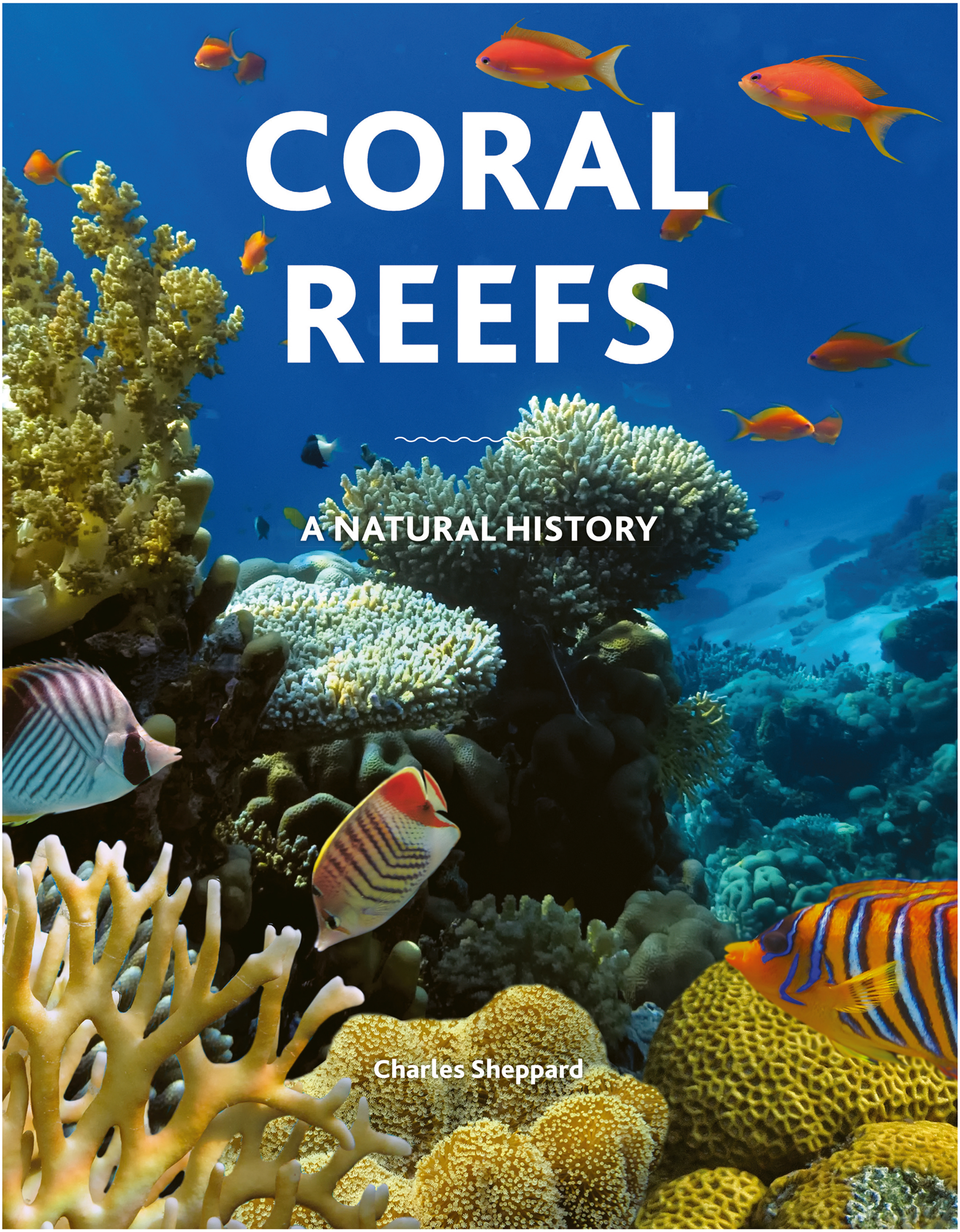
CORAL REEFS

A NATURAL HISTORY

Charles Sheppard



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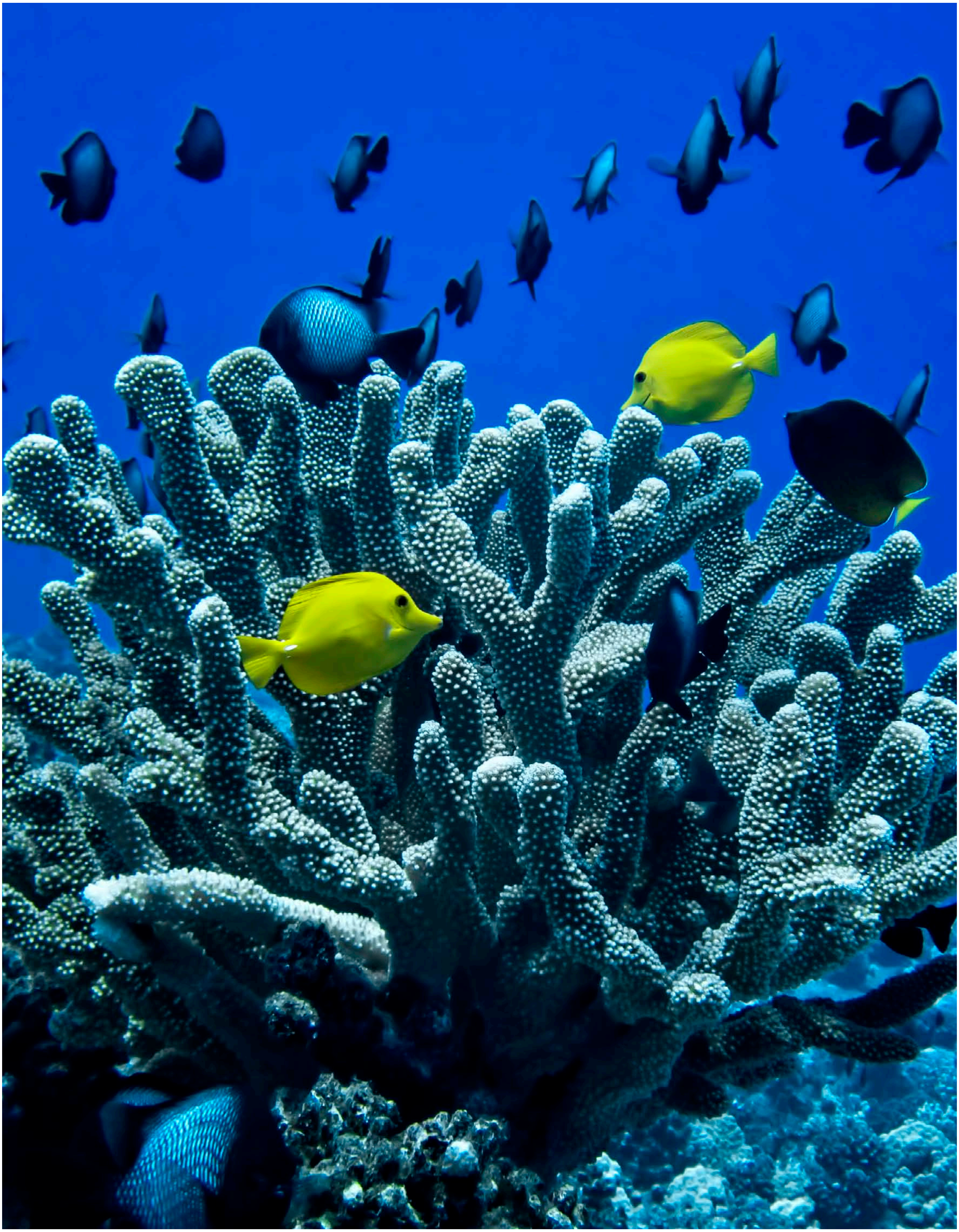

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Charles Sheppard

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Russell Kelley

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For my family.

May our many adventures,

both on land and under water,

just keep on going.

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FOREWORD

Imagine swimming in a warm, tropical sea. Through your face mask you peer down into an infinite azure abyss. All you can see are shafts of light plunging into the depths like lightsabers, and iridescent, sapphire-like flashes reflecting from invisible plankton somewhere below. Now you hear something between the lazy splashes of the torpid sea. A non-stop crackling hiss rises and falls like someone tuning a distant radio station. You kick your fins and turn 180 degrees and a vertical reef wall looms, draped in a wriggling tapestry of color and movement. Fish teem around hundreds of other kinds of reef creatures. You swim closer and gawp at the hallucinogenic patterns while the entire coral reef carnival carries on without a care for an alien visitor as clumsy as yourself.

For me, there is nothing as ineffably beautiful as a coral reef on a calm, sunny day—such scenes sear vivid memories that last a lifetime. Remarkably, the story of reefs—their origins, adaptations, and achievements in the great pantheon of evolution and Nature—is equally breathtaking.

From the study of modern reefs, we know corals are not just beautiful biological baubles, but an innovative force in Nature. Corals have solved the problem of how to create something from nothing in the middle of empty, nutrient-poor oceans using an ecology based on symbiosis and collaboration. And not just a modest "something," but the richest marine ecosystem on Earth.

The coral reef innovation derives from an extraordinary advent in biology—the ability for a plant to live inside an animal, the best known example being the algae cells laced through the tissues of every reef-building coral polyp.

Somewhere in the mists of geological time, shallow-water corals became infected with plant cells that not only survived but thrived within the coral animal. These tiny plant cells did what plants do: photosynthesise. Using sunlight, excess CO_2, and animal waste products, they flourished inside their host. In return the plant cells released sugars and the humble coral polyp suddenly had two engines for growth—a carnivore by night and a solar farm by day. Now corals had energy to burn, energy to build!

Their larvae dispersed on ocean currents to settle on the edges of sterile volcanoes where, with nothing but sunlight and microscopic planktonic meals, they combined their construction prowess with another great evolutionary achievement—cloning. In this way the arrival of a single coral larva, transforming into a polyp, could build great coral colonies. I like to think of them as colonial castles conjured from nothing in the middle of empty oceans.

On coral reefs recycling is a way of life, as is finding a home on, or inside, another species. Over many millions of years coral reefs have attracted thousands of species to come

along for the ride, weaving an evolutionary fabric so organically intricate it inspires, and deserves, the term living art.

This book explores the natural history of reefs in a human context. Written plainly and richly illustrated, it is a guide to the good, the bad, and the ugly of the coral reef story. Around the world Nature is in retreat and so it is with reefs. In the tropical world around 500 million people depend on reefs for shelter, protein, and employment. Yet in many regions reef decline is accelerating due to the impacts of growing populations of people without options.

Even more pressing is the threat of climate change and the ocean warming it causes. Underwater heatwaves are triggering mass coral bleaching, a "disease" (described on page 186) that attacks the evolutionary bond between coral and algae, the very engine of the ecosystem's existence.

Coral Reefs; A Natural History is a portrait of the wonders and dilemmas facing the richest of marine realms. If we want our children to see Nature's great gifts, and if millions of people are to avoid displacement and hardship, then it is time for humanity to take our collective foot off the carbon emissions accelerator.

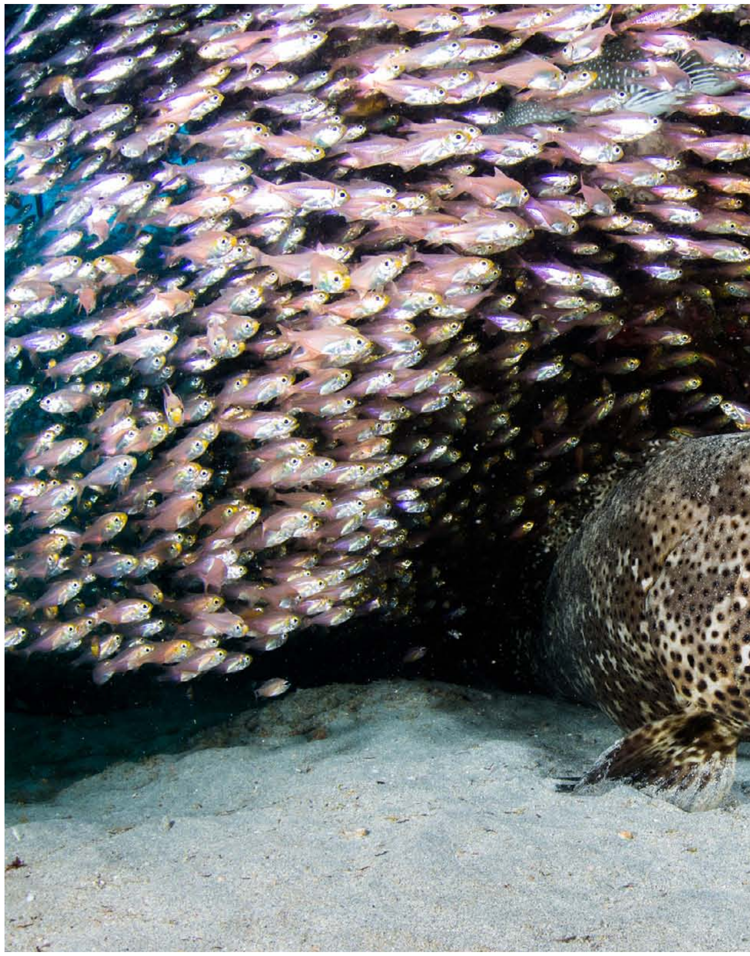
Russell Kelley
Townsville, Queensland, Australia

INTRODUCTION

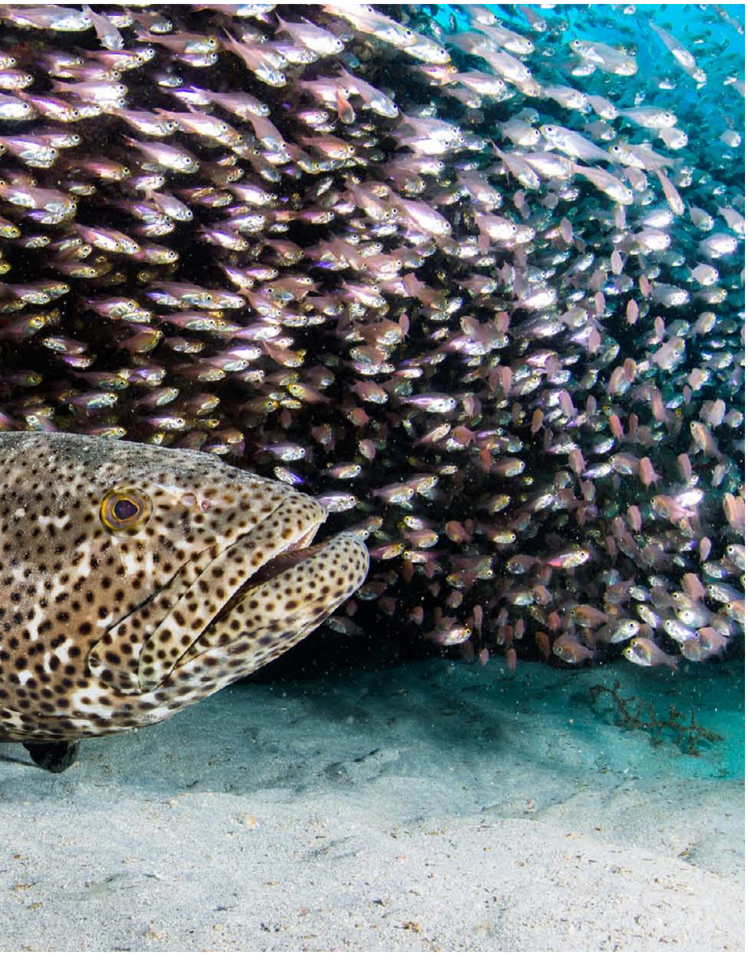
Coral reefs mean different things to different people. To a sea captain they are potentially hazardous, often poorly marked on the chart, and always lying just beneath the surface of the water. To people living in the tropics beside a reef, or on a small island perched on one, they provide both a home and food. To many divers and snorkelers who visit tropical coasts they are a kaleidoscopic wonderland of colorful fish that circle and dart above the strangest of living structures, and these tourists bring significant revenue and foreign earnings to such regions. The scientist sees something different again, a place of huge diversity in a relatively small space, of apparently chaotic pattern and movement, something to try to make sense of. A reef is all of these things and more.

Coral reefs occupy only about one percent of the Earth's surface but they contain a high abundance of marine species, and they concentrate huge densities of it too, like an oasis. Not only this, but they also construct the reef itself. A reef is made by corals and other organisms as they extract limestone from the seawater to deposit as solid rock to make their own skeletons. They have been doing this for millennia so that now some reefs are a couple of kilometers thick in parts of the Earth that have been slowly subsiding over the ages, such as in the atolls scattered across tropical parts of the Indian and Pacific oceans. The parts of the reef that are now living form only a veneer on the top. Yet that small quantity has built the structure that supports all the rest, from the thousands of species of simple animals to the swarms of fish above, and to several entire oceanic nations.

Few of us realize that around half a billion to a billion people are now wholly or largely dependent on coral reefs, because they live on them or are dependent on the protein that they produce, or perhaps because they provide sheltered waters for a mainland settlement. That number does not include many millions more who use them for recreation.



Yet there are fewer than 1,000 species of reef-building coral—a thousandfold fewer than the number of species that live among the structures they have built. Corals are the key animals that deposit the limestone rock, which they do because of help from captive, symbiotic algae, in a close association between animal and plant that has lasted for a couple of hundred million years. The far greater numbers of invertebrates on reefs include many that are hidden, and this is unsurprising given the huge whirls of predatory fish above them. Many animals are gaudily colorful. All are hunting for food and mates, and many use astonishing methods of hunting while avoiding being eaten themselves.



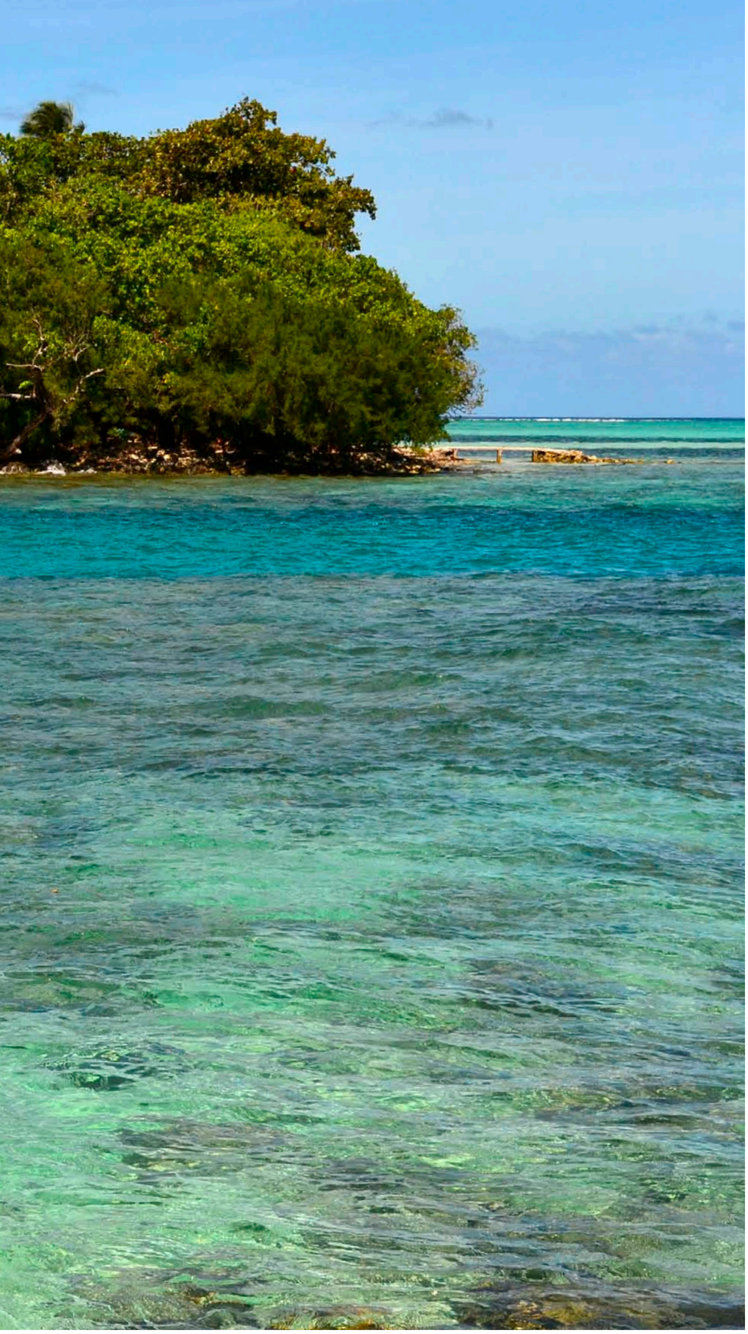
ABOVE | A grouper on a Western Australian reef. Grouper are ambush predators and commonly hide in caves, though here the cave is concealed by the shoal of small, silvery fish.

TOP RIGHT | Deeper on a reef where water is calmer, large sea fans extend into the water to trap plankton for food.

RIGHT | A rich mix of stony coral, soft corals, and fish on a reef slope.

Coral reefs have attracted people for generations, and because of that attraction to sheltered sea conditions, food, and space on which to live, they have been facing increasingly damaging pressures. So much so that by about 50 years ago probably about a fifth to a quarter had already been damaged and some destroyed. As human populations have risen steeply over the last couple of generations, this damage has increased, coming from pollution such as sewage, agricultural practices that smother reefs with too much fertilizer and sediment, and from dredging the seabed or industrial pollution because the sea has been a cheap place to dump toxic wastes. Damage has also resulted from overfishing to feed increasing populations, and overfishing is one of the most damaging impacts we inflict, because it unbalances the ecosystem.

Then, around the 1970s, the temperature of the oceans started to rise. It wasn't noticed much at first because the increase was small and within the general variation. It occurred because for the preceding century people had been burning ever more oil, which, together with the burning of



LEFT | A small coral island on the reef flat of one of the Federated States of Micronesia, in the Pacific Ocean.

ABOVE | A rich mix of soft corals on a reef slope.

coal and land clearing, added increasing amounts of carbon dioxide (CO_2) to the air. This gas traps heat from the sun. Scientists looked at every other possible cause of warming and discounted most: the temperature rise has come mainly from burning fossil fuels. Many species in tropical waters, including corals, are already very close to the maximum temperature they can survive. This warming arrives in pulses, called marine heatwaves, and repeated heatwaves are killing corals and reefs in vast numbers. Today this is the primary threat to their survival. Corals, seemingly robust because of the huge reefs they make, have a rather fragile relationship with their symbiotic algae and will die when this is disrupted. They are now facing an existential threat.

This book aims to show and describe the beauty of this most incredible ecosystem, and to explain some of the problems that it now faces and how we must respond to the threats. It is a natural history of an extraordinary but endangered ecosystem.

