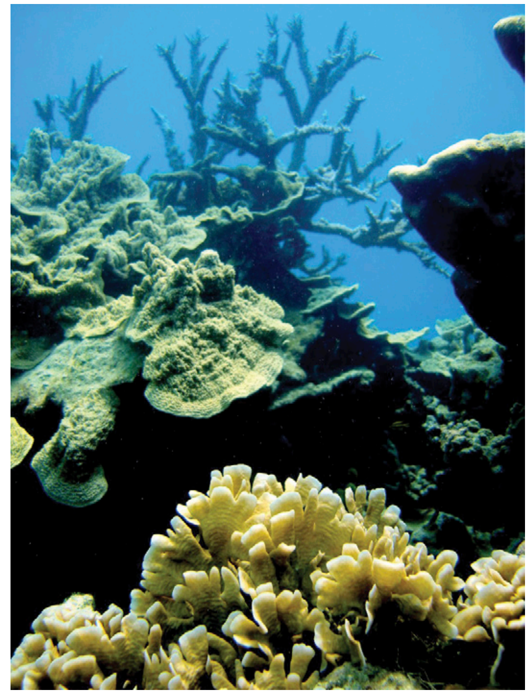

Figure 2. Diversity of coral growth forms. Photo courtesy of Ove Hoegh-Guldberg.

Corals also reproduce sexually; some corals have separate sexes but many corals are hermaphroditic. In broadcast spawning, eggs and sperm are released into the water column, often in spectacular, highly synchronized, annual events involving many species ('mass spawning'). Within-species synchrony clearly facilitates fertilization success, whereas between-species synchrony may help reduce predation on eggs. Other corals — typically smaller, weedier species — are brooders; they often reproduce for a number of months each year, with the developing eggs being held for a period of time before release. The timing of coral reproduction is not entirely understood, but is probably controlled by a mixture of cues associated with temperature, the lunar cycle, and the daily pattern of sunrise and sunset. The larvae of corals ('planulae') settle after a few days to a few weeks; brooded planulae are often larger, contain zooxanthellae and are capable of settling more quickly. Planulae require a hard surface on which to settle and in many cases prefer to settle on certain species of coralline algae.

Coral reefs are densely occupied, and competition for space, light and food is intense. Corals and other sessile reef-dwellers compete using a variety of strategies. Some invest heavily in upward growth and are capable of shading out their neighbors. For example, branching species in the genus *Acropora*, the most diverse of all scleractinian genera, are capable of growing more than ten times faster than many other corals (~1 cm per month versus ~1 cm per year). By contrast, slower growing corals often compete by killing their neighbors with their stinging cells, while other bottom dwellers (e.g., sponges) release toxic chemicals. Seaweeds are often the most important competitors of corals because they grow much more rapidly; thus corals depend on herbivores for their survival.

Corals are mostly skeleton and many organisms prefer to eat other fleshier reef dwellers, but predation is nevertheless a major source of mortality for corals. The most renowned predator is the crown-of-thorns starfish (*Acanthaster*), and other invertebrate predators include snails (*Drupella, Coralliophila*) and fireworms (*Hermodice*). Both *Acanthaster* and *Drupella* are well known for their enormous fluctuations in population size, and outbreaks can result in the loss of most of the living coral on a reef. A few fish, such as some butterfly fish, are specialized polyp feeders. Both fish and invertebrate herbivores also graze on corals to a greater or lesser extent, particularly sea urchins, parrotfish, and damselfish, some of which kill coral to provide substrates for their algal gardens. Some corals shelter crab and shrimp that aggressively defend their hosts against these predators.

Corals are also vulnerable to diseases. The symptoms of many coral diseases have been documented in recent years, but the causative agents are only known in a few cases. These include bacteria, fungi and protozoans; viruses also occur on corals and may cause disease, but viral pathogens have not been documented. Some diseases may not be caused by specialist pathogens, but rather be the result of microbial overgrowth in stressed corals. Diseases of Caribbean acroporid corals have had ecological impacts comparable to Dutch Elm disease and Chestnut Blight on land; these once dominant corals are now listed as threatened under the U.S. Endangered Species Act. Diseases of other organisms have also had important consequences for coral reefs. For example, many sponges have died from disease, and the still uncharacterized disease that killed >95% of the sea urchin *Diadema antillarum* in the western Atlantic in the early 1980s resulted in the overgrowth of many corals by seaweeds.

Corals can also be killed by physical processes. Strong storms, such as typhoons and hurricanes, are common in most places where reefs occur. Waves are the primary cause of damage, but associated fresh water and sedimentation may kill corals and other reef organisms as well. Cold spells, especially in geographically marginal reefs, and even earthquakes can also cause catastrophic mortality.

Sadly, of all marine ecosystems, coral reefs are among the most threatened by human activities. Threats are both local and global, and they often interact in a negatively synergistic way to decrease coral growth and reproduction or increase coral mortality. Even though human impacts often increase gradually, the collapse of coral reefs may be sudden and unexpected. Throughout the world, many coral reefs have become seaweed reefs; it has been estimated that 80% of Caribbean coral cover has disappeared in the past three decades, and recent analyses of the Pacific indicate that many of these reefs are also in precarious condition. In addition, positive feedback loops may make it difficult for corals to become re-established (i.e., corals and algae represent alternate quasi-stable states). Although to date extinctions of conspicuous coral reef organisms have largely been avoided (the Caribbean monk seal being an exception), smaller organisms may have disappeared unnoticed and some organisms may already be doomed because of processes such as extinction debts and Allee effects — the inexorable decline of a species once numbers of its populations or individuals fall below threshold levels.