CHAPTER 1

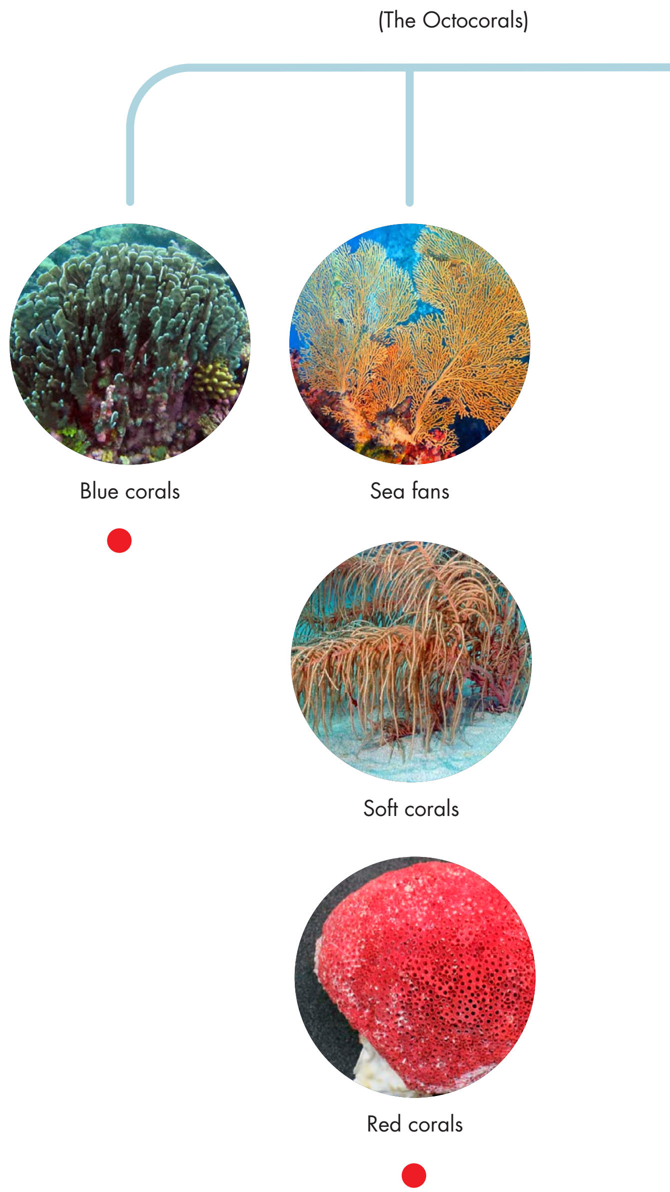
THE CORAL ANIMAL

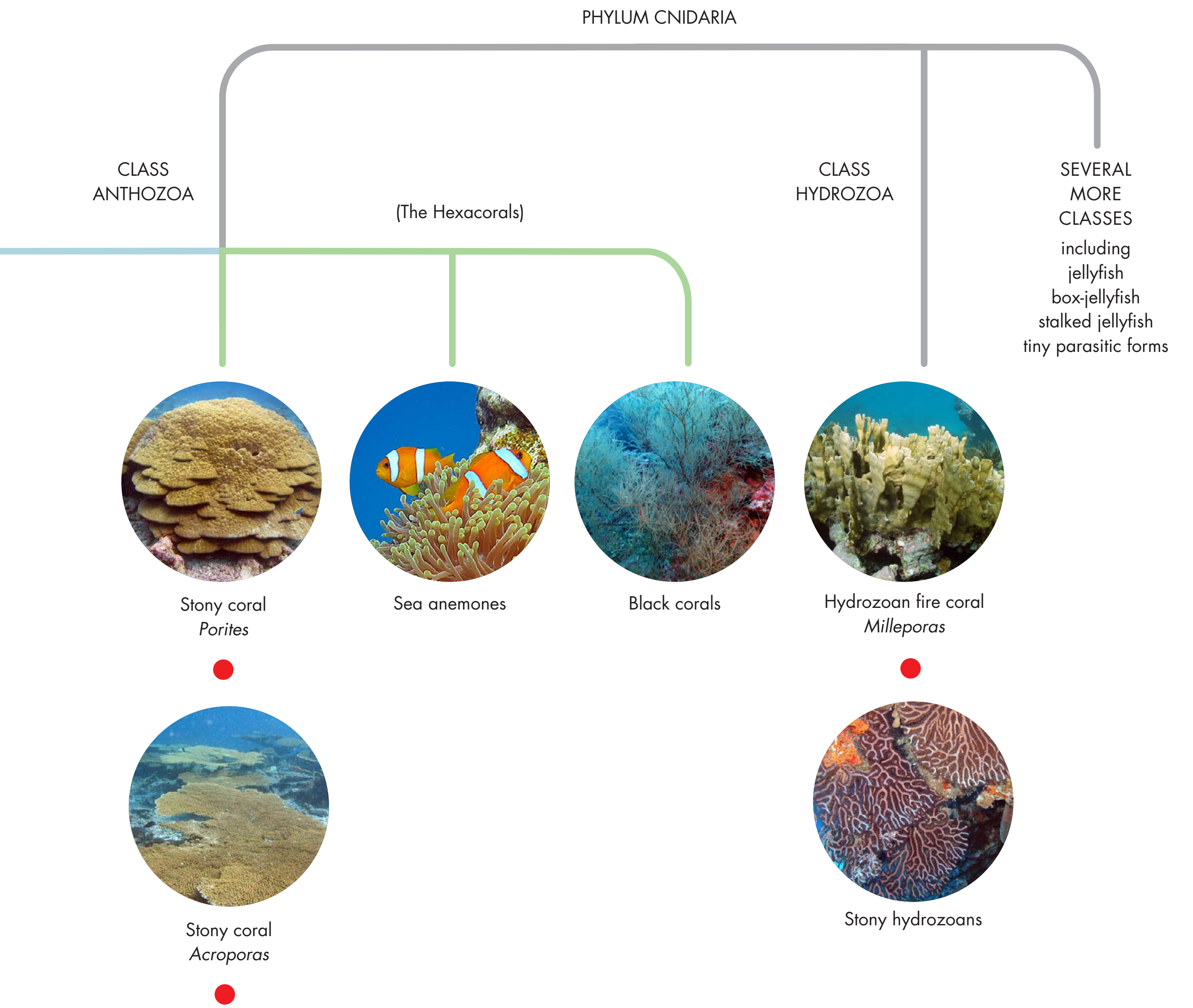
WHAT ARE CORALS AND REEFS?

Corals belong in a group of primitive, simple animals called cnidarians, a group named for the stinging cells that they all have in one form or another, in tentacles that are used for capturing tiny prey. They have an ancient lineage: over 740 million years ago, the Earth saw the emergence of the common ancestor of this group of animals, which now includes other reef-building forms as well as corals. No fossils exist from that time to confirm this age, so it has been deduced by use of the "molecular clock," which is the rate at which mutations occur in their DNA. The earliest fossil cnidarians found so far are about 580 million years old, with the forms that gave rise to today's corals appearing 100 million years later (see page 94).

Since then, divergence in the group has resulted today in several main classes, some mostly free-swimming, including the jellyfish, and at least three that are mostly attached to the substrate when adult, which includes the corals and other reef builders.

The earliest corals were, for a long time, only a minor form of life on Earth, but they were persistent. They survived through millions of years, including the greatest biological crashes that have occurred in Earth's history, not only once but on several occasions. When modern corals developed further and made their important impact on our planet, it was after the great global wave of extinction between the Permian and Triassic eras. Corals also nearly came to grief again during a later wave of extinction at the end of the Cretaceous, which saw the demise of the large dinosaurs. Modern corals then thrived at various times between 80 and 20 million years ago, and today's commonest coral genus (*Acropora*) occurs as fossils in limestones around London and Paris, among other cities. They expanded considerably and came to dominate shallow tropical seas, as we see today.





ABOVE | The animals in the phylum Cnidaria are defined by the presence of stinging cells in their tentacles. The phylum contains four to six classes, the number and characters that define each being in a state of flux and dependant on the results of new research. The diagram shows likely relationships between groups of reef-dwelling Cnidarians. Blue lines indicate the eight-segmented Octocorals and green lines the six-segmented Hexacorals, all within the class Anthozoa. The red dots next to several groups indicate the important reef constructors, the main ones being the stony corals. Other classes include mainly free-swimming and tiny parasitic forms, which are not important for reef-building.

THE CORAL ANIMAL

The basic unit of a coral is a polyp, which is like a small sea anemone. Each polyp has six radial segments—they are hexacorals—and one or more rings of tentacles surrounding a mouth on top of its cylindrical, sac-like body. Its tissues secrete limestone in the form of a cup, in which the animal lives. Each cup is called a corallite, and these polyps with their corallites grow upward, and divide as they do so.

The polyps and tentacles of most species are usually contracted into their cups in the daytime, emerging at night to capture zooplankton—tiny animals floating or swimming in the water. Each tentacle is loaded with stinging cells, called nematocysts, which have barbs on threads that inject venom and pull the trapped zooplankton to the central mouth. The wall of the body (and tentacles) is composed of a simple double layer, the ectodermis on the outside and gastrodermis on the inside, sandwiching a jelly-like mass called the mesoglea. The ectodermis in the tentacles houses the stinging cells, and that on the underside of the polyp is responsible for deposition of the limestone skeleton (see page 21).

The gastrodermis layer of the body wall contains the digestive tissues. Importantly, this layer also contains thousands of single-celled algae living in symbiosis with the animal host. These algae take up animal waste and in return provide the products of their photosynthesis (sugars and nutrients), and give a greenish-brown color to the coral. The number of algal cells is huge, and their photosynthesis commonly provides the coral animal with more food than does the captured zooplankton.

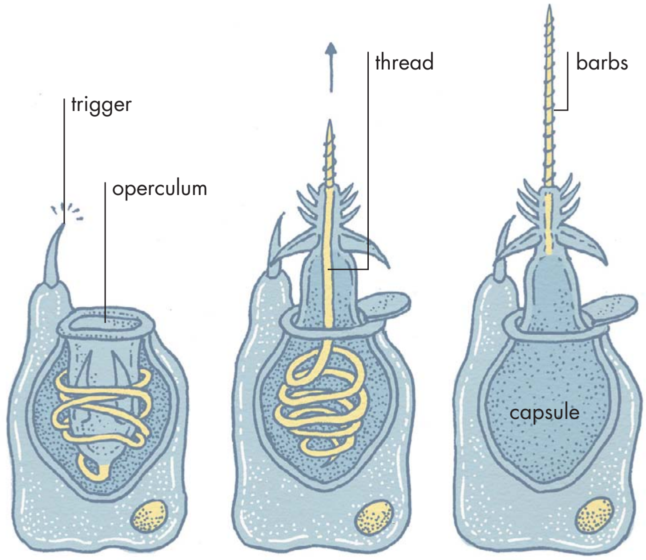
In the polyp body, vertical structures called mesenteries partly separate the space into compartments, adding greatly to the total surface area available for digestion. These develop the eggs and sperm too, commonly in an annual cycle. Some corals have separate sexes, but most are hermaphrodites (both male and female).

Almost all species divide by budding—splitting into two individuals. The "daughter" polyps may remain joined or separate completely. All tissues are served by a nerve net, which can transmit signals across a colony, as can be seen when one part of a colony is touched, causing a ripple of polyp retraction across the surface. Most corals are colonial, but many are essentially solitary—single cups with polyps.

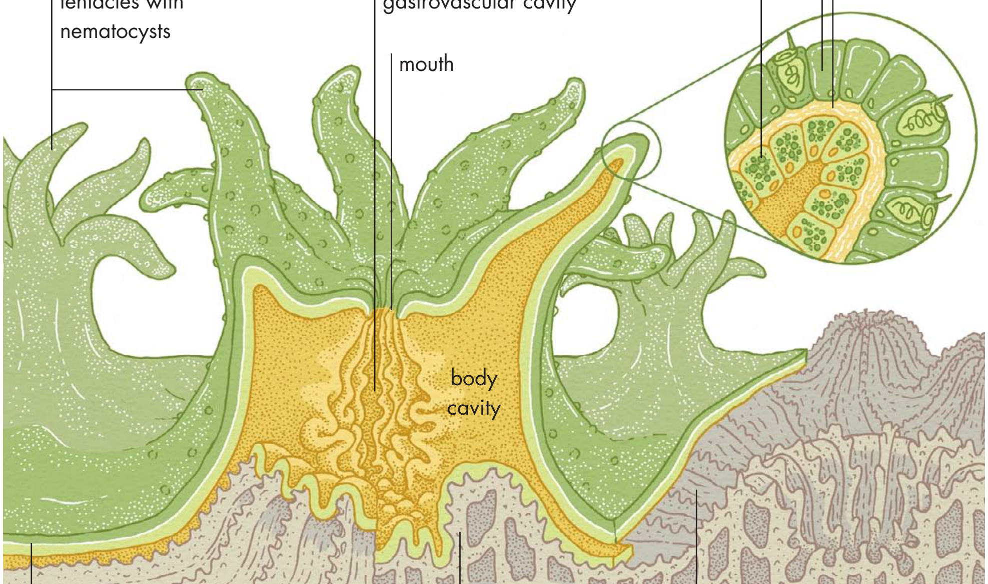
ABOVE | Tentacles of most species are small and expanded at night only, when they catch zooplankton and when browsing fish do not feed.

ABOVE | Polyps of *Goniopora* are especially long and are extended during the day. If touched they will almost completely retract.

A NEMATOCYST DISCHARGING



ANATOMY OF A CORAL POLYP



ABOVE | Touch on a hair-like trigger at the opening of the nematocyst causes the sting to shoot out.

ABOVE LEFT | One fairly large coral polyp in one limestone cup, with the polyp retracted in daytime. Tissue conceals the cup, although the radial plates (septa) show through. The green/brown color comes from the symbiotic algae in the coral. The polyp in the middle is connected to the one on the left by tissue, but not to the one on the right.

LEFT | Anatomy of several hard coral polyps with tissue (colored) overlying skeleton (grays).

CORAL SYMBIOSIS
SYMBIOTIC ALGAE

While plants form the basis of all sunlit ecosystems on Earth, on most healthy reefs there are very few large plants or algae to be seen. Where, then, are all the plants that support the life of this teeming ecosystem? The answer lies within the corals, in a symbiosis with origins at least as ancient as the Triassic period, 220 million years ago. The corals are packed with symbiotic, single-celled algae called zooxanthellae, of the family Symbiodinacea. Each square centimeter of coral surface contains a couple of millions of these plant cells. Their numbers fluctuate, but their density gives the corals their dominant brownish-green color. When you look at an expanse of coral reef you are looking at a field of captive, single-celled algae.

These algae provide much of the primary production on a healthy reef. Corals regulate the algal densities in their tissues, and there are natural seasonal cycles in density according to whether the coral surface is shaded or in bright light. The system can go badly wrong, however. When the water is too warm, the physiological activities of the algae become toxic to both the coral and plant. This causes corals to expel the algal cells and many corals go on to die, a major problem today, known as "bleaching," that is leading to massive and worldwide coral mortality (see page 186).

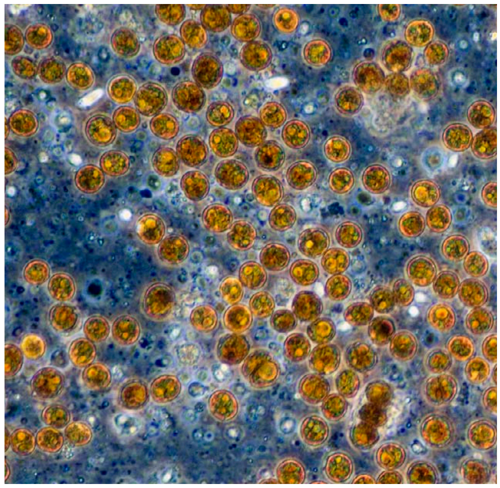
There are symbioses with other microbes too, mainly with bacteria and archaea (which are similar in size to bacteria but which have a quite different biochemistry), but also with fungi and others, that are almost as important. Numbers here can dwarf those of the zooxanthellae: 100 million bacteria can live in each square centimeter of a coral and in its surface mucus. These microbes are central to the nitrogen cycling processes for the coral. Ammonium (one form of nitrogen) excreted by animal tissues is toxic, but this is used and

rendered nontoxic by some of the microbes in a complex cycling system. However, as with the algal symbiosis, things can go horribly wrong, like when excess nitrogen is added to the environment from sewage or agricultural run-off. This will disrupt the balance of the microbe community, and can also kill the coral host (see page 20).

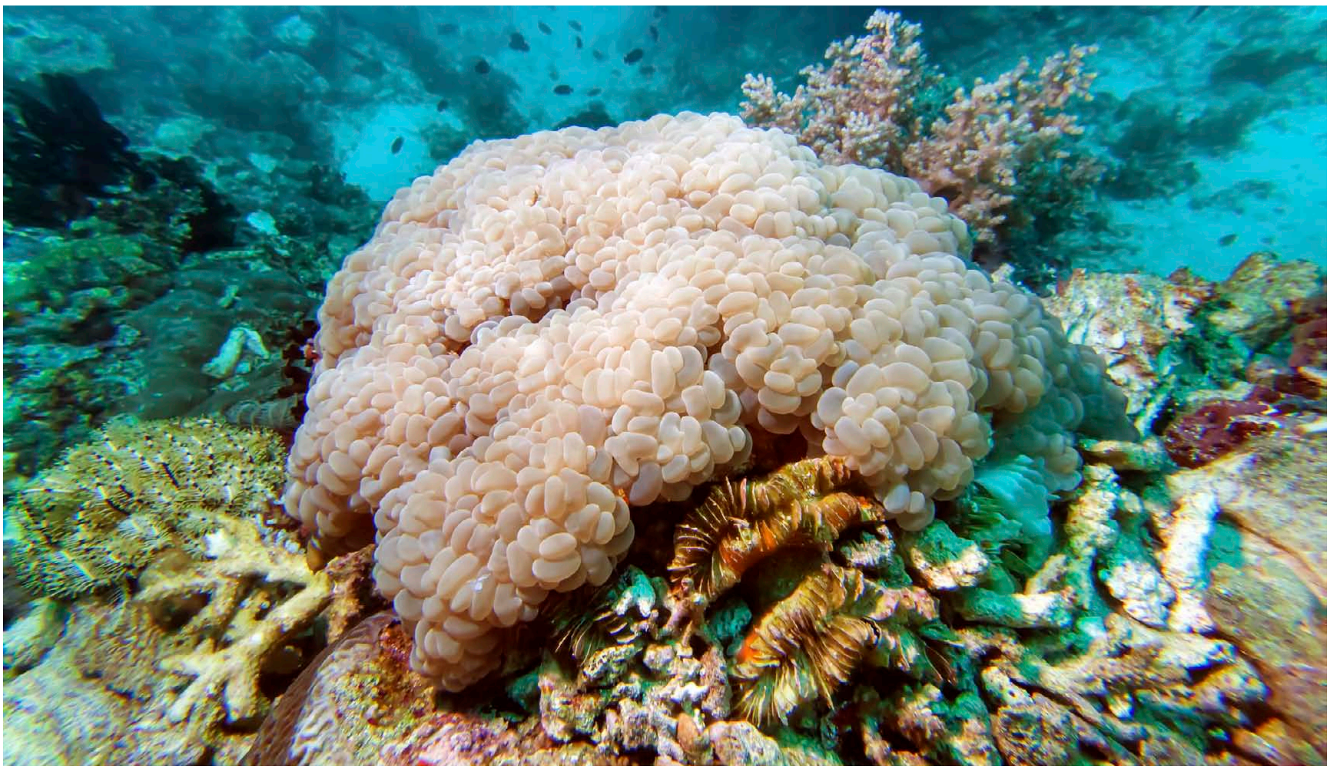
A coral's symbiotic complex is now commonly termed "the coral holobiont," all interlinked and all dependent on each component part.

BELOW LEFT | The dominant color of most corals is a greenish-brown, caused by the vast number of algal cells contained within the coral tissues.

BELOW | A few corals expand bubbles of tissue from their surface. These create a larger surface area, allowing it to house a greater number of algal cells.



ABOVE | The symbiotic algal cells in coral tissue seen through a microscope.



CORAL SYMBIOSIS
THE CORAL HOLOBIONT

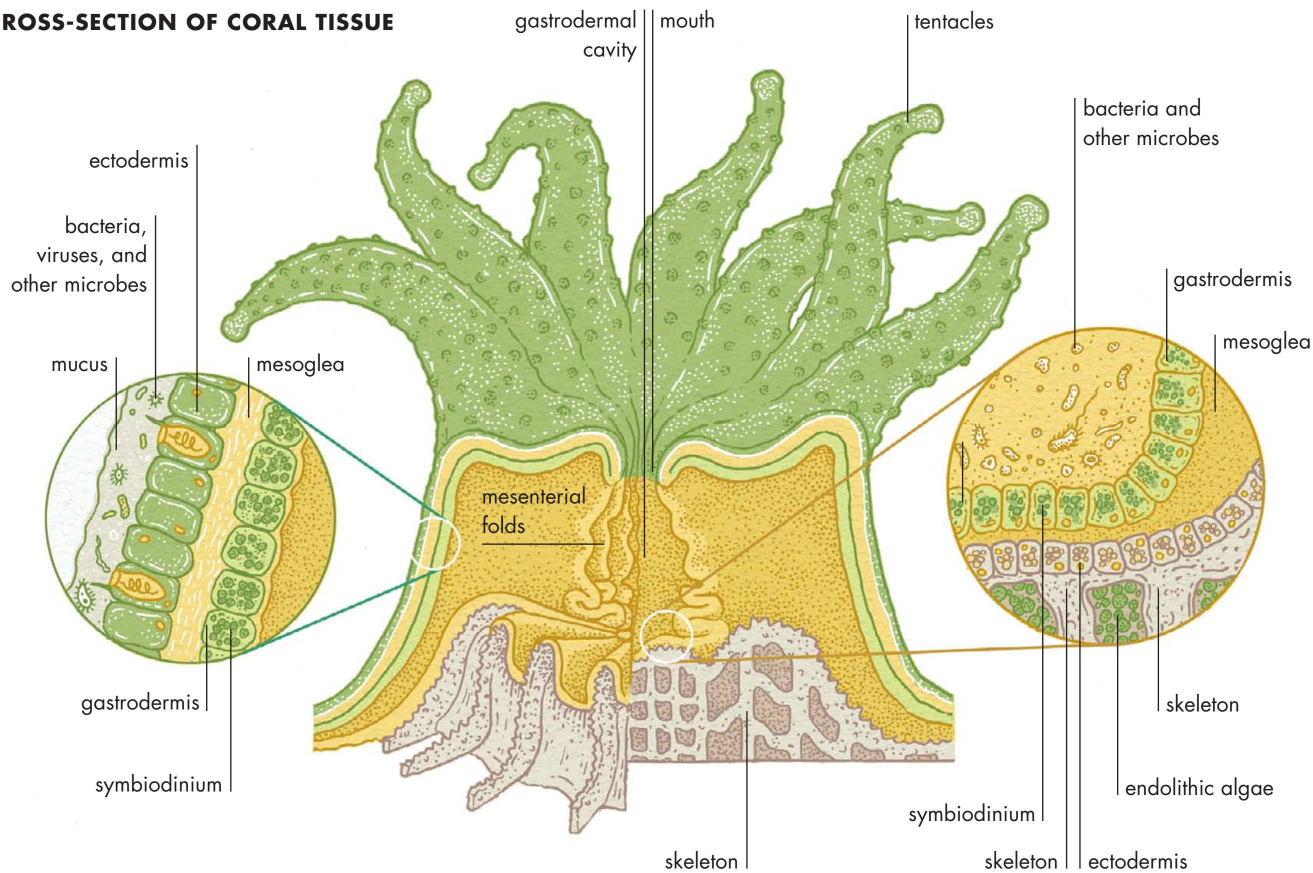
ABOVE | All corals secrete mucus from across their whole surface: from their tentacles, body wall, and the tissue-connecting polyps. This mucus usually forms a thin, invisible layer that is constantly renewed. It is packed with a range of microbial forms that carry out a number of symbiotic functions with the coral, but sometimes with pathogens. These distinctive tentacles have club-shape tips.

OPPOSITE | The anatomical parts of a polyp, emphasizing symbiotic components. The thickness of the mucus layer is exaggerated. The ectoderm on the tentacles (left inset) contains the stinging cells, while that at the base of the polyp (right inset) contains the apparatus for depositing limestone skeleton.

The coral holobiont is the assemblage of the coral animal together with its associated microbes. These include bacteria, archaea, viruses, fungi, and protists, in addition to the symbiotic algae cells (the zooxanthellae) in its tissues (see previous pages). The micro-organism component is called the microbiome. In corals these microbes provide numerous key functions, and many scientists now think that corals could be imagined as being assemblages of all of these organisms, not just the large and visible coral polyp.

The zooxanthellae are a key component of these microbes, and these provide the coral with nourishment from their photosynthesis. They are present in densities of half a million to 5 million cells per square centimeter (see page 19).

CROSS-SECTION OF CORAL TISSUE



Another abundant group of microbes are the recently discovered "corallicolids," a group of parasitic microbes. They evolved from photosynthetic cells which later lost the ability to photosynthesize and became parasitic in tissues in the coral's gastric cavity.

Very important are bacteria and other microbes, living within the coral tissues but most notably in huge numbers in the layer of mucus that all coral polyps secrete on their surface. For example, growth of the coral polyp and colony is highly dependent on nitrogen availability but corals thrive in nutrient poor seas with very low nitrogen. How they could do so was a mystery for a long time, and this was called the Darwin paradox after its first observer. It is now known that many of these bacteria can convert dissolved nitrogen into compounds used by the symbiotic algae and the coral. Others turn the toxic ammonia that is made by some of the processes into nontoxic forms. Still other microbes are involved in carbon and sulfur cycling, anti-pathogen defenses, and other vital functions.

The different coral species do not necessarily have the same component microbial species, and microbes vary also according to depths at which the coral species grows. The principle, however, is similar for all in that the assemblage of numerous microbes intimately associated with the polyps are central to their growth and existence.

CORAL GROWTH AND DIFFERENT COLONY SHAPES

As coral polyps divide by budding they grow upward. The rate at which budding occurs relative to upward growth to a large degree determines the shape of the whole colony.

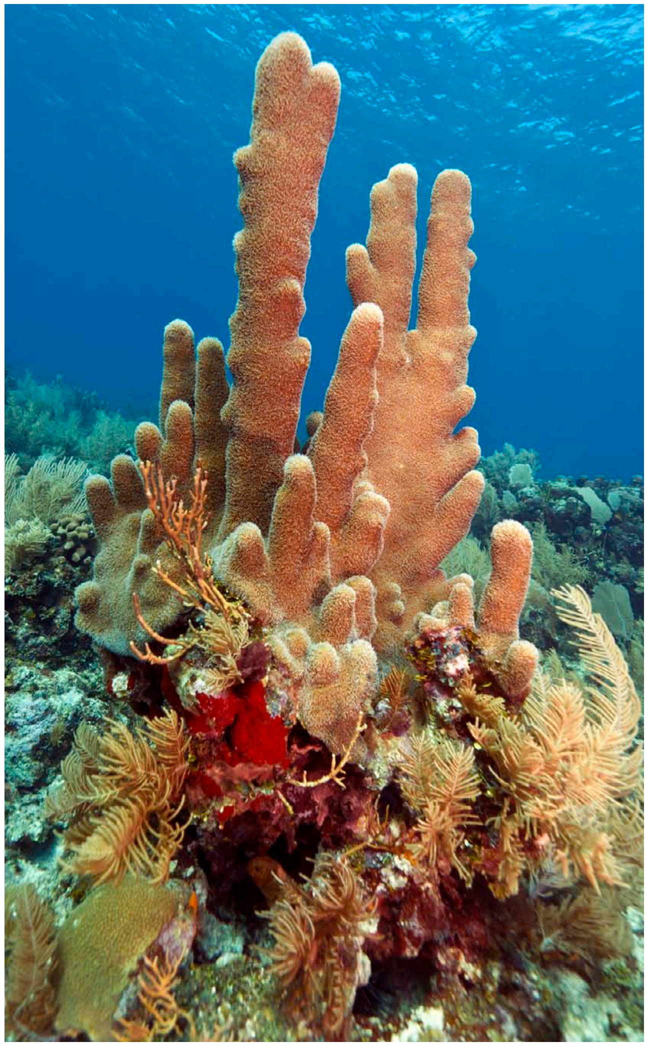
In a branching coral or one that forms columns, the upward growth is far greater than the budding. In contrast, one that buds frequently but shows little upward growth will develop into a plate or it may encrust the surface, with possibly only a few lumps here and there. A matched amount of upward growth and budding would theoretically create a perfect hemisphere.

The general colony shape is determined by the genes, but is also influenced greatly by the environment in which the colony is living. In very sheltered water, branching species will develop much more slender and elongated branches than will the same species in turbulent water. These differences may be large enough to even suggest it is a different species, so colony shape alone is insufficient to determine the identity of a coral. The size of the polyps on the branch affects the colony appearance, too. The polyps may be sparse or crowded, and branches may be pointed or club-shaped, or may all turn upward at their tips.

In leafy corals, lateral budding is profuse and upward growth is minimal, leading to a thin, expanding plate. Most leafy species, but not all, have polyps only on the side of the colony facing upward, though some species with steeply sloping leaves may have polyps on both sides.

In massive-shaped corals (see page 30), different parts of the colony may behave differently. Some have leafy edges, and others may develop a column. These different characteristics are used as an aid to identify the coral, before the more detailed structures are looked at.

In many species, the polyps or chains of polyps remain attached to each other laterally, but in others they separate as soon as a group of perhaps three or four has developed. These are termed phaceloid colonies, a kind of halfway between a massive and a branching coral.



ABOVE | The Caribbean coral *Dendrogyra cylindricus* can grow columns 9 ft (3 m) tall. Its polyps and tentacles are emerged in the daytime, giving a furry appearance.

OPPOSITE LEFT | The branching *Tubastraea micrantha* has no symbiotic algae and is entirely dependent on capturing plankton with its green polyps.

TOP RIGHT | *Pocillopora* branches are usually stubby and can live in water with strong wave action.

CENTER RIGHT | Polyps of both these *Lobophyllia (L. diminuta* left and *L. hemprichii* right) divide into groups of two or three, then separate from neighboring groups.

RIGHT | *Pachyseris speciosa* divides rapidly at colony margins and has minimal upward growth, so forms a plate. Its polyps divide to make chains, with as many as over 100 polyps in each "valley."

LEFT | Many fish species on reefs live in schools of hundreds or thousands. This helps them confuse predators and can also facilitate breeding.

RIGHT | Branching corals offer refuge from predators for numerous fish species and invertebrates. These small schooling damselfish shelter among the branches, emerging to feed on plankton and retreating back to shelter when approached by predators or divers.

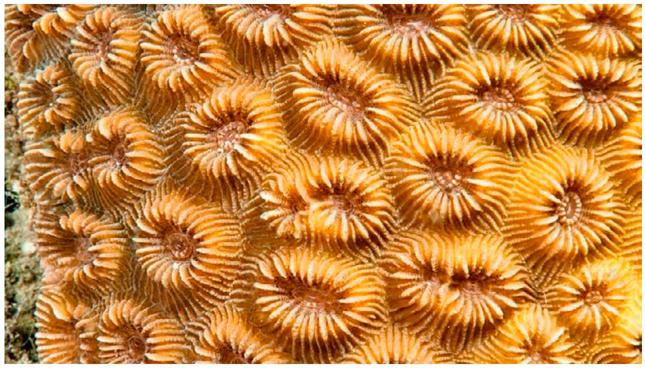
IDENTIFYING CORALS

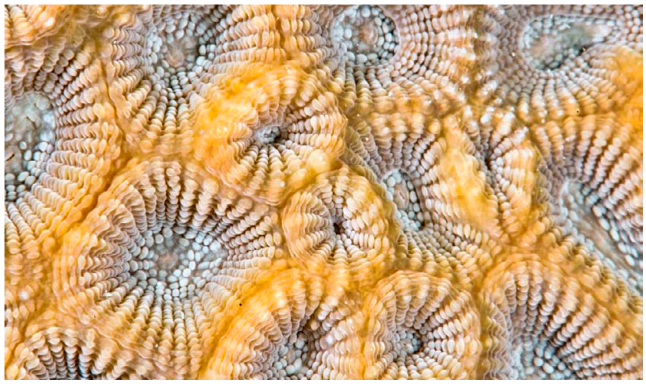
Few corals have widely accepted common names, though aquarists do use them. Latin names are used in scientific work. Difficulty arises in identifying any one species of coral because their colony shape can be highly variable, and is influenced by the colony's depth, the space available to it, the severity of wave action it experiences, and other aspects of its habitat. Corals show a high "plasticity" in this respect.

In the last two decades, molecular techniques have become increasingly important to define a species and determine its relationships to others. A coral's DNA sequence will become the definitive arbiter of a species because a coral's colony shape and polyp characters are variable, even within one colony. But for all aspects of fieldwork, visible features remain the only way for scientists to conduct their work, and this is discussed here.

After general colony shape, the type of budding— the process by which polyps clone themselves—is important. New polyps can develop within the ring of tentacles of the "parent" (intra-tentacular budding) or from outside the ring (extra-tentacular budding). Whether polyps stay single or whether they develop chains is important and, if a chain forms, how long the chain becomes.

To distinguish species, details of skeletal structures within a corallite are often needed, often visible only with a lens. The basic skeletal cup in which each polyp is located is called the calice. Usually dish-shaped, its details are especially important. Structures on the surface between corallites, and indeed whether there is any surface between them, are important too.





TOP | The cups (corallites) of this species, *Dipsastraea laxa*, are dividing at the edge of the colony by intra-tentacular budding, whereby two polyp mouths develop inside one polyp.

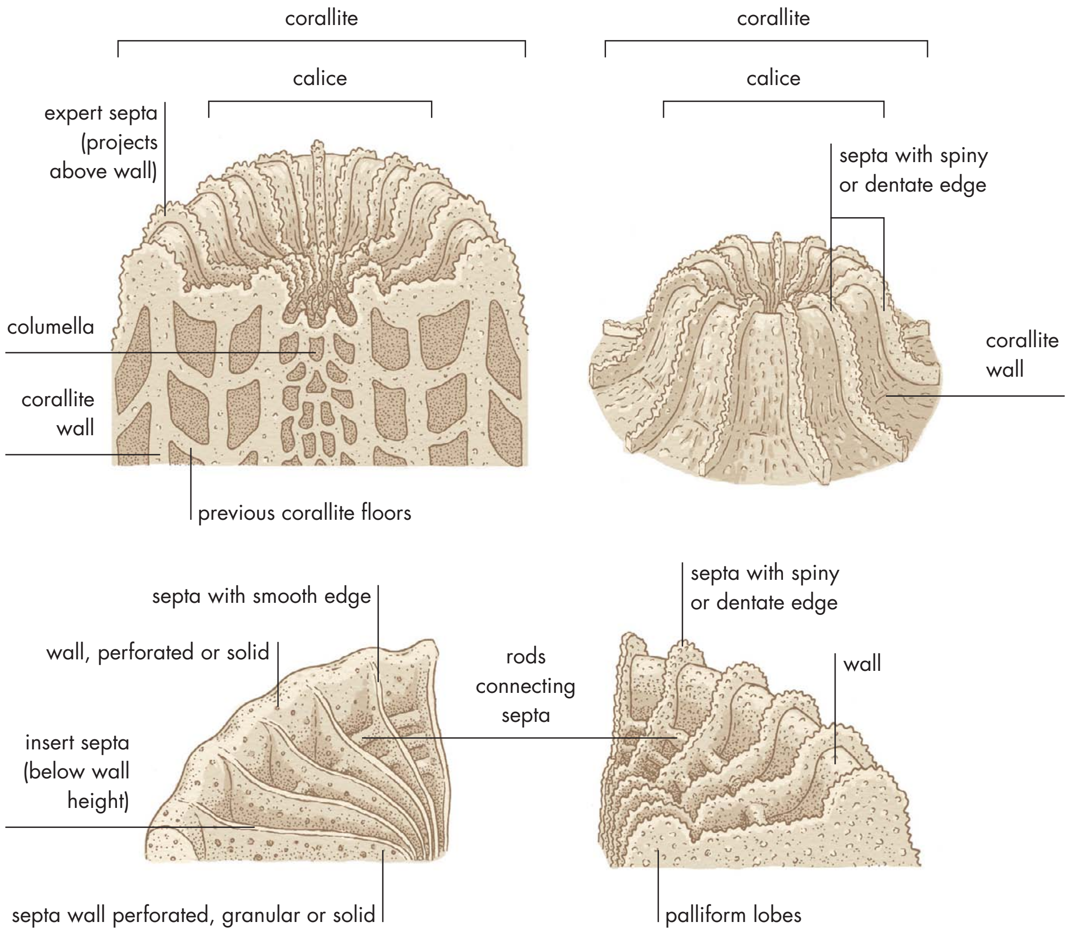
ABOVE | In *Phymastrea magnistellata*, the polyps are budding extra-tentacularly, whereby polyps bud from the space outside the parent's tentacle ring.

The arrangement of vertical skeletal plates, the septa, which radiate like spokes in each cup, is significant. There may be six septa or multiples of six, of decreasing or alternating sizes. In a brain coral, septa are parallel with one other. Septa may extend prominently up and over the corallite wall, and the septa may be smooth or adorned with spines.

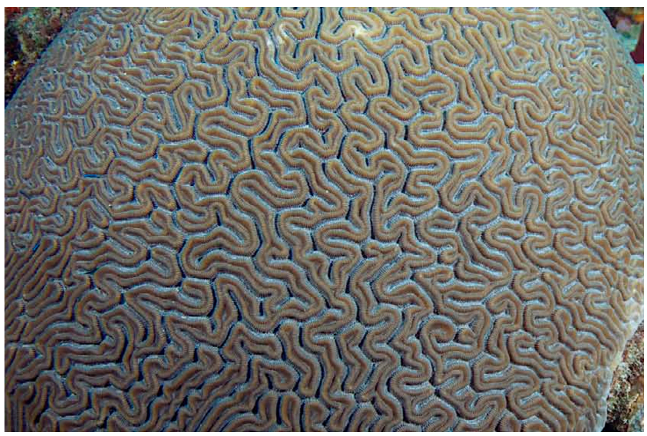
Where corallites are separate from each other, ridges may run down the outside of the wall, or not, possibly with small spines or beads. And in the center of each corallite there may be a bundle of twisted skeletal plates, or a single small pillar, or none.

There are over 800 different species of coral in the world that can be found on reefs and which grow sufficiently to build the reef itself. And there are even more species from greater depths, where it is dark, cold, and below the depths where reefs can grow. Errors in naming species are common.

KEY ELEMENTS OF A CORAL SKELETON



ABOVE | In *Lobophyllia hemprichii*, budding is intra-tentacular. Each multiple-mouthed chain of two to four polyps becomes separated from adjacent ones.



ABOVE | In the Caribbean brain coral *Diploria*, polyps only partly separate, forming chains up to 100 polyps long.

CORAL REPRODUCTION

Most coral species spawn large numbers of eggs and sperm into the water, which fertilize externally to form planulae—egg-shaped, free-floating larvae. Planulae can swim a little using the beating hairs that cover their body, and can adjust their buoyancy to move vertically to different depths. However, mostly they are borne by ocean currents and disperse passively.

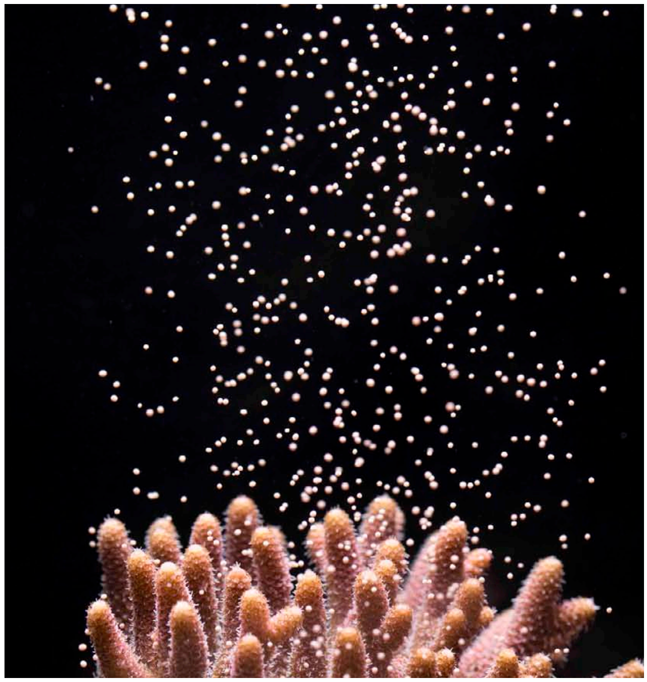
Corals synchronize their spawning to maximize the chances of fertilization, and huge slicks of spawn and fertilized planulae can be seen the next day in calm weather. Corals reproducing this way are commonly termed "broadcasters." The remainder are "brooders," which retain and fertilize eggs internally, resulting in fewer but better-developed planulae, which commonly do not travel as far. One species can use different modes in different places, and some use both.

Planulae usually last up to three or four weeks, and can stay in this larval stage for much longer under conditions of nutrient limitation, in which case they can travel many hundreds of kilometers on currents from their parents.

Eventually, the small proportion that survive the journey settle and develop into adults. They may have inherited symbiotic algal cells of their own from the parent egg, or may acquire them later from the surrounding environment.

Coral planulae can detect suitable substrates. They can sense a reef chemically, and can detect sounds of a reef nearby. They will settle preferentially on old coral limestone and calcareous red algae, and use their limited ability to swim to help them find the right spot. This is an essential ability because, as part of the zooplankton, planulae make ideal food for other adult corals, soft corals, and sea fans, and indeed for any filter-feeding animal, so an ability to select a substrate to some extent helps survival at this precarious stage. After settling, they transform into a simple, single polyp which soon commences dividing to form a colony.

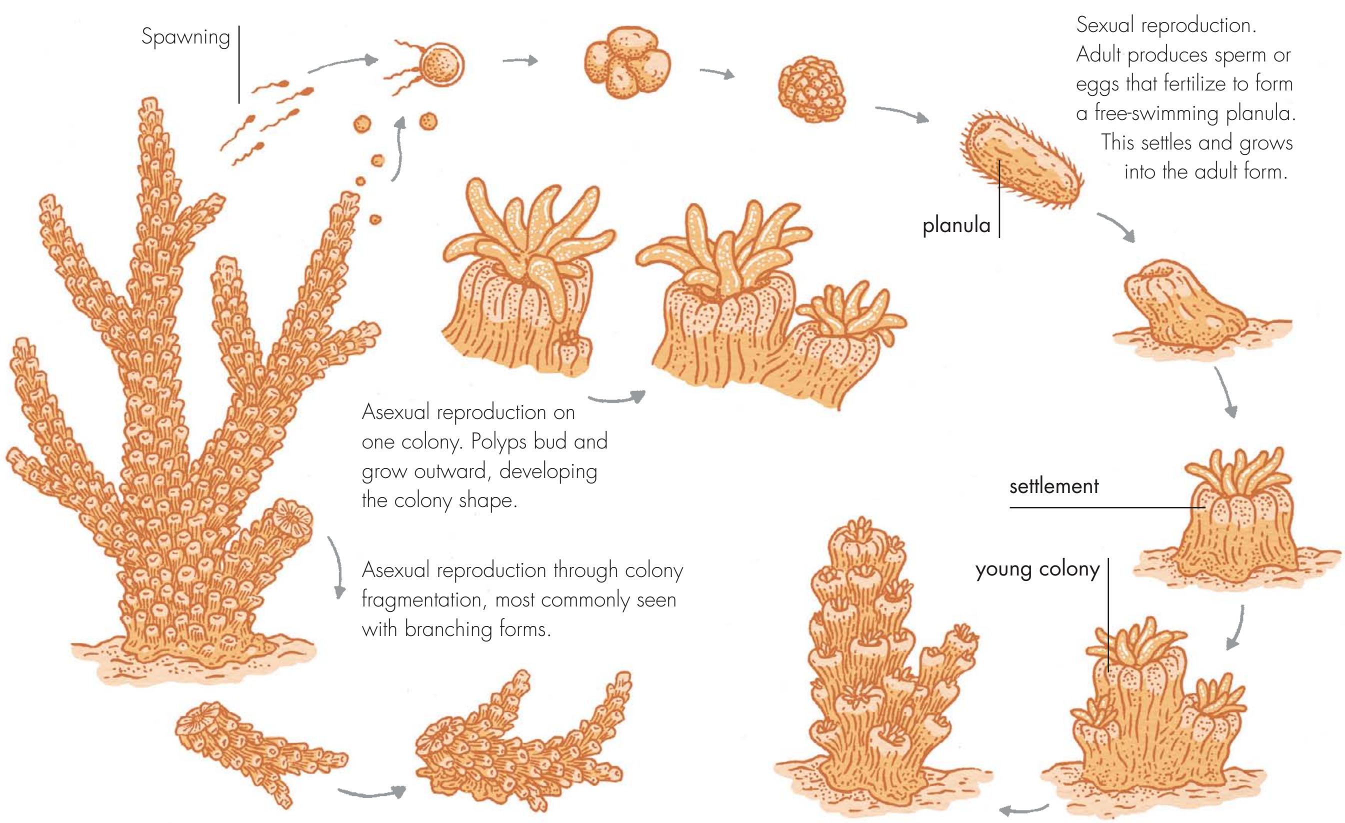
Asexual reproduction by fragmentation is common too, whereby branches break away and re-establish a new tangle of branches, and huge "supercolonies" of a branching coral may develop. Some other unusual methods also exist. One very fleshy coral, *Goniopora*, develops tissue-covered lumps of skeleton on its colony surface which then fall off and roll away, to create an independent colony elsewhere. Another, *Seriatopora*, has small fleshy polyps that can "bail out" of the skeleton when the colony is stressed and settle somewhere else, to develop a new skeleton and colony.



ABOVE | Mass spawning by a colony of *Acropora millepora*. Many different species spawn on the same night, determined by the phase of the moon, so that predators that feed on the sudden, rich food source are swamped.

OPPOSITE BOTTOM | A supercolony of *Acropora*. Hundreds of square meters may result from one single planula because of repeated fragmentation of the delicate branches.

METHODS OF REPRODUCTION IN CORALS



CORAL SHAPES

MASSIVE CORALS

Massive refers to the shape of a coral rather than its size. Basically it means that they are usually hemispherical. Adult colonies of different species of massive corals range from the size of a golf ball or a fist to several meters across and high.

Most spectacular are the giant members of the genus *Porites*. Perhaps unexpectedly, these largest of colonies are built from some of the smallest polyps—a colony 10 ft (3 m) across will be built by polyps only about 1 mm in diameter, so that a single colony will contain many millions of adjacent polyps. Together these will expand their colony's radius by up to ½ in (1 cm) per year. In many areas they dominate a reef, both visually and ecologically, and commonly form a clearly defined zone in shallow water that experiences moderate or calm conditions. This is becoming more common today as some of them are good survivors of the marine heatwaves that cause coral bleaching (see page 186), making them very important reef builders.

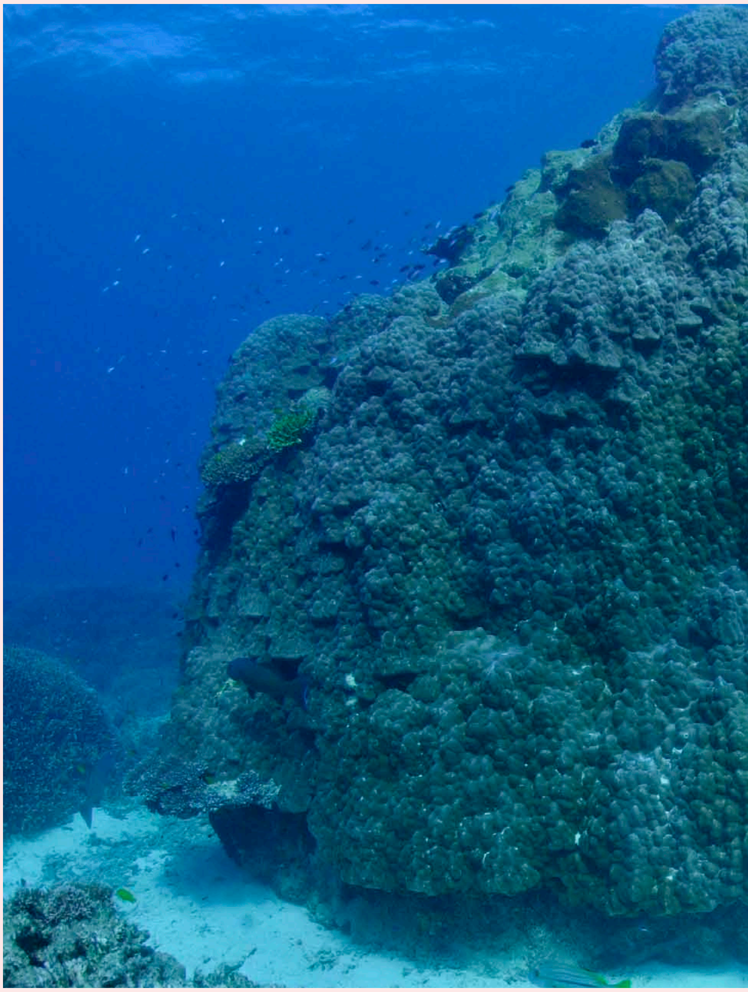
Colonies may be lobed or undulating, depending on the species, but, in general, it is difficult to distinguish species of *Porites* without being able to examine the tiny skeletal features in the corallites of dried and cleaned skeletons, and these characteristics can vary around a colony. For this reason, it has been common in surveys to lump massive *Porites* species together.

Many genera include species with massive shapes. Their surface features may be lumpy or smooth. They may contain spires arising from their upper surfaces or grow leafy plates from around their edges, or even both. Many have surfaces with brain-like patterns (see page 38), though most have individual and circular polyps. In some species of massive corals, the polyps may be fairly fleshy and expanded. One group has bubbles of tissue on its surface, presumably to expand its surface area for photosynthesis.

Usually colony surfaces have some dead areas, commonly embedded with burrowing tube worms including the "Christmas Tree Worm," or by bivalve mollusks, small crabs, or other filter-feeding animals. Many larger colonies have very eroded and indented bases, under which are found large schools of small fish and crustaceans.

Some grow much taller than they are broad, forming pillars, and several, which bud far more than they grow upward, form only very low domes, becoming what is termed "submassive."

BELOW | *Porites* corals form the largest massive coral colonies of all. They grow about ½ in (1 cm) in a year, so large ones are hundreds of years old.



TOP | *Porites* colonies are built from millions of individual polyps, all about 1 mm across and budded from one initial planula, and can reach several meters across and high. Beneath them, erosion commonly hollows the coral to form shelter for numerous fish.

ABOVE | Massive coral *Astreopora myriophthalma* forming pillows on its large colony.