Locally, the most important threats are associated with fishing and the consequences of land use and waste disposal. Severe overfishing is typical of reefs today throughout the world, and in many places large vertebrates were removed long before ecologists began to study coral reefs. In some places, cyanide and dynamite are used to fish, killing many other organisms as well. Fishing of spawning aggregations has put some snappers and groupers in extreme jeopardy, and sharks are globally threatened because of the trade in their fins. Poor land use (e.g., deforestation and coastal construction) and the lack of sewage treatment result in nutrients, sediments and toxic materials being transported to reefs. Together, these impacts result in coral death either directly or indirectly by favoring the competitors (especially seaweeds), predators and pathogens of corals. In addition, oil spills and anchor damage associated with tourism can in limited areas do much harm.

Globally, increasing levels of CO_2 in the atmosphere pose grave threats. The most extensively studied of these is global warming. The symbiosis between corals and zooxanthellae starts to break down when water temperatures rise ~1˚C above local seasonal maxima; prolonged or severe warming results in coral 'bleaching', due to the loss of the pigmented algae from coral tissues (Figure 3), and eventually coral death. Although some types of zooxanthellae are somewhat more resistant to high temperatures than are others, mass bleaching events have been increasing in frequency and severity since the 1980s. Warming oceans are also associated with increased levels of coral disease. In addition, warming threatens reefs because stressed reefs may not be able to keep pace with rising sea levels, and because serious storm damage may become more common. More recently, ocean acidification has been recognized as a potentially catastrophic threat, because projections suggest that pH may drop to the point that skeletal formation will be difficult or impossible. Although recent studies suggest that some corals might survive such a change in pH even if they lose their skeletons, the existence of reefs and the diversity they support depend on the structure that the skeletons of corals provide.

Reefs are like cities, with growth and destruction occurring side

Figure 3. A partly bleached coral. The coral is still alive, but the polyps in the bleached parts have lost their symbiotic algae. Photo courtesy of David Kline.

by side. Conservation measures must thus work to ensure that on balance growth outpaces destruction, and that the natural ability of reefs to recover from disturbance ('resilience') is maintained. To date, marine protected areas have been the focus of most attention. Conspicuous successes include placing about one third of the Great Barrier Reef in no-take zones, and protection of the Northwest Hawaiian Islands. Marine protected areas do result in the rebound of most fish populations, and although documentation of the positive effects on corals is as yet more limited, there are promising signs. However, globally less than 2% of coral reefs are largely protected from fishing, and even these are often threatened by poor water quality. Moreover, localized protection alone cannot save reefs. In developing countries, traditional management schemes may be more effective given socio-economic constraints, and management of reefs outside marine protected areas is also clearly critical, with improved land-use and protection of herbivores being top priorities. Techniques for restoring reefs are being developed, but they are necessarily small in scale and expensive, and will only work if the original causes of decline have ended. Given that even the best scenarios for reducing CO_2 emissions suggest substantial and rapid deterioration of the physical environment, improvement in local conditions coupled with action to reduce global threats are essential if reefs are to survive into the next century.

Protecting and restoring these ecosystems are thus among today's biggest environmental challenges. Reefs are not only of scientific interest — they provide many ecosystem services and are critical components of the economies of many (mostly developing) countries — tourism, fisheries, and coastal protection being the most prominent. Success will depend on collaborations between natural and social scientists — we need to know not only what kills coral reefs, but also their economic value to people.

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Stereotypical resting behavior of the sperm whale

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Though very little is known about sleep in wild cetaceans, toothed cetaceans in captivity sleep with one side of their brain at a time [1]. Such uni-hemispheric sleep is thought to enable swimming, voluntary breathing, predator avoidance and/or social contact during sleep at sea [2,3]. Using suction cup tags, we discovered that sperm whales (*Physeter macrocephalus*) worldwide conduct passive shallow 'drift-dives' in stereotypical vertical postures just below the sea surface. Bouts of drift-dives accounted for 7.1% of recording time, or 36.7% of non-foraging time. Drift-dives were weakly diurnal, occurring least from 06:00–12:00 (3% of records), and most from 18:00–24:00 (30% of records). A group of vertically drifting whales were atypically non–responsive to a closely-passing vessel until it inadvertently touched them, suggesting that sperm whales might sleep during these stereotypical resting dives.

We measured the underwater activity level of 59 sperm whales worldwide using data-logging tags attached with suction cups for a total of 562.9 hours (see Supplemental data available on-line with this issue for further details). Predominantly (80.6% of time), tagged whales conducted foraging dive bouts, which differ from non-foraging shallow dives (19.4% of time) in depth or the presence of echolocation clicks [4]. Although it has been suggested that sperm whales may rest at depth [5], we found that they swam steadily, or continually produced clicks during deep dives.

Instead we discovered that 31 of 59 whales across all tagging locations conducted inactive