CORAL SHAPES
ENCRUSTING CORALS

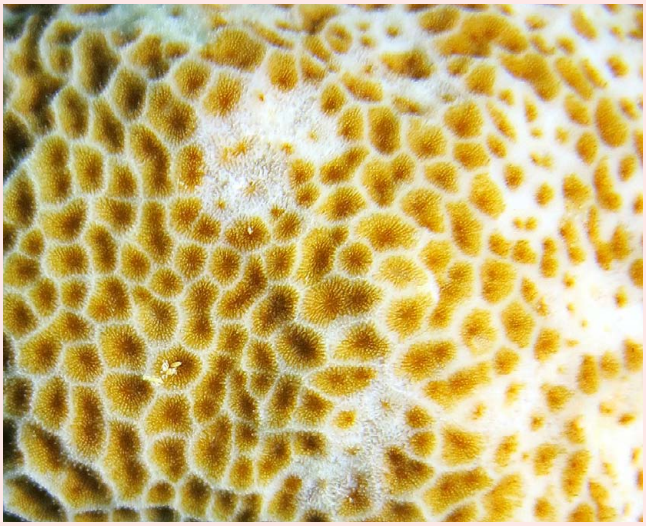
Species that encrust the surface of the reef are found in several coral genera. Many are small and relatively inconspicuous, but some may develop fairly large colonies and even become dominant. Most corals have encrusting portions when very young.

Most encrusting corals do not usually have very attractive colors or dramatic shapes, being drab browns and greens and fairly small, though some have almost luminous parts with reds, blues, greens, and yellows. Their skeletons are mostly hard and dense, meaning that their limestone is solid and without the lattice or porous texture seen in faster-growing species. Because of this they add substantially to the solidity of the reef. Another important role they play is to grow over and bind patches of sediment, allowing it to be turned into the solid rock that forms most of the matrix of a coral reef.

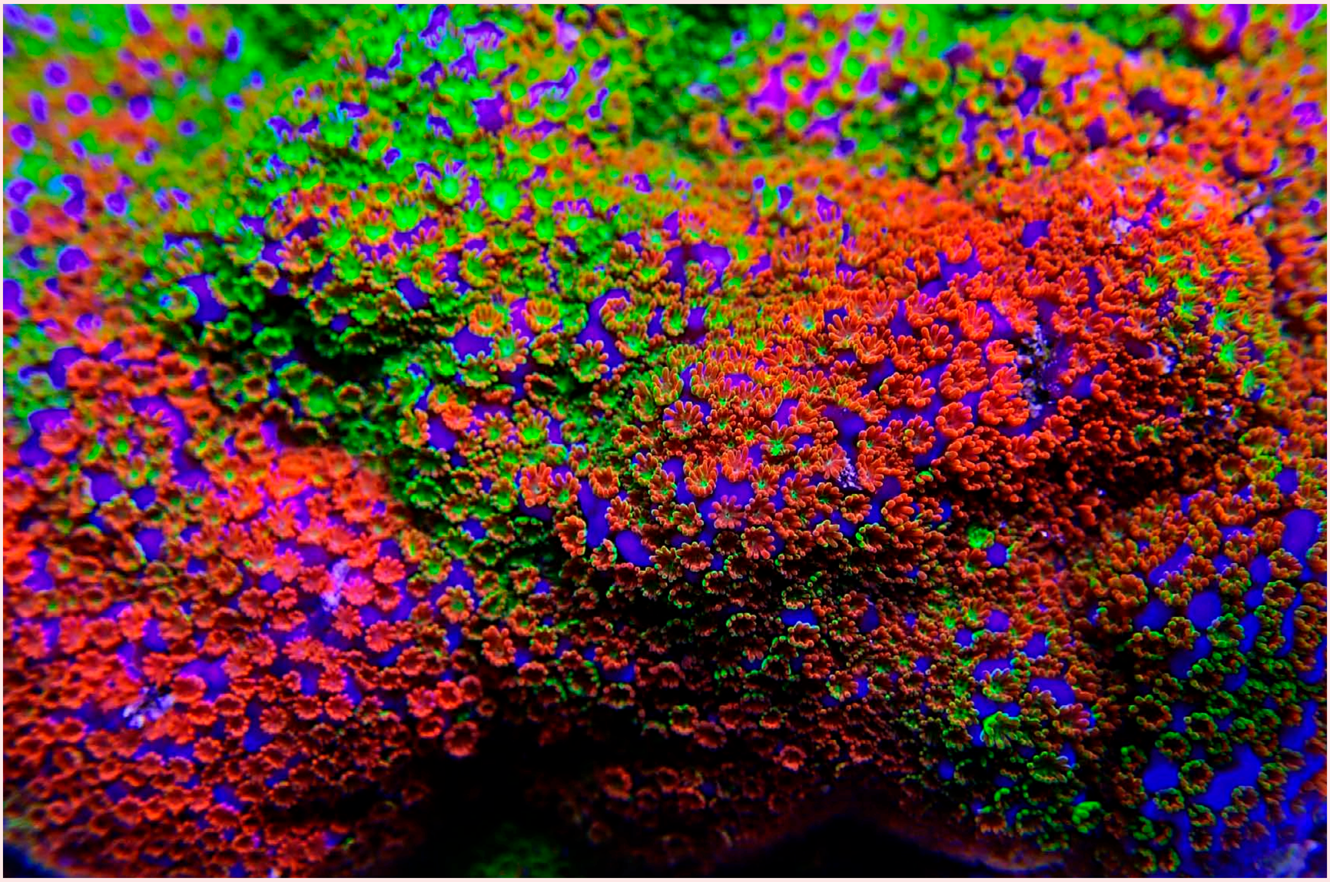
In some parts of the world, the encrusting *Pavona varians* has the greatest number of colonies of all. They are usually small and are an inconspicuous greenish brown, although this species, like many others, has beautiful surface detail with intricate whorls and ridges that are captured only with a camera's macro lens. Others show spines and bumps of almost every conceivable kind in close-up detail, and these features, which are different for each species, are used in identification.

One encrusting genus with many species, *Montipora*, contains species whose polyps are usually only 1 mm across, and are located among exquisite skeletal structures on the colony surface. They are commonly bright colors, often yellow. Other "minor" genera such as *Psammocora* remain a dull gray throughout their lives. Several corals, mostly those with small polyps, such as *Cyphastrea*, are entirely encrusting even when they may cover several square feet of reef; they may have some small vertical lumps but most do not grow far vertically.

Curiously, perhaps, although the encrusting form is the shape that is most resistant to severe wave action, few will be found in the most turbulent water or among crashing waves. Like most other corals, they prefer slightly more sheltered water, but with enough water movement to prevent them from being smothered by sediment, an easy fate for something reef-hugging and encrusting.



RIGHT | Another encrusting species is *Psammocora profundacella*, which usually forms small colonies and has beautiful petal-shaped corallites.



ABOVE | *Montipora* has many species, mostly encrusting. The species are all distinguishable, albeit with a little difficulty, based on features of the cleaned colony. All have tiny polyps.

LEFT | The coral *Cyphastrea* is sometimes boulder-like but commonly grows in low, encrusting forms. It is an abundant and important component of reefs in the Indian and Pacific oceans and has a particularly hard skeleton.

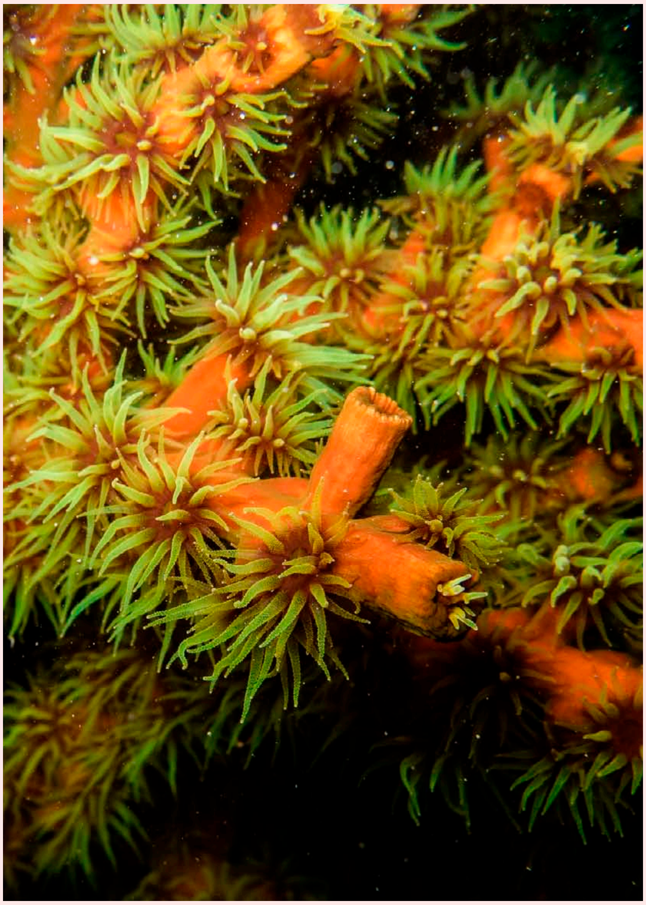
CORAL SHAPES
BRANCHING CORALS

Most branching corals are in the genus *Acropora*, the most diverse genus of corals, containing well over 100 species. Many other genera contain species that are exclusively branching too, while others contain a few branching species. This is a common form of growth.

Acropora colonies range from "staghorn" in shape, becoming nearly 6 ft (2 m) tall, to many smaller bushy forms, and some that form "tables" up to 6 ft (2 m) across that are attached to the substrate by a central pillar (see page 36). One species, the Elkhorn Coral (*Acropora palmata*) in the Caribbean, is the largest of all branching corals, developing very large branching plates in "forests" that, in the past at least, extended vertically by 6 ft (2 m). *Acropora* are the most "architectural" corals in that they have a much more predetermined colony shape than most others. This is largely because each branch has two kinds of polyps: one large apical or axial polyp at its tip, and many more radial polyps along each branch. Axial polyps provide the growth, direction, and length to the branch, while the smaller radials have more limited growth but are the polyps that thicken the branch. As a branch develops, one or more radial polyps may turn into an axial polyp, developing another branch that then grows away from the original at an angle. This branching is highly directional, determined by its genetic instructions.

Many bushy and staghorn forms develop into "supercolonies," whereby hundreds of square meters of reef surface, especially in relatively sheltered water such as lagoons, become covered with the same species in one enormous mass. In these cases it may be impossible to see where one colony ends and another begins. For these species, fragmentation is a major method of reproducing. The lower parts of branches in such cases are commonly dead, covered with encrusting algae, other seaweeds, or sponges.

Branching species of other genera usually form much smaller colonies. *Stylophora* and *Pocillopora* form very solid finger-shaped colonies which, in shallow water, are stubby and strongly resistant to the stronger wave action found there. *Seriatopora*, in contrast, prefers more sheltered locations where it forms tangles of very fine, needle-like branches. Even genera which are mostly massive, such as *Porites*, have one or more branching forms too.



ABOVE | A branching *Acropora*. There are several dozen species in this genus that form dense thickets.

TOP RIGHT | Branching corals provide a three-dimensional habitat and good shelter for fish and invertebrates.

RIGHT | This deeper water *Tubastraea micrantha* does not have symbiotic algae but has large polyps that only catch zooplankton. The branches hold their polyps into currents to better trap plankton for food.

CORAL SHAPES
TABLE CORALS

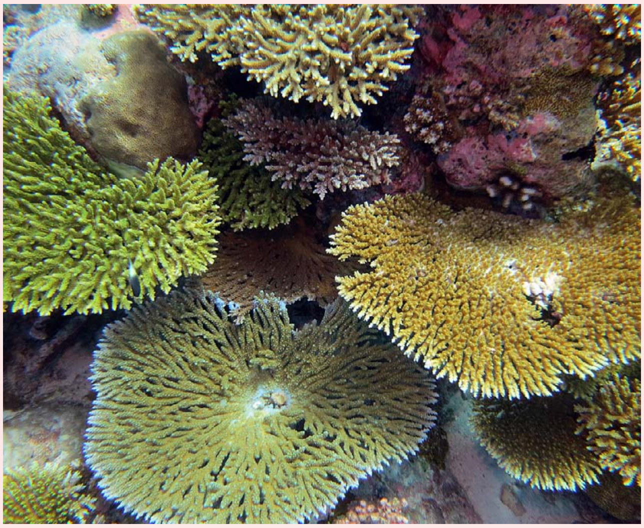
About a dozen species of the coral genus *Acropora* develop table-like structures that can grow to 3–6 ft (1–2 m) in diameter. They are supported by a solid central column and can form perfectly circular tables if their development is unobstructed, or may become irregular or semicircular if crowded. The central columns are solid in all cases, but the table tops vary. With some species the table tops are a loose lattice of fine branchlets, while others may be nearly solid as these branchlets fuse during the course of their growth over several years.

These table corals are particularly "architectural" corals in that they have very predetermined shapes. As with all *Acropora*, they are common in the Indian and Pacific oceans, but the table form is not found in the Caribbean region.

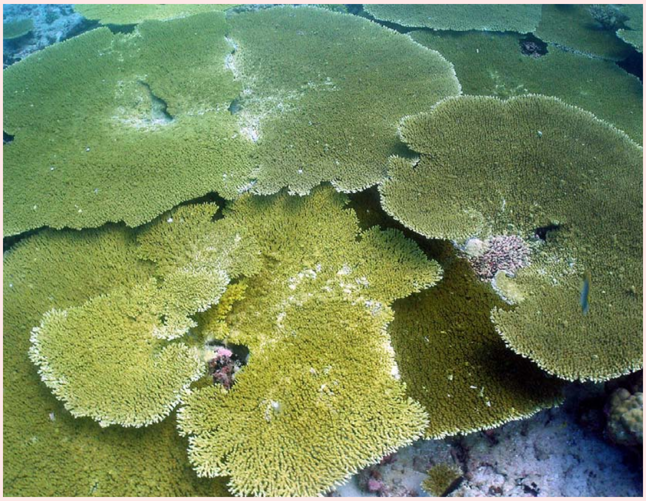
Table-shaped *Acropora* grow quickly. Each branchlet can extend outward by around 4 in (10 cm) each year, thus increasing the colony's diameter by 8 in (20 cm). This rapid extension is helped by the fact that their skeletons are very porous, so the density of the branchlet is comparatively low, making it relatively brittle. So rapid can be the extension of the table's edge that the rim around it is commonly bluish or white rather than yellow-brown or green, indicating that the coral tissue has not yet been colonized by symbiotic algal cells; the algae have not yet caught up with the fast-growing tips to add their characteristic green-brown color. This rapid horizontal growth enables the coral to overgrow and shade its coral competitors.

The tables also help build a three-dimensional structure on the reefs, which is very important in maintaining the high biodiversity. Many fish, large and small, shelter beneath the tables, and the shaded floor is also carpeted with numerous smaller species of corals. The effect of the tables can be likened to that of a tree canopy in a forest, and although this canopy may be only 20 in (50 cm) above the seabed, it results in an extra dimension and a range of habitats.

Some table corals can grow like "weeds" given the chance, rapidly colonizing clearings on the reef after a large disturbance. Within just a few years of widespread mortalities a reef may become dominated by one species in particular, *Acropora cytherea*, over its favored depth range of about 30–50 ft (10–15 m). Where it grows it can provide a very high cover of the substrate.



RIGHT | Many smaller *Acropora* species exist. Each table is 2—3 ft (about 60—90 cm) across.



LEFT | Table corals can grow their branchlets rapidly and expand their diameters by over 8 in (20 cm) each year. This species of table *Acropora* is like a weed, growing in bare patches very quickly so that it rapidly occupies a lot of the reef after a disturbance has killed off other corals.

BELOW | The rapidly growing tips of the branchlets at the rims of the tables are commonly pale because the darker pigmentation given by the symbiotic algae has not yet reached them.

CORAL SHAPES
BRAIN CORALS

Brain coral refers to a surface pattern of long, meandering valleys found when polyps develop long chains. It is the name given to massive-shaped corals only, although a similar meandering pattern on the surface can be found on several leafy and columnar shapes as well.

Resembling the pattern of a human brain, each long, winding valley, a form called meandroid in corals, is the result of intra-tentacular budding where newly budded polyps do not separate to any degree. The resulting polyps do not pinch off to form their own circles of tentacles, so all those in a chain lie within the same very elongated ring of tentacles, in the same valley on the coral surface. In this type of cloning, individual polyps each have their own mouth, separated by a few millimeters along the valley floor. Each separate polyp has its own body cavity—it is only the tentacles that are shared.

Meandroid polyp chains may be anything from three or four polyps long to over 100, and the longer ones meander

BELOW LEFT | A Caribbean brain coral, *Diploria labyrinthiformis*, with wide, valley-like areas between each chain of polyps. The narrower valleys contain the polyps, as can be seen by the tentacle tips, and the unique double chain pattern is caused because adjoining chains are separated by a deep groove.

BELOW RIGHT | A large Caribbean brain coral, *Colpophyllia natans*.

across the surface of the colony forming mesmeric patterns. The length, breadth, and ornamentation of the polyp chains are used to distinguish between different species. The longest chains are found in the leafy corals of the genus *Pachyseris*.

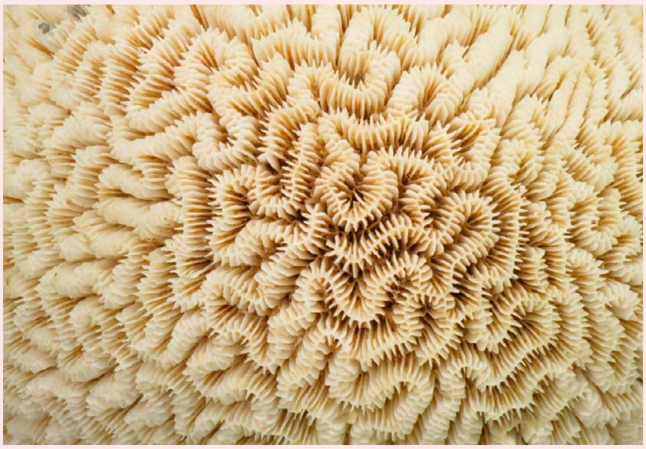
The argument has been well aired about whether each chain is one polyp with several bodies, or whether each chain contains multiple polyps within one shared encircling set of tentacles. No clear conclusion is possible—they are both! The individual nature of the polyps lying within one chain, however, is reflected in the skeletal structures seen in valleys of a cleaned skeleton. On the valley floor the location of each polyp body is clearly marked by a "center," perhaps a small clump of limestone knobs or spines (spicules), and by the way the vertical plates, called septa, converge toward them. Occasionally individual centers are not defined and there may be a simple ribbon-like plate running along the entire valley instead.

In meandroid corals, adjacent polyp chains may have a common or separated walls. In taxonomic terms, meandroid polyps on stalks with separate walls are termed "phaceloid," rather than "brain" or "meandroid." This character is also used to identify and separate different species.

LEFT | A brain coral in the Indian Ocean.

BELOW LEFT | The brain coral *Ctenella chagius* has regular valleys with smooth-edged septa. This is a cleaned skeleton.

BELOW RIGHT | The leafy coral *Pachyseris* has the longest chains of all.



CORAL SHAPES
FREE-LIVING MUSHROOM CORALS

Most species of this unusual family of corals—the Fungiidae—are unattached to the seabed for most of their adult lives. Some are huge, single polyps, though others are colonial. They form round or oval disks of 16 in (40 cm) in diameter to skateboard shapes. Forms with many small polyps can develop large domes 20 in (50 cm) across and tall.

Most species are a single large corallite, best imagined as being a cup that has been flattened. From a central, oval mouth, they have vertical skeletal plates (their septa) that radiate out toward the edges; their top surfaces correspond to the upper, inner surface of the corallites of most other corals. Their underside corresponds to the outside of the more usual form of cup, and these too have ridges (the costae) which may bear spines or beads.

There are several genera and more than 30 species that consist of these circular or oval disks with a single polyp. During the day the polyps show some small tapering tentacles scattered over the upper surface. Other genera of mushroom corals are colonial, and may be oval or domed. Their multiple polyps may live in a central furrow or they may be scattered over the whole surface.

Although adults are free-living, they start life attached to the reef by a stalk. Even in older adults, the scar of the attachment point may be still visible underneath. Some mushroom corals may have a distorted disk because they previously fragmented into two parts. Some of the small species of the genus *Diaseris* use fragmentation as a means of reproduction. The largest single polyped forms are the largest polyps seen in corals.

Mushroom corals can move to a limited extent by inflating their tissue on one side, and can even climb a gentle incline. Some can also right themselves if turned upside down by a large foraging fish. Being free-living, they are one of the few kinds of corals that can live on sandy or rubble areas of the reef as well as on solid reef substrate.

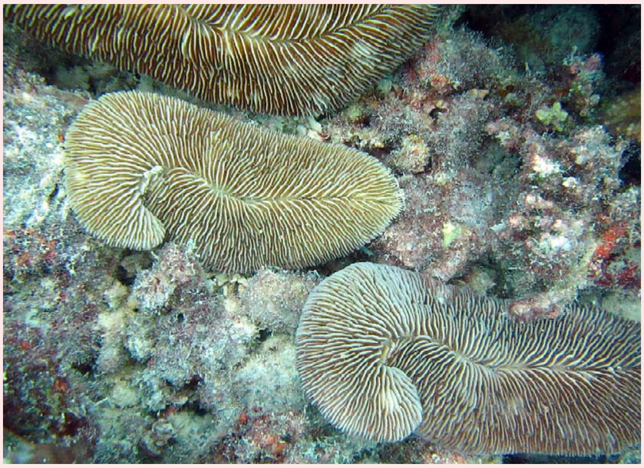
Each is usually either male or female, and some are known to have changed sex over the course of their life. One studied coral even changed sex back again later.

ABOVE | A Fungiid coral showing a typical disk that is one single, free-living corallite and polyp. It has one mouth in the middle furrow.

ABOVE | A jumble of a large Fungiid species. The disks contain a single polyp, whose mouth is in the center. This species (*Fungia fungites*) also has numerous tentacles across the top surface of the disk.

ABOVE | *Polyphyllia* has numerous tentacles emerged during the day, making it very distinctive. In this genus there is no central furrow, but there are many mouths scattered across the entire surface.

ABOVE | *Halomitra* has numerous small polyps over a large dome.



ABOVE | The elongated corals of *Herpolitha*. The central furrow has a chain of mouths. Usually straight or perfectly elongate oval, these two (perhaps siblings) have the same curious distortion and twist at one end.

ABOVE | The disk of a *Cycloseris*, a genus with smooth edges on the radiating septa.

CORAL SHAPES
LEAFY CORALS IN DEEPER REEFS

The deeper and darker parts of most reefs are commonly dominated by corals that spread out semicircular or leafy-shaped whorls and plates. In many species, the plates form overlapping tiers like tiles or shingles on the roof of a house, though some also slope upward in the form of vases. Light is dim in these parts, and the only light that can make it down here is blue because the water has filtered out all other colors, particularly the reds. The corals all look gray-brown until you turn on a flashlight or video light, which "paints" all the colors back wherever the beam alights.

Less light at depth means less energy is available to a coral to build its skeleton. A thin plate needs relatively little limestone, and the thin whorls extend out into the water to intercept whatever light is available. The plates are relatively fragile, so are not found in turbulent shallow water.

The whorls are rarely horizontal. Their angle varies according to the location of the coral and the slope of the substrate. Although a horizontal plate would be best at intercepting light, it is unfortunately also the best for trapping sediment that continually rains down from above, which would smother and kill it. Therefore, the "leaves" are generally slanted at an angle that is optimal for both factors: flat enough to trap sufficient light, but sloped enough to help it shed the falling sediment. Corals do have an ability to actively remove sediment by sloughing it off using beating hairs (cilia), but it is energy intensive. For light-trapping and sediment-shedding, a trade-off is reached.

Leafy corals are often dark brown because they are rich in chlorophyll to trap the limited light (shallow corals can have an excess of light and often have brightly colored pigments to help filter its wavelengths). While over half or more of their energy might come from photosynthesis, they still need some zooplankton prey for a balanced diet, which they catch with their polyp tentacles. Their polyps, however, are usually small and in some species are scattered fairly sparsely over the surface.

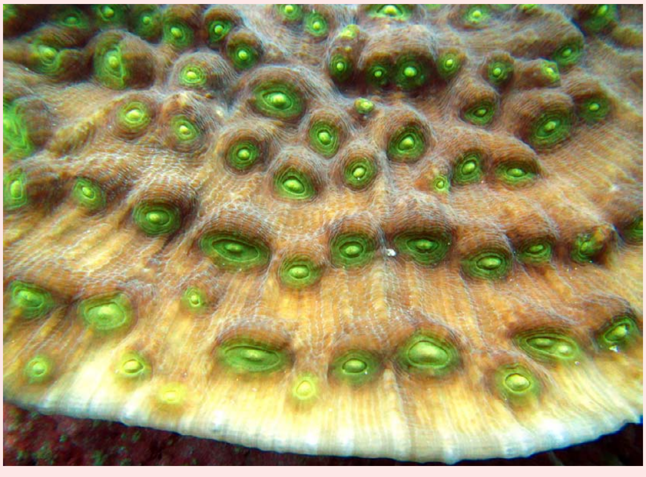
As with corals of other shapes, the polyps may be individual or in meandroid chains. In some genera the photosynthesizing surface between polyps may be adorned with multicolored spines and beads.

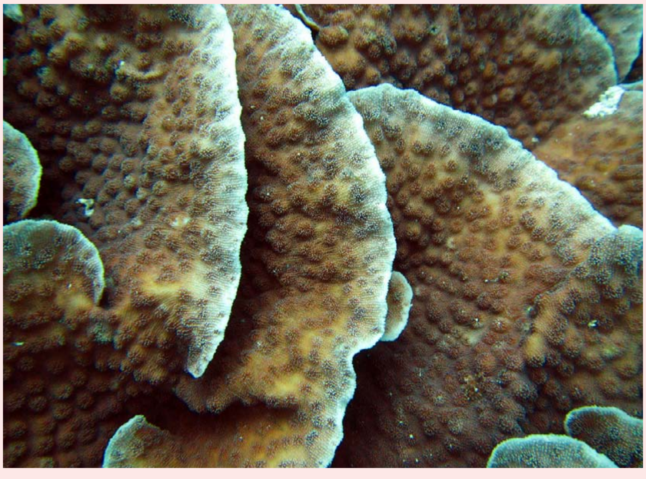
LEFT | Leafy corals like this deep water *Leptoseris* commonly hug the reef surface closely.

OPPOSITE TOP | Some leafy corals form "vases," like this *Turbinaria* species.

OPPOSITE BOTTOM LEFT | This species of *Mycedium* is leafy, with much larger corallites than many. Each is widely spaced, in rows, and inclined toward the edge of the leaf.

OPPOSITE BOTTOM RIGHT | A group of "leaves" of the coral *Echinopora*, with moderately large polyps. In this case they are uniformly inclined upward to achieve their ideal slope because they are attached to a horizontal surface rather than a steep slope.





LEFT | Polyps of a coral expanded at night. Tentacles of the polyp center-left have captured a small prey animal, which is being dragged to the mouth in the center of the polyp.

ABOVE | An extreme close-up of tentacles of a coral polyp. Some of the markings on the tentacles show the batteries of stinging nematocysts.

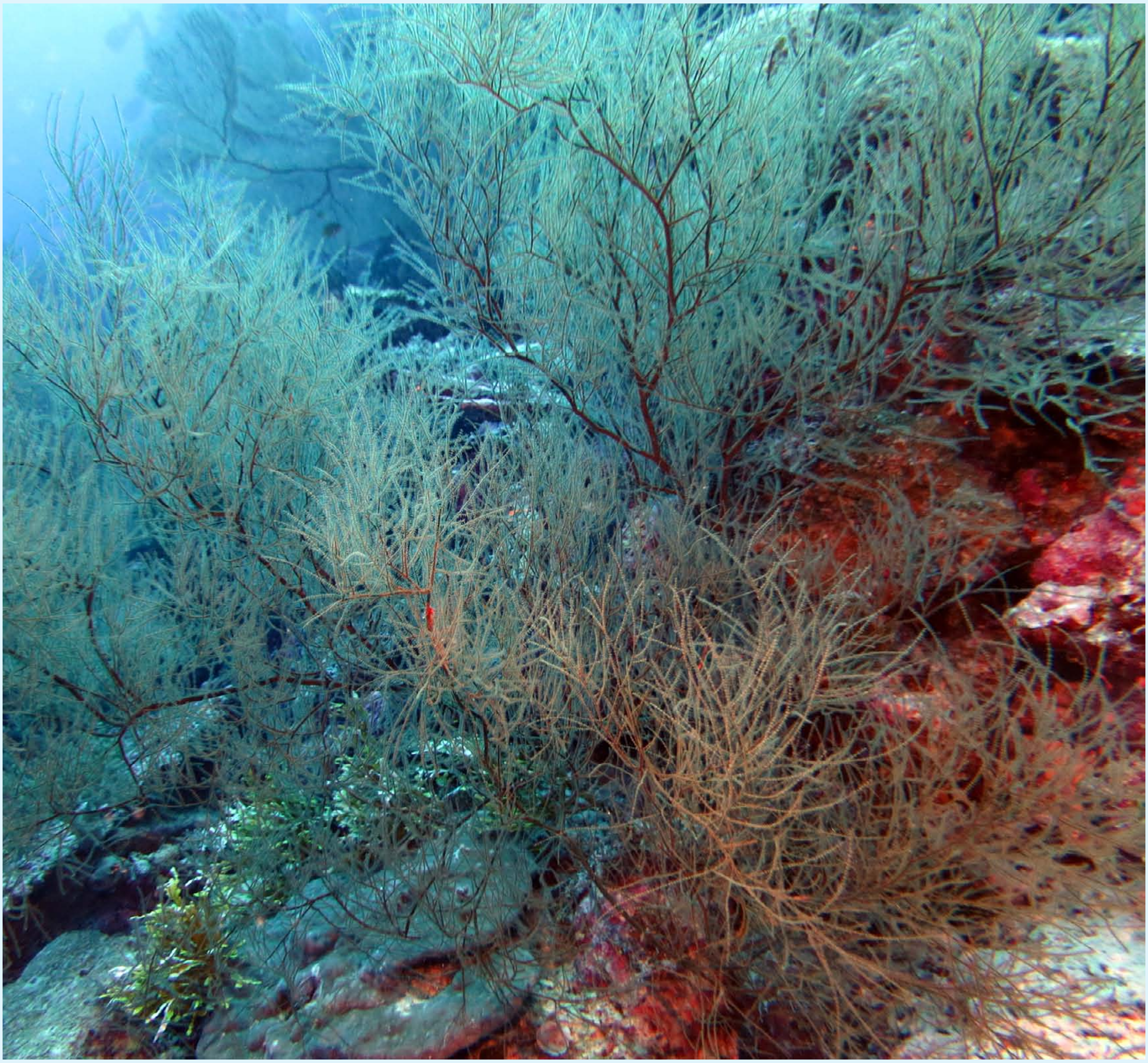
OTHER REEF CNIDARIANS
BLACK CORALS

Black corals are antipatharians (in the order Antipatharia), not stony corals (order Scleratinia). Their colonies can be tree-like, coiled whips, or bushy ferns. They usually grow on deeper reef slopes and walls, and down to great depths. There are about 300 different species, mostly in tropical and subtropical oceans. These are colonial animals, and their black skeletons can take a lustrous polish, making them valuable for jewelry. When living, their branches are covered with white or brightly colored polyps, each bearing six simple tentacles. Like in all Cnidaria, the tentacles have batteries of stinging cells to catch tiny zooplankton prey. The tentacles cannot retract, and this gives the branches a fuzzy appearance.

Some species, termed wire or whip corals, are not tree-like but have single, often coiled, and very flexible stems. All antipatharians grow extremely slowly, and large specimens (with thicker stems that are the most sought-after for jewelry) may be over 1,000 years old; the present record holder was dated to be about 4,250 years old. The skeletons are made of protein and chitin rather than limestone, which is why they can be polished.

As well as black corals, some more distantly related groups can also be polished and used for jewelry, unlike the true, reef-building corals. So-called pink coral, bamboo coral, and gold coral join with black coral to supply the jewelry trade. Harvesting black coral has caused problems for populations because of their slow growth. Replenishment of a depleted "forest" cannot occur in mere human lifetimes, so collectors hunt for it from ever-increasing areas and depths. When new populations are discovered, the trade can follow a boom and bust cycle. In Mexico's Caribbean, substantial collecting in the last century caused black coral's present scarcity, and even where its collection has long been prohibited it has shown no notable recovery. In Hawaii, black coral is the official state gem. The trade is now better regulated, but even so, the slow growth of these colonial animals means that recovery of decimated populations is very slow. In past centuries, they were considered to hold both mystical and medicinal properties, so they have been much sought-after for a very long time.

Black corals can provide important habitats where many are found in a crowded forest, offering a three-dimensional habitat, shelter, and cover. Several species appear to be particularly associated with certain fish and other invertebrates.



LEFT | A necklace made from precious black coral. It is slow growing and the coral stems need to be many years old to prduce this kind of thickness. They take a polish, which is why they have value in the jewelry trade.

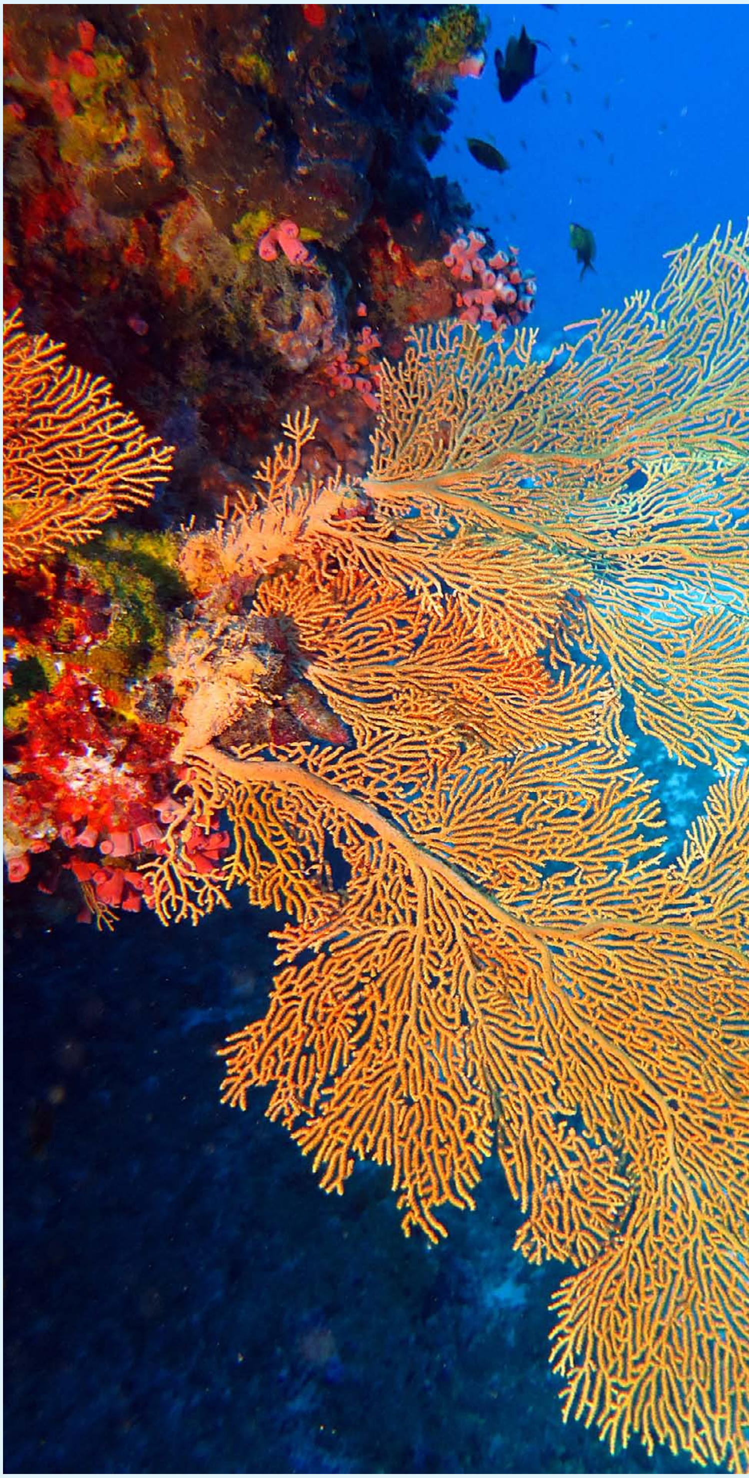
ABOVE | Black coral from relatively shallow water has a bushy appearance, commonly with white or yellow "fuzz" over the branches, caused by protruding polyps. The stem of the collected specimen is black, but in life they have a covering of brighter-colored living tissue. They might be mistaken for sea fans and, indeed, share a similar ecological function.

OTHER REEF CNIDARIANS
SOFT CORALS AND SEA FANS

All this varied group are "octocorals" (meaning their polyps have eight feathery tentacles). The commonest reef dwellers are the soft corals, sea fans (gorgonians), and sea whips. They all lay down an exoskeleton, but this is a matrix of gelatinous material, either rubbery to the touch, or thin and stiffened. Within the matrix are countless tiny spicules of limestone which, in some species, fuse into more solid lumps. They have very varied forms, from fleshy lobed masses to fans over 6 ft (2 m) tall.

There is a marked difference in the appearance of soft corals between the Caribbean region and the Indo-Pacific. In the Indo-Pacific, the shallow soft corals are mostly fleshy, lobed, or encrusting colonies. Deeper down, sea fans become common and often grow in spectacular forests on steep slopes. Sea fans are commonly oriented across the prevailing current so their polyps can better trap plankton. In the Caribbean there are many octocorals too, but mostly they are branching and fleshier forms (see photo on page 72, left).

Polyps of all of this group have exactly eight tentacles (not six or multiples of six as in stony corals). Each tentacle is feathery, fringed with numerous pinnules. Mostly, polyps are



of a single kind, though some, mainly in the Indo-Pacific, have a second tiny kind of polyp without tentacles, which is thought to be involved in helping to move water through the colony.

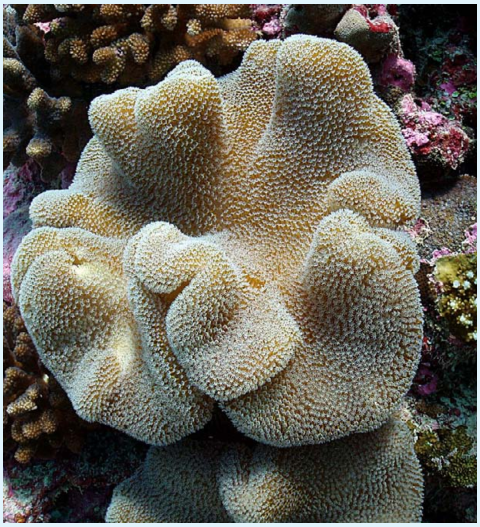
Collectively, soft corals can occupy as much space on well-lit parts of the reef as stony corals, and sometimes more. Individual colonies of some species can cover several square meters. Although they add to reef diversity, only one genus has species that contribute significantly to building the reef itself. Most of those found in the well-lit regions of the reef contain symbiotic algae in the same way stony corals do. Their tentacles also capture plankton, though usually smaller-sized microplankton than stony corals, including phytoplankton (plant plankton) and bacteria too. Most reproduce in ways similar to stony corals, but with some variations. "External brooders" retain fertilized eggs in a mucus pouch outside the parent for the initial growth stages. Another variation in some is to extend a runner, or "stolon," which attaches to the rock 4–8 in (10–20 cm) away from the parent. This develops into a new colony, which then breaks off the connecting stolon.

OPPOSITE FAR LEFT | Some soft corals, especially in the family Nephtheidae, are extremely colorful, and do not contain symbiotic algal cells.

LEFT | Sea fan on a vertical cliff. Fans extend out into the current to trap zooplankton.

BELOW LEFT | Fleshy soft coral typical of the Indo-Pacific.

BELOW RIGHT | A sea fan *Menella*, showing expanded polyps that give a furry appearance to the branches.



OTHER REEF CNIDARIANS
FIRE CORALS AND OTHER STINGERS

Fire corals, named for their painful stings, are not true corals but are yellowish stony hydrozoans—a group more closely related to jellyfish than to true corals. They do, however, develop colonies that build stony skeletons on coral reefs in a similar manner to the true corals. Different species may be encrusting or mixtures of plates or branches.

If touched, they can leave a rash on the skin that persists for several days, and in some people dangerous allergic reactions can also arise. They sting not necessarily because the toxin that the nematocysts (stinging cells) inject is more potent, but because they are powerful enough to penetrate human skin to a degree not managed by the true corals. Like true reef corals, their surface contains high densities of symbiotic algae that photosynthesize and supply energy to the colony.

Their polyps are microscopic, live in pores, and are connected to each other by a network of canals beneath the surface. The polyps are in two main sizes. The smaller ones, zooids, contain polyps with stinging structures that capture passing prey, and on most species these hair-like projections give the appearance of a fine "fur." The larger polyps are those that digest the prey that is passed to them by the surrounding stinging forms.

Fire corals reproduce using a two-stage process. There is a third type of polyp that produces tiny, free-living, jellyfish-like medusae that are short-lived. These medusae contain the cells that produce eggs and sperm, which fertilize in the water to form planulae that drift away from the parent before settling and developing into another adult colony.

Other stinging relatives are the hydroids, a diverse group whose adults appear as clumps of feather-like structures or isolated polyp clusters on a common stalk. Their colonies differ from those of true corals in that some polyps have specialized functions rather than all being identical clones. The polyps are connected by tubes in the central stalk. Most polyps are specialized for feeding, using stinging cells to capture passing zooplankton, and the digested result is partly passed to the central colony via these connecting tubes. Other polyps are specialized for reproduction, and one colony is usually either entirely male or female. The stings from contact with these feather-like structures can be painful, and the rash produced can also last for several days.

BELOW LEFT | Fire coral (*Millepora*) from the Indian Ocean.
BELOW CENTER | A feathery hydroid from the Indian Ocean.
BELOW RIGHT | Hydroid from the Indo-Pacific.

OTHER REEF CNIDARIANS
COLORED REEF BUILDERS

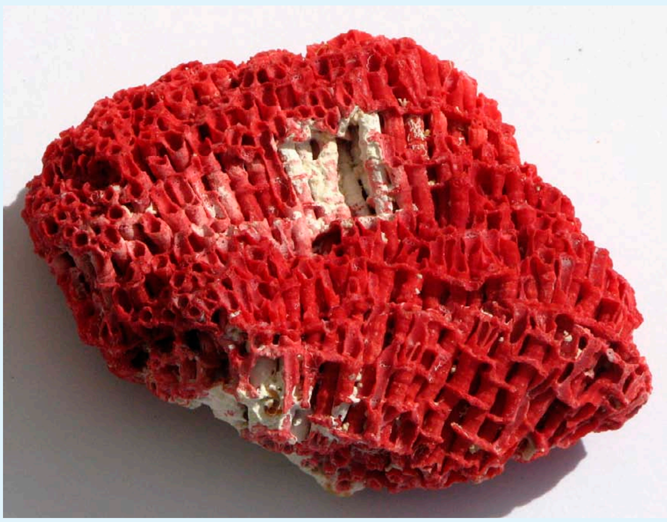
Most skeleton builders are either the true corals or fire corals, but a few other colonial animals of the Cnidaria also deposit limestone. While all the true corals have skeletons that are pure white, several of these more distant relatives have strongly colored skeletons. Two colored species in particular can become important contributors to building the reef.

Blue Coral (*Heliopora coerulea*) is an octocoral, a form of soft coral. It has a bright blue skeleton because of iron salts that are deposited in it while it is growing. In some places this species can dominate the shallow reef and reef flats. When it is alive, however, the skeleton looks brown because it is covered by the living tissue and small tentacles. It is the only octocoral that lays down a truly solid skeleton. Its range includes most of the Indian Ocean and West Pacific.

Organ Pipe Coral (*Tubipora musica*) is even more closely related taxonomically to the soft corals. It has a bright red skeleton formed by a collection of vertical pipes a couple of millimeters in diameter, connected by thin horizontal plates. Each pipe houses a polyp at its upper end. Its dried, bright red skeletons are conspicuous on a white sandy beach, but underwater they are covered by extended gray polyps with eight feathery tentacles, about ¼–⅓ in (0.5–1 cm) in diameter. The skeleton is formed by a remarkable pattern of fusion of the calcareous spicules (minute and very angular or lumpy pieces of limestone). This is an Indo-Pacific species only.

Some soft corals concentrate limestone spicules toward their base so densely that they leave behind some solid material when they die. Apart from the Organ Pipe Coral, some species of *Sinularia* in the Pacific have very dense spicules, to the extent that they leave behind appreciable amounts of fused and solid skeleton, spiculite, on the reef.

A few other species with small, delicate colonies are notable. Related to the fire corals are the finely branching hydroid *Stylaster*, and the sometimes slightly larger and sturdier *Distichopora*. Globally there are several species of each, mostly purple, red, or orange, found in darker parts of the reef such as under overhangs or in caves, where they do not have to compete for space with the faster-growing corals or soft corals.

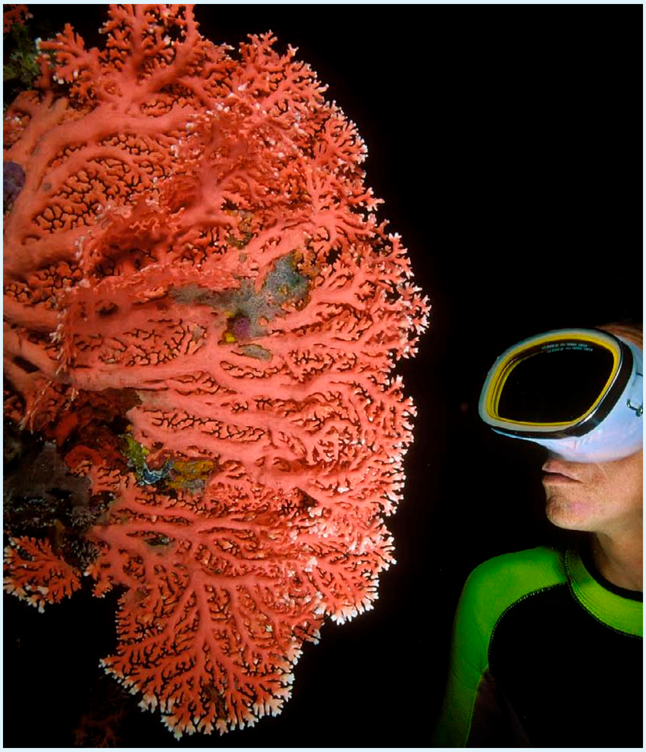


LEFT | The red skeleton of *Tubipora musica*.

OPPOSITE TOP LEFT | A large colony of a red hydrozoan, *Distichopora violacea* is not a true coral but is fairly solid. It has a reddish skeleton.

OPPOSITE TOP RIGHT | A live Organ Pipe Coral (*Tubipora musica*). These are covered with gray to pink flowery tentacles, each polyp being in one tube. Cleaned, they are bright red (as seen left).

OPPOSITE RIGHT | Blue Coral (*Heliopora coerulea*) forms colonies of collections of vertical plates that are brown-gray in life, though bright blue on snapped tips and when cleaned.



CORAL FLUORESCENCE

The dominant color of corals is generally shades of greens and browns, generated by the chlorophyll in their symbiotic algae. However, if far blue or ultraviolet light is shone on them, they will appear in a stunning range of colors. This is because they contain proteins that can absorb the light and re-emit it as different colors; that is, they fluoresce—in this case, absorbing ultraviolet and re-emitting it as red, cyan, green, blue, and yellow.

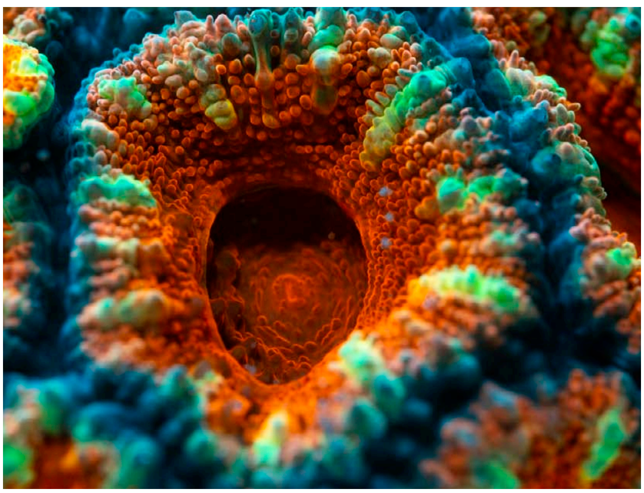
Water absorbs light differentially, meaning that different wavelengths of sunlight disappear from the spectrum at different depths. Infrared (which we don't see) is absorbed immediately. Red is absorbed rapidly, so that by about 16 ft (5 m) depth there is nearly none left in the light we see. Greens are absorbed next, leaving blues and the invisible ultraviolet. This is why scenes filmed underwater are nearly all blue, except where strong lights are used. A beam of light adds back all the colors wherever it touches.

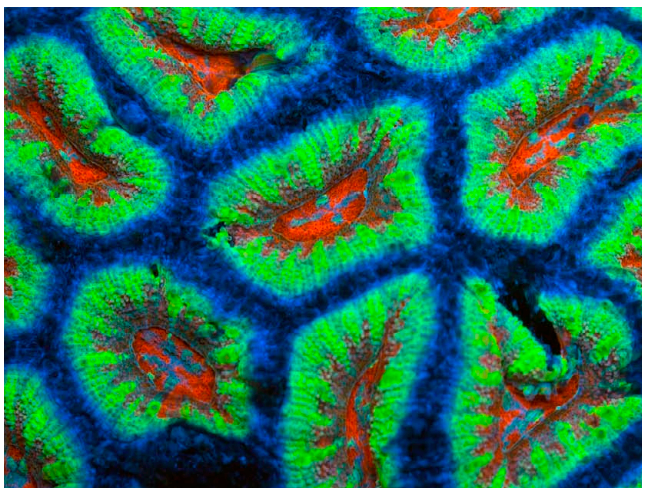
The ultraviolet wavelength that is left stimulates several chemicals in a coral so that they fluoresce in other colors. In shallow water these are swamped in bright sunlight and remain invisible, but deeper, where it is dimmer, they are commonly noticed—and they are certainly noticed in an aquarium under UV lighting.

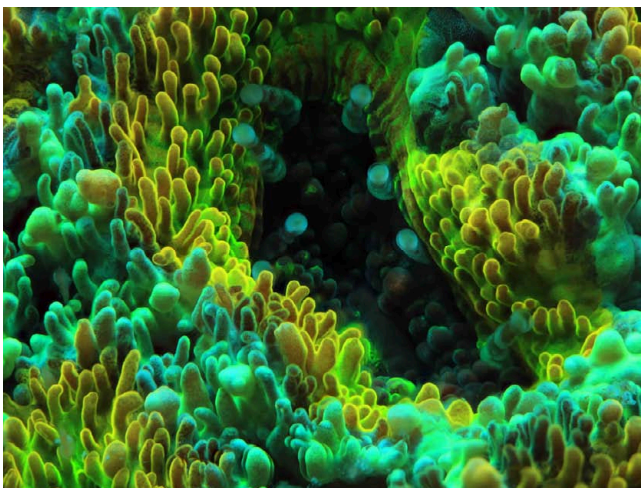
The reasons for these chemicals in corals are not just to make a beautiful display, but are still partly speculative. Some chemicals act as a sunscreen, absorbing the damaging ultraviolet light in shallow water and protecting the coral tissue and its essential symbiotic algae. However, the effect happens in deeper water too, where there is little ultraviolet left. It is thought that the chemicals are there to convert the ultraviolet into other wavelengths that trigger the process of photosynthesis better than ultraviolet alone would do—the chemicals are enhancing the efficiency of photosynthesis where the light is too dim on its own.

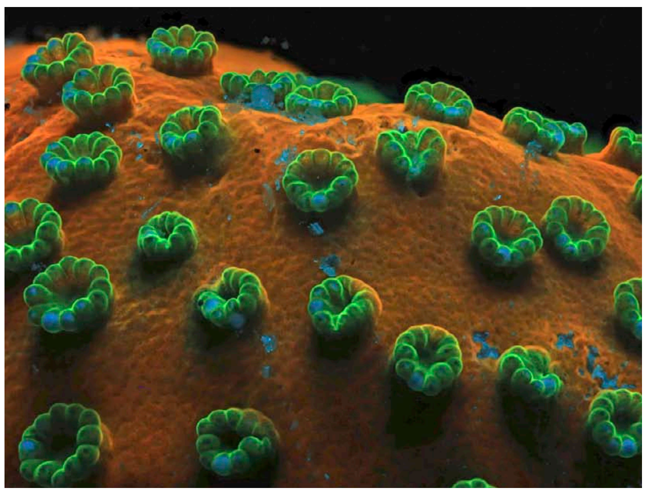
It could also be that some of the pigments are there for completely different reasons, and their emission of colored light is merely a coincidental, but attractive, side effect of whatever it is that they are doing.

BELOW AND RIGHT (ALL) | Coral polyps fluorescing under far-blue and ultraviolet light. They absorb this light and re-emit it in a range of colors that are visible to humans. Different parts of the polyp and the connecting tissue contain different fluorescing proteins, so show up as different colors.







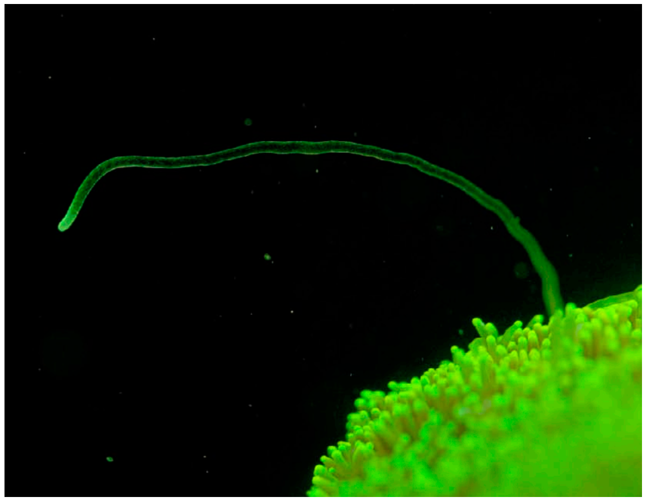


CORAL COMPETITION

Corals on a reef may look static, but in reality their positions are fairly dynamic. As the edge of each colony grows, it comes into contact with others, and when it does the two corals will compete for space. There is an ebb and flow of species on any one spot all the time—it is just that it is done in slow motion in our terms. In one year the reef substrate may be 50 percent covered with corals, and it may be similarly covered a few years later, but that 50 percent may be largely different. Previously bare patches will now be occupied, some corals will be dead and gone, and some corals will be partly killed on one side where more aggressive neighbors are encroaching on them.

Corals use different methods for this. Most rapid is when one coral ejects digestive filaments from the side of its body, throwing a net over the encroaching neighbor, which it digests. This can happen overnight, and is likely used mostly when a coral is dislodged and pushed close to another. The range is only a very few centimeters, but it is fast.

A second common method takes a couple of weeks and is mostly used when edges of corals grow slowly toward each other. Here, "sweeper" tentacles develop in polyps nearest the other coral; these tentacles are several times longer than normal ones and are packed with stinging cells. Although this is a slower method, the range is much greater, and sweepers can reach a competitor 4 in (10 cm) away, coming from polyps only ¼ in (0.5 cm) across. In the genus *Goniopora*, which has long polyps already, the whole polyp grows rather than just the tentacles, but the effect is the same.



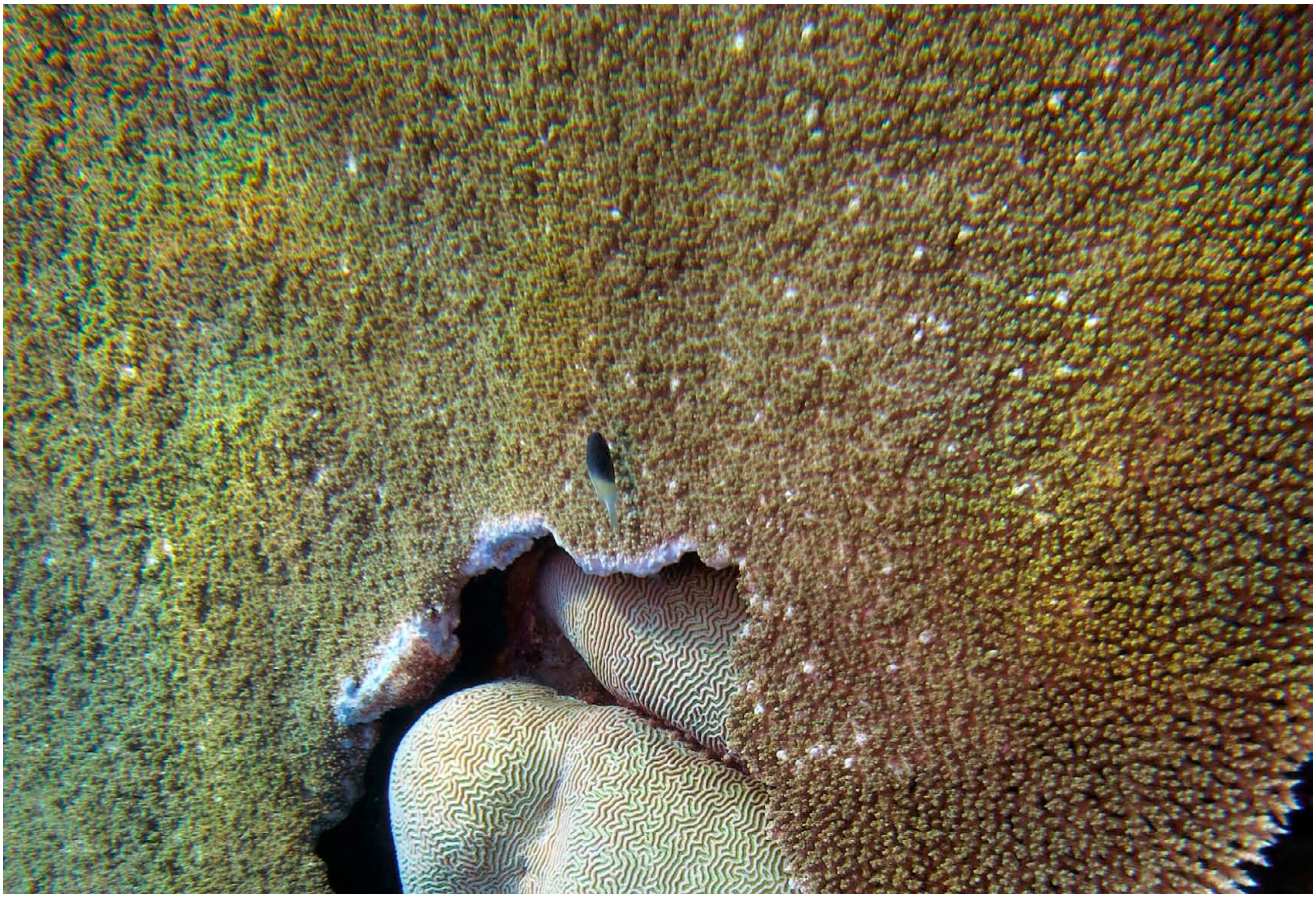
These battles take place at night so are rarely seen on the reef. There is a consistency between species, where species A always kills B, and B always kills C, but C might always kill A, so a circular hierarchy exists. Aquarists know to keep certain corals well separated. When two colonies of the same species touch, they may meet at a line of white, distorted tissue, which is an immunological response, or may simply fuse together.

Other mechanisms are also used, for example, secretion of toxins, which is more common in soft corals. All corals must have some competitive advantages or they would not still exist.

ABOVE | A sweeper tentacle some 20 times longer than the normal tentacles of this coral.

TOP RIGHT | A slow-growing brain coral (*Leptoria*) is holding its own and preventing a faster-growing *Acropora* table from overgrowing it. It will be using long sweeper tentacles that emerge at night to kill the encroaching edge of the table.

RIGHT | Mesenterial filaments from polyps at the end of an *Acropora* tip, being ejected to cover and kill another encroaching coral.



HOW CORALS DEPOSIT LIMESTONE

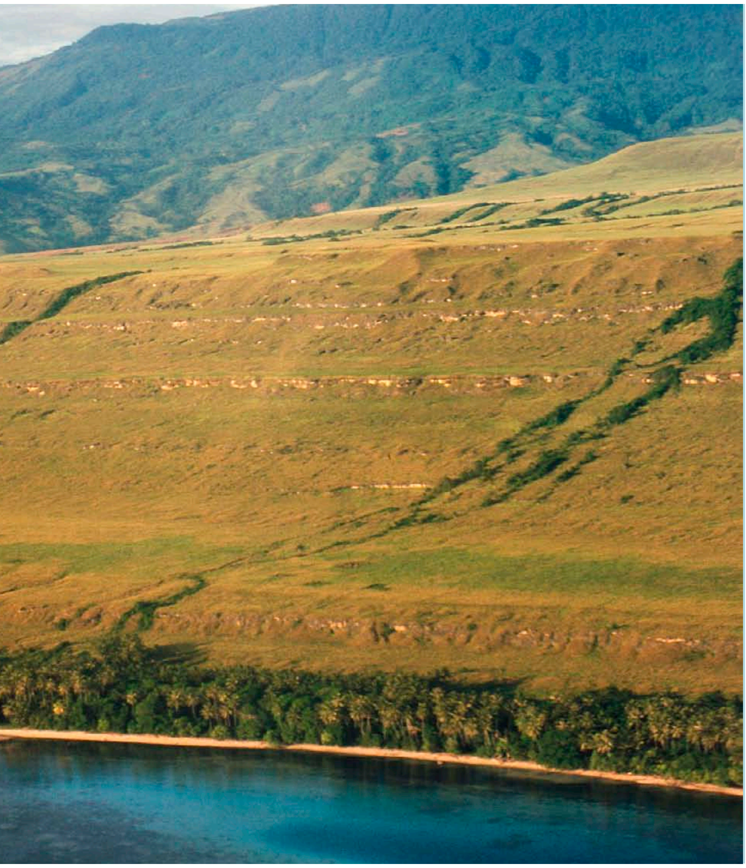
The process by which corals make their limestone skeletons is complex. Limestone (calcium carbonate) comes in several different forms, two of the most common crystal forms deposited by marine life being aragonite and calcite. The reef-building corals deposit aragonite. Calcite is a harder and more stable form, and mollusk shells, for example, partly make this variety. Most soft corals produce tiny needles and irregular structures of calcite limestone embedded in the gelatinous matrix. The different forms are simply different crystal arrangements of the mineral.

The production of aragonite by a coral is the key starting point for making its skeleton, and eventually the whole reef. However, a coral does not excrete this mineral directly; instead a multistage process is involved. The lower layer of cells in a coral polyp and in the tissue connecting polyps together contains cells which secrete an organic matrix into the minute space between the polyp and the existing skeleton. This is a mix of proteins, sugars, and lipids that forms a kind of "scaffold" in which limestone then precipitates from the surrounding water. Some of the proteins bind the calcium component of limestone, and the limestone crystals develop from that. Each coral species has its own specific pattern of cells that secrete the initial organic matrix, and the pattern of the resulting limestone deposition matches that.

The quantities of the calcium and carbonate components of the limestone are controlled to a large extent by the cells on the underside of the polyp. The process only works, however, if the water the coral is in is very rich in dissolved limestone to start with—it must be "supersaturated" with it. If the seawater becomes a little more acidic (has a lower pH), this saturation becomes less, and limestone deposition is reduced and even becomes impossible. This is important today

with CO_2 dissolving more and more in seawater, making it more acidic. In fact, a drop in acidity by just 0.1 pH, which has already happened over much of the ocean, means a measurable 30 percent drop in the ability of corals to calcify.

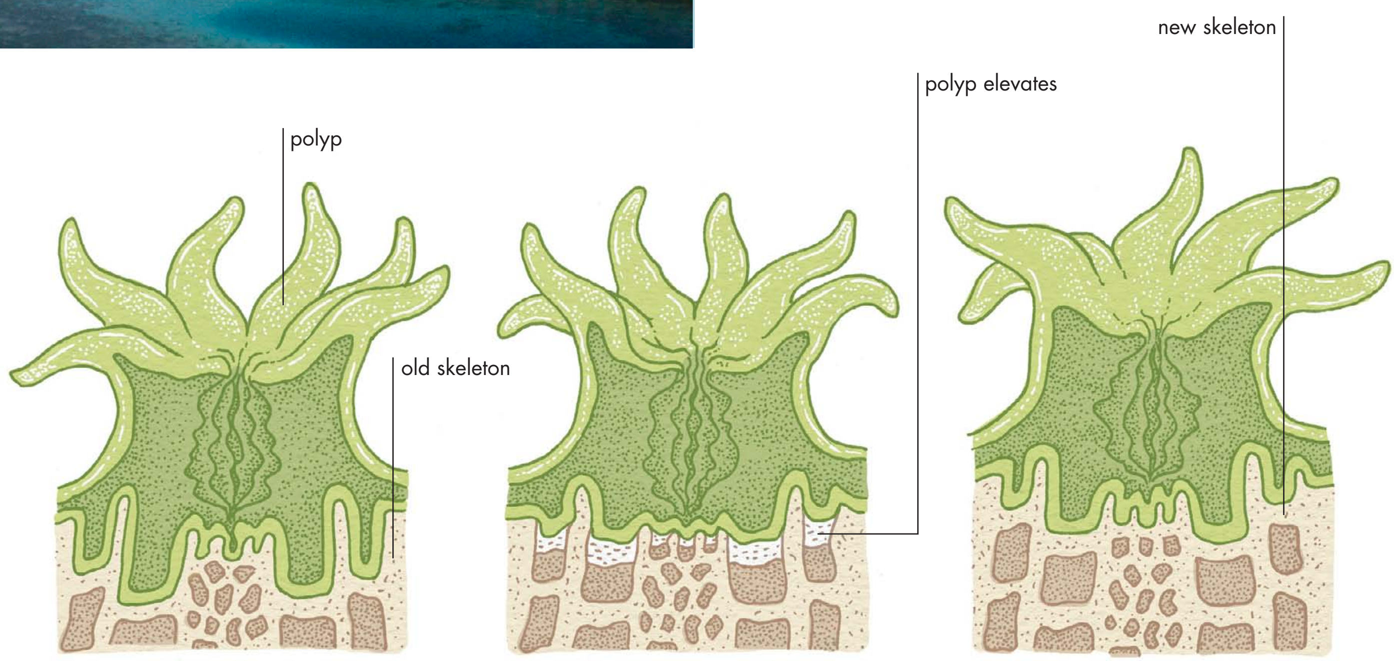
All reef construction ultimately depends on this. Aragonite is not a very stable crystal, but over many years the aragonite deposited by corals turns into the more stable calcite form that old and fossil reefs are made of.



LEFT | The raised limestone reefs of the Huon Peninsula, on the north coast of Papua New Guinea, are a series of reefs that have been successively lifted out of the water by tectonic jolts. Kept free of trees by anthropogenic burning, these flights of reef terraces reveal the capacity of tiny coral polyps to generate immense structures. The modern reef and lagoon at the bottom of the hill are alive and active. The terraces up the hill record reefs built at previous sea level stages and uplifted by earthquakes over the last 500,000 years.

BELOW | Corals grow upward in a series of steps. The base of the polyp rises from the limestone it deposited previously. It deposits another "floor" beneath its base and lives on that before repeating the process. As it rises, it may also bud to divide into two. The area of active crystallization between the old skeleton and the base of the living polyp is a fraction of millimeter.

THE PROCESS OF UPWARD CORAL GROWTH



CHAPTER 2

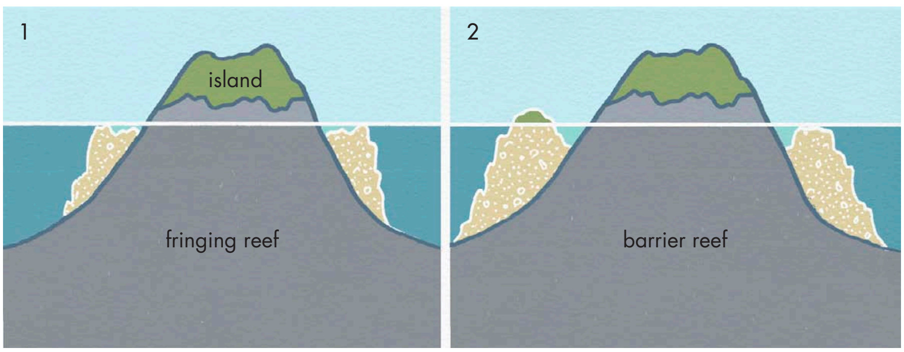
DIFFERENT KINDS OF REEFS

DARWIN'S SCHEME

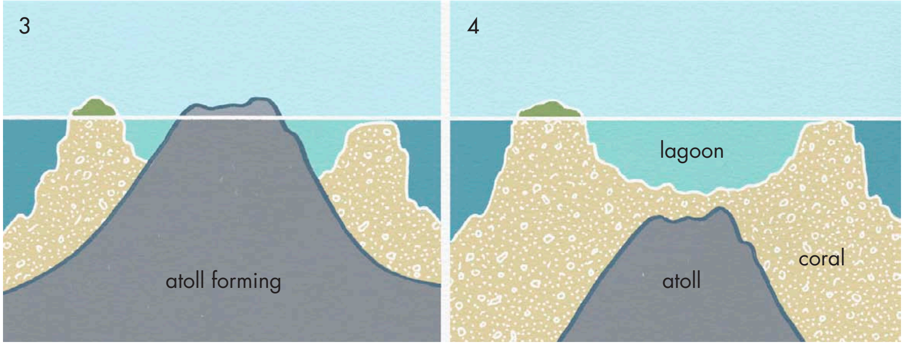
It was Charles Darwin who came up with the basic idea of how corals make reefs. In the nineteenth century there had been much debate about why reefs always grew up to the low tide mark and no further, why coral islands and especially atolls, of which hundreds were now known, were always just a few meters above sea level, and how the rings of atolls actually formed. Recognizing that islands can slowly subside and that corals build reefs as they grow upward toward the light, Darwin traced the progression of development through the series: (1) a fringing reef that develops in shallow waters beside an island or around a volcano; (2) a barrier reef as the land subsides farther and reef development progressively moves away from the shore until it is far enough from the land for navigation by a small ship; and finally (3) an atoll—when the land submerges completely, leaving only a ring of reef. This happens because volcanic islands and other land sinks, and because corals keep growing upward toward the surface. Darwin recognized that land moves vertically over large distances, observing this earlier in his journey around the world. His ideas on reefs were as original as his thoughts on evolution, and helped change the way people thought of Earth's long history.

There are other kinds of reefs—like those found on continental shelves—but all are really no more than variants of this. Over millions of years, land can continuously sink, as occurs with volcanoes in mid-ocean, or it can move vertically in either direction, both upward as well as downward, in bursts near continental landmasses as well as gradually. In the Red Sea, for example, both shorelines are moving apart and they jolt upward at geological intervals, leaving a series of reef terraces extending increasingly upward on either side. Also, absolute sea level changes by well over 330 ft (100 m) during ice ages, when ice caps melt or expand. Both factors combine to ensure that the position of shallow habitat suitable for corals is continuously changing over geological timescales. As a result, reefs come in a wide variety of forms—patches, rings, ribbons, and barriers—all a result of the reef-building ability of corals.

STAGES OF DEVELOPMENT OF AN ATOLL



RIGHT | Stages of reef development into an atoll: 1) A volcanic island develops a fringe of coral reef, forming a fringing reef. 2) The volcano subsides and deepening water appears between the reef and land, leaving a barrier reef. 3) The volcano almost disappears, so an atoll is forming. 4) The volcano has subsided below the sea surface, leaving only a ring of reef: an atoll.



ABOVE | In addition to formation of the atoll rim (shown left), many atolls also develop pinnacles and islands in the lagoon. The Maldives consist of a chain of atolls in the Indian Ocean containing many of these. The reefs have grown for tens of millions of years as the volcanoes underneath them have slowly subsided. In lagoons, the water is shallow, rarely deeper than a couple of hundred feet, even though the outer slopes plummet to depths of several thousand feet.

REEF COMMUNITIES AND REEF DEVELOPMENT

Just as there are many kinds of forest, so too there are many kinds of reef communities. Sheltered water favors forests of branching corals, coral tables, and those with fine finger-like projections. Stormy water favors the more solid and massive forms; branching corals do occur, but these will grow with dense skeletons and are usually quite squat. As depths increase and the degree of exposure to waves and light fades, so there is a gradation of coral shapes and species. In deep water there are leafy and finely branched forms that could not survive shallow, turbulent water, making up a quite different community. Just as lowland tropical forests differ from high-altitude mountain forests, so reef communities differ almost as markedly.

These coral communities grow on a near-infinite variety of reef shapes and profiles. The present profile of any reef is a result of alternate growth and erosion over millennia. Thousands or millions of years ago different climate, energy, and rainfall patterns eroded reefs in different places to different extents: today some reefs slope gradually while others may be vertical. Both kinds, and several stages in between, may be found on one reef within a relatively short distance. Over time, conditions may have become more or less favorable for reef growth. During ice ages, huge volumes of water became locked up at the poles, substantially dropping oceanic water levels, which would drop the position of new coral growth. A common sight at depth in

some places is a long line of undercut reef, even caves, cut deep into the reef slope when that depth was at the ancient sea level for centuries or thousands of years, so that waves eroded the reef at that time. An understanding of "deep time" helps explain the widely varying slopes and coral communities that are quite different but which many might simplistically lump into the one term "reefs."

Reef rock itself builds in a more complicated way than simply corals growing on corals. Reef rock may be mostly composed of an amorphous matrix of limestone rather than coral skeletons. Skeletons may well be seen embedded in the matrix, but usually as a minority component. The matrix itself is formed from sand grains derived from ground-down coral skeletons, which become bound there, changing slowly from aragonite into the harder rock calcite by chemical solution effects, driven partly by bacterial action.

OPPOSITE | Fields of branching corals in shallow water. The fact that some are relatively fragile species shows that this reef is located in relatively calm water, protected from stormy waves. Most species here are from the diverse genus *Acropora*.

BELOW | In water of similar depths, a more exposed reef, subject to much stronger wave action, supports coral communities with more robust forms. Behind the massive corals in this Caribbean scene are colonies of fire coral (*Millepora*) and the now uncommon large elkhorn coral.

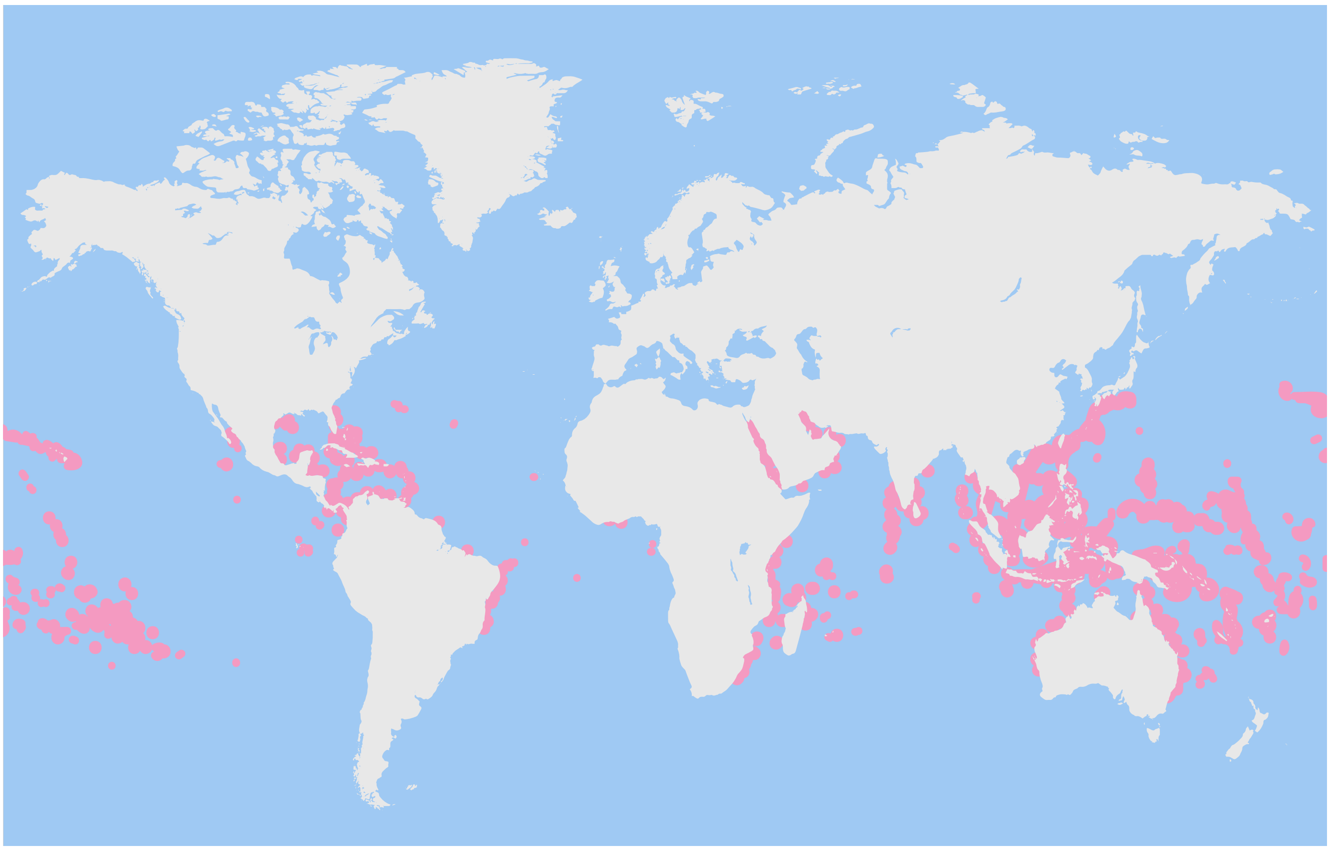
GLOBAL DISTRIBUTION OF REEF-BUILDING CORALS

Coral reefs are located in the equatorial belt, mostly between the tropics of Cancer and Capricorn. Extensions to the north and south occur where warm currents flow beyond these tropics along suitable coastlines. Warm currents take reef-building corals north to southern Japan and to the coral-rich northern Red Sea. Australia sees the farthest extension south down the Great Barrier Reef on its east coast, and along the Houtman Abrolhos Islands on its west coast. In the Atlantic, coral larvae travel to Bermuda in the Gulf Stream, and in the South Atlantic Brazil has reefs too, with several endemic species.

Other limitations to where corals grow and reefs develop come from freshwater inputs from giant river systems, and muddy substrates. Few corals inhabit the West African coast because of the muddy conditions, and in South America the Amazon acts as a barrier to most coral species. On the Pacific coast of South America, corals grow toward the equator, but cold upwelling currents inhibit them over most of the Pacific coast of the Americas.

BELOW | Map showing the global distribution of coral reefs.

OPPOSITE | A shallow reef in the South Pacific island of Alofi, French Polynesia. Here the diversity of corals has fallen considerably from the high-diversity region farther west, but the reefs are just as substantial, with high biomass.



With present-day warming (see page 182), places previously at the margins for coral growth are becoming warmer, so one or two places, such as Bermuda, may see increasing diversity.

There are no coral species in common between the Atlantic and Caribbean region and those of the Indo-Pacific, apart from one that has made the journey recently, possibly in ballast water of a ship, and one, possibly different, that was taken across in earlier transplant experiments. In the Indo-Pacific, the richest diversity lies in the "Coral Triangle" (see page 76) in Southeast Asia. From here, coral diversity declines fairly evenly eastward through the Pacific island groups. In the Indian Ocean, the pattern is more mixed, as diversity rises again around Madagascar and Mozambique, and in the Red Sea.

There is no relationship between the diversity of corals and the strength and substance of the reef that they build. Massive atolls in the Pacific are built by reef communities with many fewer coral species than those of the Coral Triangle. This is partly because wave-resistant reef-building relies on several factors, such as growth of coralline algae (see page 102) as well as coral growth. The coral skeletons provide bulk and structure, but it is the way coralline algae act as a binding cement that determines how a reef resists ocean swells.

FRINGING AND BARRIER REEFS

Fringing reefs, especially some of the smaller ones, are some of the simplest reefs in structure and formation. They offer a restricted range of habitats to corals. Because they are connected to the shore by an expanse of reef flat, they have very limited back-reef constructions like lagoonal areas. The simplest consist only of the reef flat extending from land, followed at its seaward edge by a slope that descends into deeper water. The northern two-thirds of the Red Sea (see page 74) is lined by fringing reefs along both its African and Arabian shores; in total, these form the longest fringing reef in the world, if you ignore the occasional breaks and interruptions. Off the coast of Western Australia, the Ningaloo Reef is also long, extending 160 miles (260 km), always attached to the continent except in a few bays. Ningaloo is the longest fringing reef along one single country, and part of it is a World Heritage Site.

A barrier reef is a development of a fringing reef and similarly has a reef flat and a reef slope that descends from it into deep water. However, it is separated from the land by a navigable channel and so it will include more extensive and sheltered back-reef areas, many more expansive sandy areas, and numerous pinnacles and small patch reefs within its back-reef areas. It may even contain a fringing reef within it that runs along the shoreline itself. Many reefs in the world are in fact small barrier reef systems, sometimes simple linear systems and sometimes complex and convoluted. One good example is the "Little Barrier Reef" of the Red Sea that extends offshore from the fringing reef, down much of both sides of the northern half of the sea. It lies about 6¼–19 miles (10–30 km) offshore, a rich ribbon of reef that is a consequence of ancient sea levels and of geological faulting that affects the Red Sea as it continually

widens. The Great Barrier Reef of eastern Australia is another, but is somewhat different (see page 80).

In some cases, such as the Red Sea, the slopes are vertical and extend to depths of several hundred yards (meters), although corals only grow in the top shallow region. In others, like Ningaloo, the reef slopes do not extend more than 66–100 ft (20–30 m) deep before reaching the sandy floor of the Australian continental shelf.

BELOW LEFT | Part of the long fringing reef of the Red Sea. This shows the reef flat adjoining the arid landscape. The reef then slopes steeply down to great depths, and is home to rich marine life.

BELOW CENTER | The Ningaloo fringing reef off northwest Australia extends for 160 miles (260 km), hugging the coast all the way.

BELOW | A fringing reef on the volcanic island of Komodo, Indonesia. This thin fringe hugs the shore and plunges steeply. Despite the relatively small aerial extent, the slope supports a huge diversity and abundance of life.

ATOLLS

It is often supposed that a ring of reef, or an atoll, is formed simply by corals growing on the rim of an old volcano, but it is rather more complicated than that. There would have been a volcano tens of millions of years ago, and it will have had corals growing around its flanks. But it has been subsiding since then, and over the immensity of time sea levels have risen and fallen repeatedly by over 330 ft (100 m) during each ice age and interglacial period. Today the limestone caps on the ancient volcanoes might be 1–2 miles (more than 2–3 km) thick, and are now so deep that there is no direct trace of the old volcanic rim visible at the surface.

Much happened over the intervening time. Corals formed on the rim once it was below the ocean surface, and probably inside the rim at various times too. Further subsidence, growth, and erosion by waves and rain, simultaneously or sequentially, have all shaped and cut the ever-increasing mass

BELOW | Maiana atoll in Kiribati is 9 miles (14 km) wide. There is a single island on the rim along its northern and eastern side, which has habitation, while the western rim supports a few small islets. Its low elevation has put the islands at high risk from sea level rise.

BELOW RIGHT | The coral atoll Penrhyn, in the Pacific, seen from the air. Atolls form pinnacles in the ocean with islands just above sea level. The lagoon is a fairly shallow basin, but surrounding it the reef slopes downward to great depths.

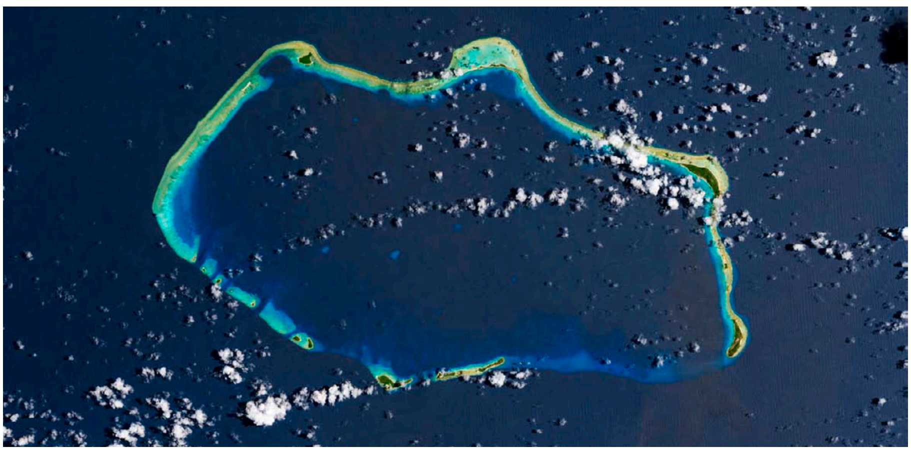
of coral reef that was forming as the volcano sank. This process is continuing. There are around 440 atolls in the world, of which about 60 percent have islands on their rims.

Key to the formation of atolls is that limestone, being a calcareous rock, dissolves in rain, which is always slightly acidic. During periods of very low sea level during ice ages, rain dissolved giant depressions on the emerged reef limestone, with drainage channels leading out of the developing basin. These depressions became lagoons after sea levels rose to where they are today. The variety is endless: small atolls can have deep lagoons, while some large atolls can have lagoons just a few meters deep; some lagoons are over 200 ft (60 m) deep, and over 100 atolls today have lagoons that are now not even directly connected to the outside ocean.

Over millions of years the combination of episodic growth and erosion has resulted in a huge variety of atoll rings, each on a column of limestone rock resting on the old volcano. Closely positioned atolls can be separated by water several kilometers deep. This method of formation was predicted by Darwin and confirmed a century later by drilling into Enewetak Atoll in the Pacific in 1952, when the old volcano was found at over ¾ mile (1.25 km) deep.

LEFT | The small atoll of Saint Joseph, which has a small, shallow lagoon. Vegetated islands have accumulated in just a few places on its broad rim, which is more or less continuous, with no channels leading into it.

BELOW | Bikini atoll in the Pacific. This satellite image shows islands dotted at intervals all around the rim, with the rest of the rim being reef that is submerged, broken by a few channels seen in the bottom left side. Nuclear testing took place over a decade from 1946 on this atoll, and the clear indentation in the rim at the top left, is the crater of one testing site.



FIVE CONTRASTING REEF SEAS
THE CARIBBEAN

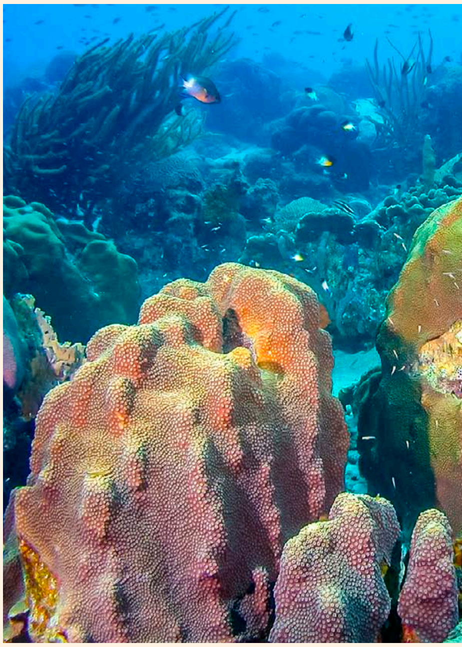
The Caribbean is the main coral province of the Atlantic Ocean. It includes Bermuda farther out in the Atlantic, as well as a fairly distinct group of reefs in northwest Brazil that are partly isolated from the rest by the freshwater barrier of the Amazon and Orinoco rivers.

The reefs here are mostly fringing reefs surrounding the numerous mountainous islands. Many coral islands called "cays" exist too, as well as reefs on pinnacles that reach near the surface. The Caribbean is a young sea: the land bridge of Central America developed about three million years ago to join North and South America and isolate the Atlantic from the eastern Pacific.

The Caribbean has no corals in common with the much larger and richer Indo-Pacific (apart from a species of *Tubastraea* that does not need light and which probably made the journey with shipping). There are only about 50–60 reef-building coral species in this region, or fewer than one-tenth of the number in the Indo-Pacific. The relatively small size of the Caribbean Basin has much to do with this. Most species occur along the Antilles islands and on the northern coast of South America.

Biologically, Caribbean reefs are distinctive because they are heavily dominated by tall, branching soft corals, which do not themselves help to build the reefs. They are also home to many more sponges than are generally seen in the Indo-Pacific.

The Caribbean and its reefs have been heavily used. Up until the 1980s, shallow reefs were largely dominated by the giant branching Elkhorn Coral (*Acropora palmata*), which formed impenetrable and majestic forests from low water to depths of about 12 ft (4 m). However, these are now largely absent, "white band disease" having reduced most of them to rubble in a few years. This disease may have originated from human sewage. Later, the crucial grazing Long-spined Sea Urchin (*Diadema antillarum*) more or less completely died out from disease (see page 162), in a wave radiating out from



roughly the entrance of the Panama Canal, allowing algae to flourish and inhibiting corals further.

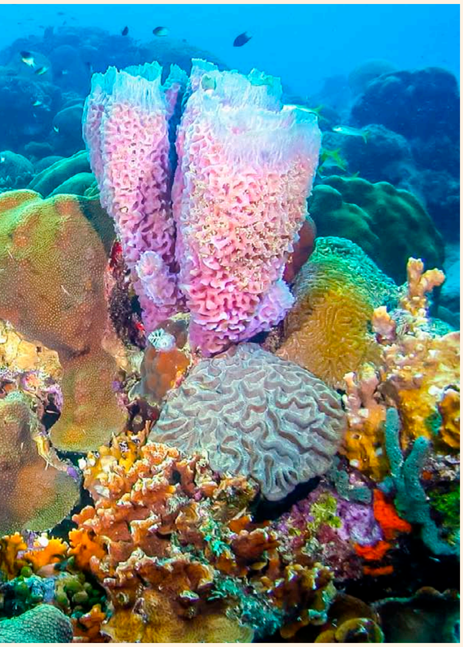
The state of corals in most of the Caribbean region has now been reduced further by ocean heatwaves—the cause of coral bleaching—and it remains heavily fished. This removes grazing fish species, helping seaweeds further outcompete corals. As it is a very heavily used body of water, the prognosis for reefs in the Caribbean is not good.

ABOVE | The Caribbean Sea.

BELOW LEFT | This British Virgin Islands reef scene, dominated by tall, waving soft corals and sea fans, is typical of the Caribbean.

BELOW CENTER | Another reef scene in the Caribbean, where sponges (the pink cylinders seen on the right) can be nearly as prominent as corals and soft corals.

BELOW RIGHT | Elkhorn coral (*Acropora palmata*) used to dominate shallow reefs in the Caribbean, but over recent decades have suffered greatly from disease. They can form some of the largest coral colonies in the world.



FIVE CONTRASTING REEF SEAS

THE RED SEA

At the far northwestern extremity of the vast Indo-Pacific, the Red Sea extends considerably beyond the Tropic of Cancer and deep into the arid regions of the Middle East. The northern part is today home to several substantial tourist recreation areas, in Egypt, Jordan, and Israel, where many people take the chance to visit the nearest coral reefs to Europe. For political reasons, only the northern tip of the sea is much visited.

The Red Sea is a part of the Indo-Pacific realm in terms of its marine life, and in many senses it has only recently rejoined it. In the last ice age it was isolated, cut off because the sea level was over 400 ft (130 m) lower than it is now and the shallow entrance at the south of the Red Sea dried out. Before the ocean flooded back, the sea's waters became far too salty from evaporation to support any life other than salt-tolerant microbes and simple animals.

However, 17,000 years ago when the Red Sea began to flood again, corals and other reef life entered it from the Indian Ocean. The Red Sea is widening by several centimeters each year because Arabia is moving, partly pushed by a spreading center deep in the sea, where water temperatures can be over 175 °F (80 °C). Because of its widening, the newly forming sea is actually an ocean.

Coral reefs extend along both shores, mainly in the northern two-thirds. In total, they form the longest fringing reef in the world, and in many places have very shallow and narrow reef flats before plunging vertically to hundreds of meters. Their coral and fish diversity is high, possibly enhanced because water containing larvae flows continuously into the sea to replace the water lost from intense evaporation, so the sea acts as a kind of trap for entering species. Offshore in the north is also the "Little Barrier Reef," which is not commonly visited.

In its southern third, the Red Sea is shallower and muddy, precluding much reef development, though the Farasan and Dahlak archipelagos have substantial coral.

The reefs support large quantities of soft corals as well as hard corals, including characteristically large amounts of red, bush-like soft corals and finger-shaped corals with clouds of small fish that shelter in the branches. The sea's relative isolation has led to numerous endemic coral species, which are not found outside the Red Sea and probably evolved within it.

ABOVE | The Red Sea.

BELOW LEFT | Beyond the reef flat the reefs of the Red Sea usually plunge steeply, often vertically, to depths of thousands of feet. This is the result of a deep rifting of the Earth's crust, and tectonic forces that continue to push Arabia away from Africa.

BELOW CENTER | Red Sea reefs usually have clear waters, allowing rich growth of corals and soft corals at depths of over 150 feet (50 m). They are also home to numerous sharks and turtles.

BELOW RIGHT | Water-based tourism, such as diving and snorkeling, is popular in parts of the northern Red Sea, where the rich reef life is in marked contrast to the arid desert landscape above water.

FIVE CONTRASTING REEF SEAS

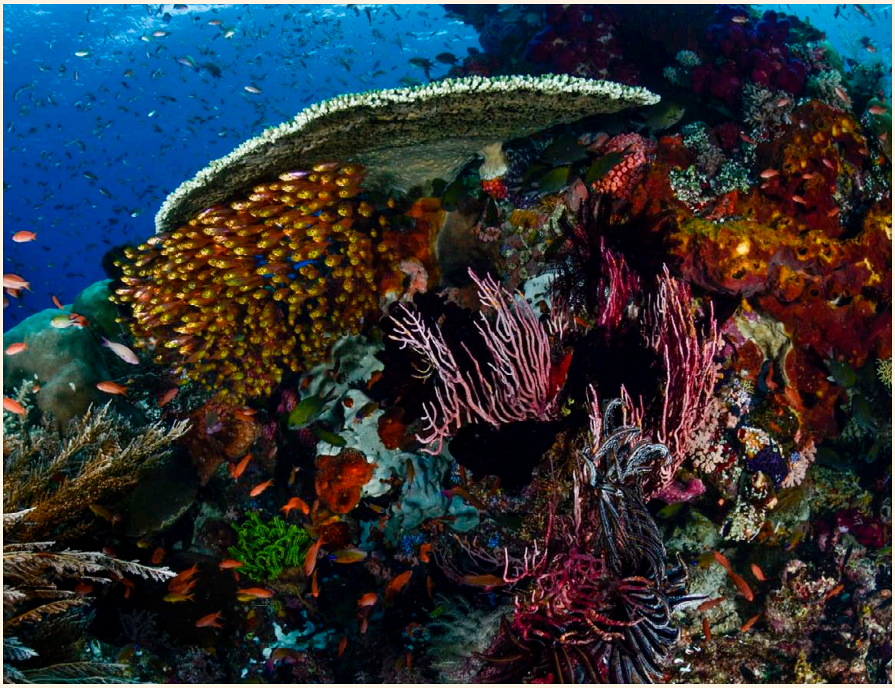
THE CORAL TRIANGLE

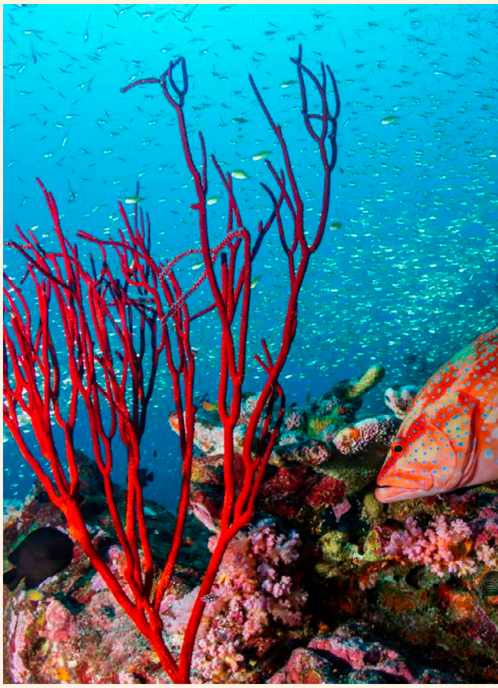
The "Coral Triangle" is the roughly triangular region of Southeast Asia which is richest of all in terms of the number of coral species. Encompassing Malaysia, the Philippines, Indonesia, Papua New Guinea, Timor Leste, and the Solomon islands, it is a 2.3 million square mile (6 million square kilometer) area of archipelagos, islands, and reefs. Perhaps surprisingly, much of Australia's Great Barrier Reef does not lie within it. The area of peak coral diversity within the Coral Triangle is a band including the Sulu Sea and the Bird's Head region in west New Guinea.

Within this area there are at least 620 species of corals, or about three-quarters of the world's known shallow-water species. It also has more than 2,000 species of reef fish, about one-third of the world's total. Most of these species occur farther afield to the east and west, but the number of species fsrther away roughly declines with distance from the triangle.

Reasons for this high diversity have been researched for many years, and the pattern is similar for most other marine and terrestrial groups of animals and plants; this region has the highest biodiversity in the world for almost all groups. There are several explanations. It is in the geographical center of the Indo-Pacific, and has experienced several repeated recolonizations of species as sea levels dropped, drying out large portions of it, and then flooded again, bringing in colonizers from a much greater area, and concentrating them.

The changing location of the tectonic plates has also been important, with many coral and fish groups having their origins in a region of the now extinct Tethys Ocean that once lay between Africa and Eurasia. Today's Coral Triangle may also have been less affected by the last of the world's great species extinctions. Populated by archipelagos with thousands of islands, it has a longer coastline and a



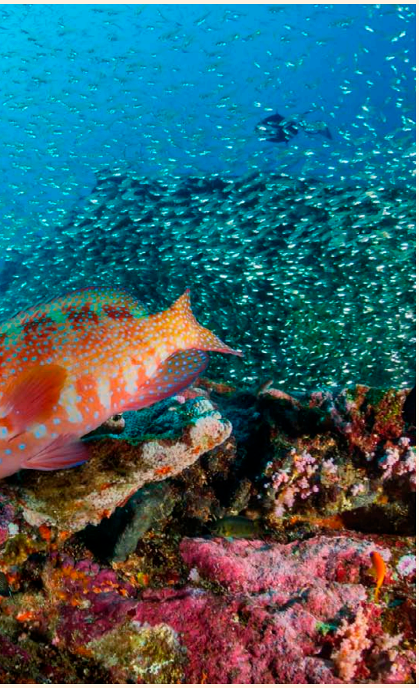


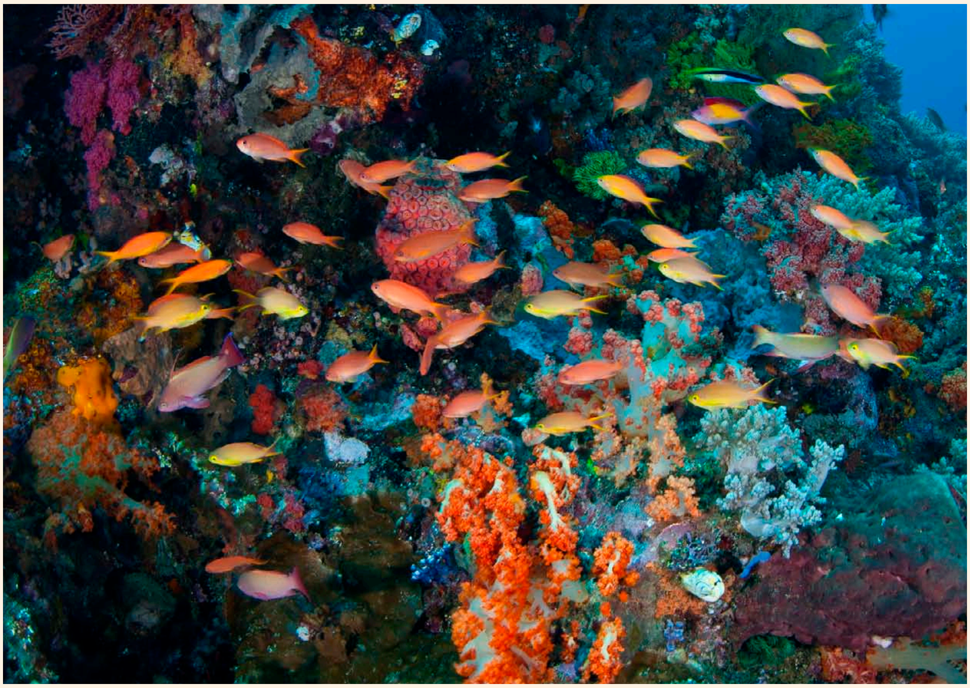
wider range of suitable habitats than do more uniform coasts, so it simply has far more suitable coastline than most places of similar area.

Several hundred million people now depend on Coral Triangle reefs for their protein. The ever-increasing human population has pushed people to use unsustainable methods of resource extraction, such as fishing with dynamite and poisons. Today large areas of degraded reefs can no longer supply the needs of people to the same extent as they once did (see chapters 4 and 5).

BELOW (ALL) | In the Coral Triangle, corals, soft corals, and reef fish are abundant. The rich reefs here have the highest diversity in the world and, if undisturbed, some of the greatest biomass.

RIGHT | The Coral Triangle in Southeast Asia includes some, but not all, of the Great Barrier Reef (shaded pink).





FIVE CONTRASTING REEF SEAS
PACIFIC ISLAND REEFS

The huge Pacific Ocean occupies almost half of the Earth's surface, and a tiny proportion of it consists of islands. These islands are in several different groups. Nearest Asia lie Micronesia and Melanesia, with Polynesia covering the largest expanse of ocean farther east. Each area includes several different archipelagic countries and territories. Each has its own cultural characteristics, and there are linguistic differences also, though each grades with adjacent regions.

Melanesia has many volcanic island chains and includes part of the Coral Triangle at its western end (see page 76). Micronesia consists mainly of low-lying atolls and cays, while Polynesia consists of many high volcanic islands, including Hawaii.

All of the Pacific's tropical volcanic islands are rimmed with coral, and the numerous atolls are made from coral. All are geographically part of what is termed the "Oceania realm," and there is no continental landmass within the area (except for New Caledonia in the west). The volcanic landmasses are mostly of relatively recent geologic origin.

Coral diversity diminishes eastward across the region (see page 66), and as few as 50 coral species form several atolls in the east, although these reefs and islands are as substantial as those with several times more coral species in the west. The most easterly atoll, Clipperton, has only about 15 species. Most of the area was never connected to the Asian landmass, so all species have reached the archipelagos through planktonic dispersion from Asia subsequent to the islands' formation. In the eastern Pacific, cooler water inhibits corals, which is partly why there are many fewer species and limited reef development.

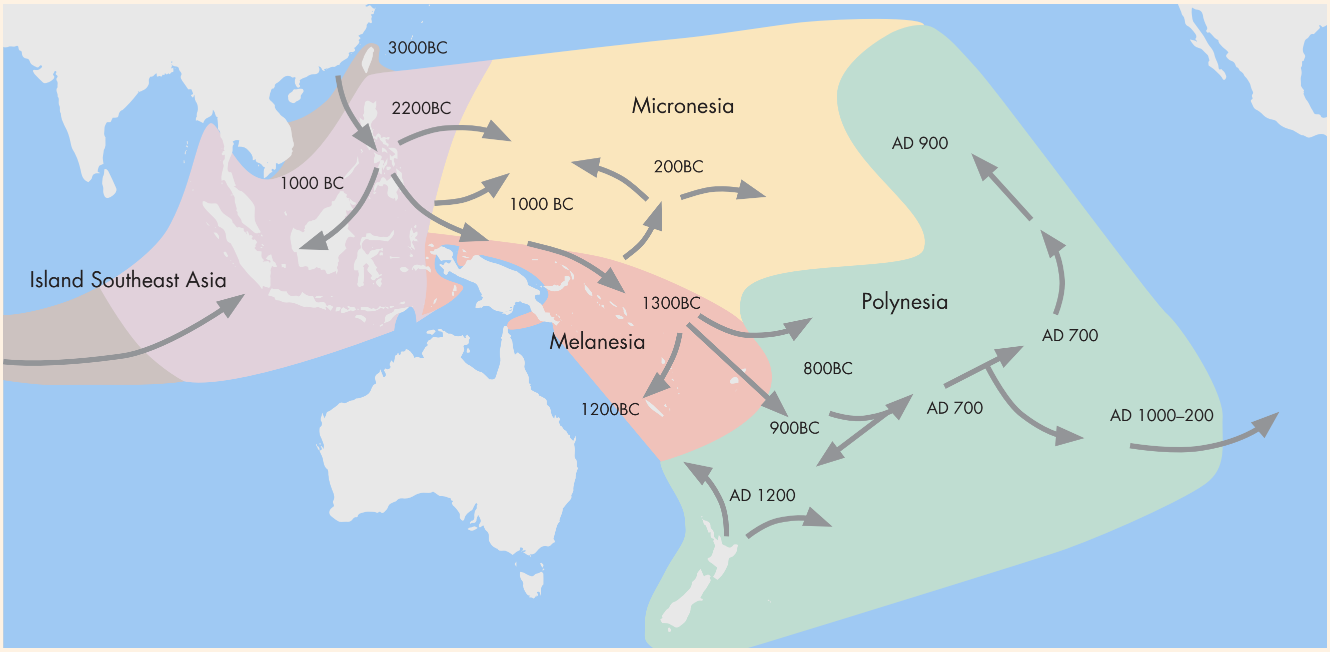
A classic island arc is seen in Hawaii, where a volcanic hot spot deep in the Earth's mantle is creating a series of islands as the Earth's crust moves over the relatively stationary hot spot. Corals have colonized each of these, the older ones in the west now being classic atolls.

Many of the inhabited islands are atolls, lying precariously close to present sea level—which is rising. High spring tides, called king tides in some countries, now flood well inland at intervals on several islands, destroying water tables and plants, causing erosion, and making life increasingly difficult or impossible. Recent widespread marine heatwaves have been killing the corals that build the reefs and protect the islands. The atoll peoples of Oceania are likely to be some of the first climate refugees of a warming world.

RIGHT | Kure atoll, in the Hawaii archipelago, is a typical undersea mountain of coral reef on top of a deep volcanic base. It is the northernmost atoll in the world and lies in cooler water where the rate of reef growth only just exceeds the rate of subsidence.

OPPOSITE TOP | The three main cultural groups of Pacific islands, Melanesia, Micronesia, and Polynesia. Overlaid on the map are the tracks and approximate dates of human divergence and settlement onto the islands from Southeast Asia, it is thought from southern China.

OPPOSITE BOTTOM | Tutuila island in American Samoa, in the Pacific, is a "high island," composed of a central volcanic core and fringed by coral.


3000BC
2200BC
Micronesia
AD 900
200BC
1000 BC
1000 BC
Island Southeast Asia
1300BC
Polynesia
Melanesia
AD 700
800BC
1200BC
AD 700
AD 1000–200
900BC
AD 1200

FIVE CONTRASTING REEF SEAS
GREAT BARRIER REEF

The Great Barrier Reef is a reef system of superlatives, commonly included as one of the seven natural wonders of the world. It is huge, extending 1,430 miles (2,300 km) along eastern Australia, sometimes close to land, and sometimes 185 miles (300 km) distant. It is not really one reef at all, but about 3,000 individual reef systems of many shapes. It has over 1,000 islands, one-third being coral cays and mangrove islands, with most others being continental islands fringed with coral reefs. The whole complex extends southward from just south of the Coral Triangle to Lady Elliot Island at 24 degrees south.

The Great Barrier Reef developed as Australia drifted north into the tropics, with reef growth commencing in the north, where the carbonate limestone is now up to 1 ¼ miles (2 km) thick. Today, reefs comprise only about ten percent of what is known as the Great Barrier Reef region, with the areas between individual reefs supporting vast seagrass and algae beds (including the calcareous *Halimeda*), mangroves, sponges, and thousands of square kilometers of sand and mud that support commercially important species of fish. The reefs are integral to all these habitats and enable the existence of most. The Great Barrier Reef's wealth of life has ensured that much of it is listed as a World Heritage Site.

However, today it has severe problems. Agricultural run-off containing pesticides, sediments, and nutrients that stimulate seaweeds has long been a known source of damaging pollutants; and some major outbreaks of the Crown of Thorns starfish (see page 164) have also damaged the reefs. Most of all, the effects of climate change have had such a massive impact that the authority that manages the reef has downgraded its outlook from Poor to Very Poor. There have even been calls to revoke its World Heritage status. Waters have warmed over the entire Great Barrier Reef over the recent past, resulting in the northern third—its most pristine region—losing about one-third of its corals in one year. Overall, about half of the corals of the Great

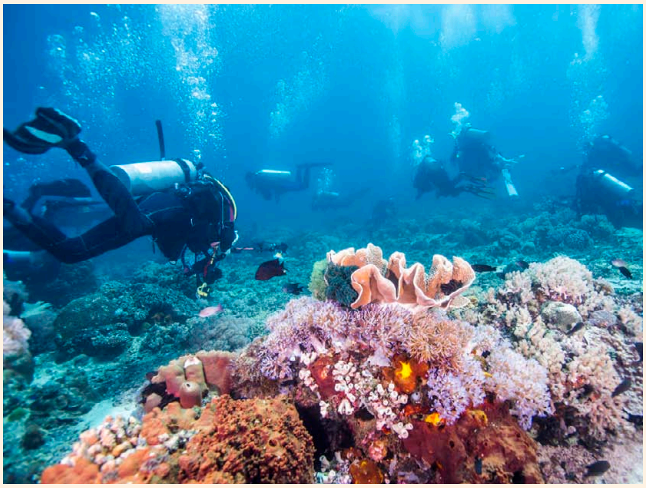
Barrier Reef were killed because of the marine heatwave of 2015–16, and more from the heatwave of 2020. Recovery might be possible given time, and there is a very well-developed system of management to try and ensure this. But only a concerted effort by the world to reduce emissions and prevent global temperature rise from exceeding 2.7 °F (1.5 °C) will prevent further, more regular, coral bleaching.

BELOW LEFT | Rich coral growth on part of the Great Barrier Reef.

BELOW CENTER | The Great Barrier Reef is a collection of about 3,000 individual reefs, stretching along the shallow shelf off northeast Australia.

BELOW RIGHT | As well as corals, the Great Barrier Reef is rich in soft corals. Most of the Great Barrier Reef is not actually part of the Coral Triangle, due to its more southerly latitude.

ABOVE | The Great Barrier Reef extends along most of the northeast Australian coast, closer to land in the north, where it includes fringing components, and sweeping farther away from shore toward the south.



CORAL ISLANDS AND CAYS

Perched on top of many coral reefs, from fringing reefs to atolls, are coral islands. Some may be transient and last only a few decades, while some may have lasted several thousand years. Many are built up by storm-tossed coral sand and rubble, the product of the breakdown of coral colonies and myriad other reef creatures. Piles accumulate on the reef flat at the summit of the coral reef, just above the high tide level. Some never develop any further than this and remain as piles of sand, vulnerable to a major storm that could wash them away.

However, some remain, grow larger, and are visited by birds that nest on the sand and deposit guano (droppings) rich in organic matter. Wind-blown seeds germinate, and there gradually develops a thin topsoil capable of sustaining other plants until, over decades and centuries, a richer island vegetation becomes established. Freshwater tables develop a few meters beneath the surface due to accumulation of rainwater, which further increases the potential for the number and diversity of plants, including trees when the water becomes sufficient. People may visit and settle, leading to entire island communities and nations.

Such cays are usually small, never more than several hectares. Plants are zoned across them all the same, with salt-tolerant species, usually shrubs and grasses, around the rim, and larger trees less tolerant of salt nearer the middle. Across the world, these low islands now support millions of people.

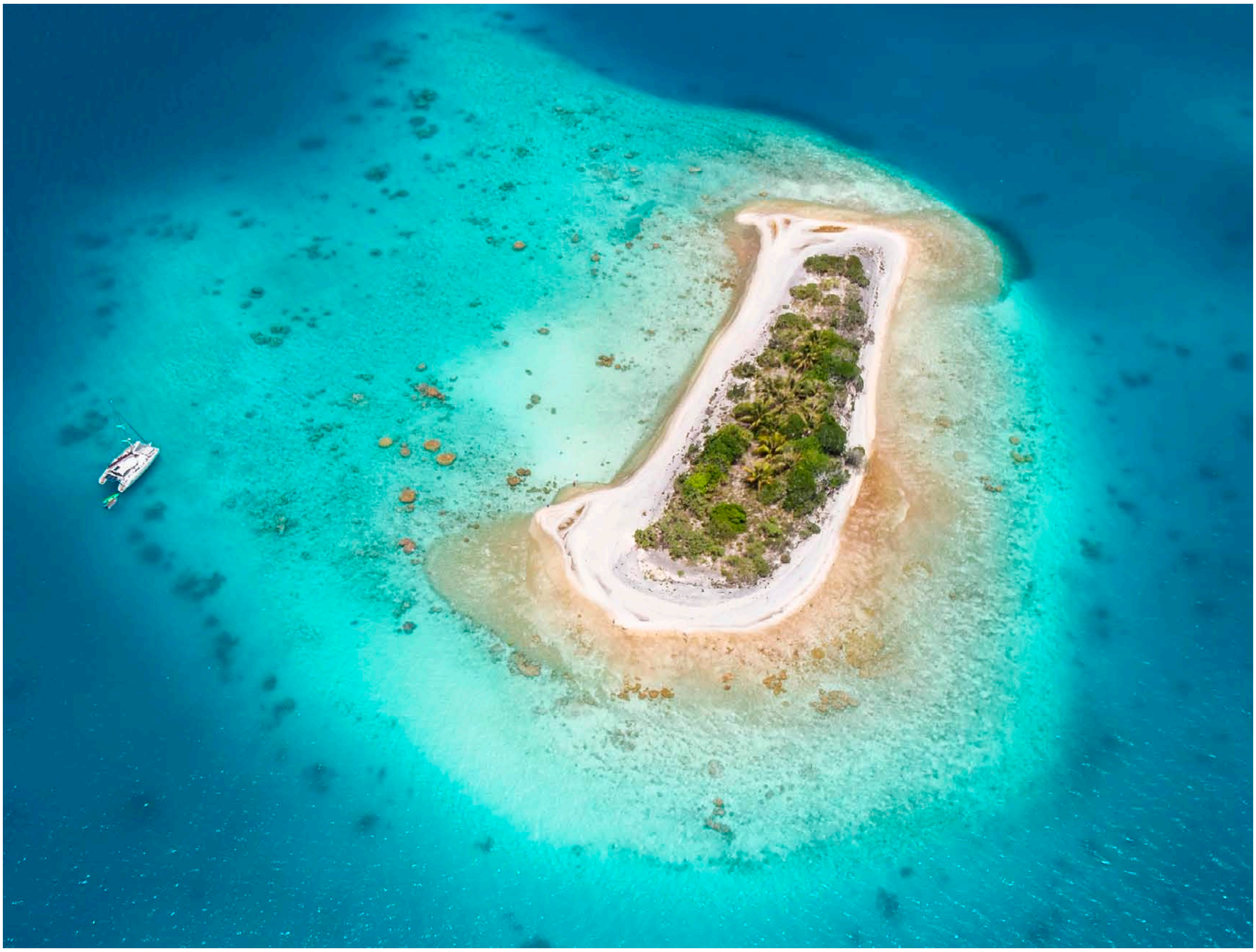
Some coral islands do have a central core of consolidated limestone. This is old coral reef that is now uplifted, usually because of vertical geological movements and because the original reef became exposed when sea levels dropped a little. Some entire atolls are uplifted in this way, but again, usually to no more than a few meters.

Cays are never more than a few meters above high tide, though drifts of sandy dunes may extend a little higher, and may even consolidate a little and become fairly stable. They are very vulnerable to storm surges and now also to sea level rise.

RIGHT | A typical coral island or cay is very low-lying. It is entirely made up of coral sand and rubble, later colonized by vegetation.

LEFT | A coral island perched on a reef grows by the accumulation of sand derived from ground-down corals and other calcifying organisms. The birds bring seeds, more seeds arrive on currents, and vegetation starts to grow, in turn attracting further life.

BELOW | A small coral island perched on a coral atoll rim in Rangiroa, in the Pacific. It accumulates sand by wave action acting on growing coral on its surrounding reef.



LEFT | This ancient reef, now on dry land in the Kimberley region of northwest Australia, grew in Devonian times.

RIGHT | Fossil sponge reefs in Lion-sur-Mer, France, built up in Jurassic times. They also contain fossils of many reef-dwelling species of the time, such as echinoderms, brachiopods, and bivalves.

THE RICHEST PARTS OF REEFS

On any one reef, the zone with the highest diversity of reef-building corals and soft corals is likely to be deeper than about 15 ft (5 m) down to about two or three times as much. This is determined by several factors, so the exact depth range differs in different parts of the world, and will even vary on different parts of the same reef.

One of the most important controls is wave energy, and this declines with depth. Storm waves near the surface eliminate many species, and many branching species that are common in shallow water in sheltered lagoons, for instance, are absent where the reef faces strong waves.

Light is another key factor. This dims as depth increases, and with fading light comes fading energy for photosynthesis. The term "mesophotic" refers to depths where light is very dim, the realm of leafy corals whose shape allows them to collect most of the limited light that reaches there.

With depth, sedimentation also generally increases, and many species are poorly tolerant of the rain of silt that descends, while others have colony shapes that allow silt to slide off more easily. Those that can survive the silt are generally more delicate colony forms which could not survive in shallow water with high wave energy.

There are especially hostile conditions on a reef flat, where monsoonal rain in some regions can dilute seawater, and fresh water is not tolerated by many species. On a low tide near solar noon the temperature in shallow water can become lethally warm, and another constraint comes from too much light, especially ultraviolet. Few coral species can tolerate living in these shallow areas.

So, the preferred space to live on a reef is where it is shallow enough for sufficient water movement to keep corals clear of sediment but not rough enough to smash them, where there is not too much light to "burn" the corals but not too little for sufficient photosynthesis, and where there is not too much sediment to smother them. Most coral species prefer these "middle depths" where conditions are most benign. However, because most want to live in this optimal band it is also where there is most competition between species, and that requires biological characteristics of faster growth, aggressiveness, or more reproduction to survive.

ABOVE AND OPPOSITE (TOP AND BOTTOM) | Sometimes sheltered and sometimes exposed to wave energy, the richest parts of reefs lie just below the strongest wave energy and extend down to where light or sediment becomes unfavorable. These rich parts of the reef are the preferred habitat for most reef-dwelling species.

HIGH- AND LOW-DIVERSITY REEFS

There are about 850 different species of reef-building corals in the world, around 60 of which are in the Atlantic region (mostly in the Caribbean), with the rest being in the Indo-Pacific. As previously noted, the "Coral Triangle" in Southeast Asia (see page 76) contains about 620 of these, a number that falls as distance from that region increases.

This drop is smoothest and most obvious heading eastward across the numerous islands of the Pacific. A reduction does also happen to a certain extent going westward, too, but less regularly, and this is once again followed by increases in diversity nearer the African coast, partly due to the appearance of several regionally endemic species. Also, in the Red Sea there are well over 300 species. That ocean basin seems to be a trap for corals, as well as having several endemic species (see page 74).

However, the size of a reef and the strength of its construction—its solidity—have little to do with the number of different species of reef-building corals that make it. Entire atolls and archipelagos in the mid-Pacific are made from only a few dozen species. Conversely, in the Southeast Asian region, a far greater number of species can sometimes develop into only modest reef structures. Between 10 degrees north and 10 degrees south of the equator there are no trade winds or tropical revolving storms. Here reefs often take on a looser, less bound, more unconsolidated character. Sometimes coral reefs can be more like coral communities

with little solid reef formation, even though they still draw on hundreds of coral species in the region.

Perhaps several reasons are at play. Making a solid reef structure from the available corals is a complicated process. The abundance of coral is important, regardless of how many species are present. Their breakdown into rubble and sand is important too. Then, a number of factors convert this to solid reef, and convert the aragonite limestone to the harder calcite. Sand grains are stabilized; bacterial films coat the grains and change the acidity of their microenvironment so that they bind together. The sand may partly dissolve and reprecipitate. The result is a solid reef, regardless of the number of corals living on it.

OPPOSITE | Off Panama's Pacific coast, in the far eastern Pacific, there are only a couple of dozen reef-building coral species, of which fewer than half a dozen are particularly important to reef building.

BELOW | A reef with a high diversity of coral life in the more central part of the Indo-Pacific.

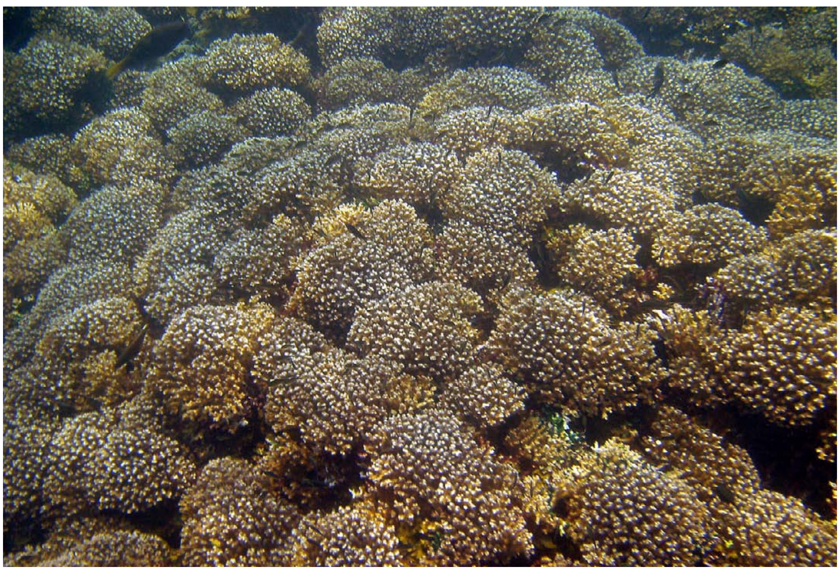
WHEN CORALS CANNOT BUILD REEFS

There are many instances where corals clearly thrive, yet do not develop into substantial reefs. These may be at extremes of latitude, but might also be in areas of high coral diversity, including in the Coral Triangle. Two groups of examples exist: firstly, where corals simply do not attach firmly enough to the substrate for reasons that remain unknown; and secondly, where corals simply pile on top of each other but with little cementation between them. In either case, the coral community may look fairly similar to a "proper" coral reef, and certainly may support similar assemblages of fish, mollusks, and echinoderms, but something is lacking that prevents much reef formation, perhaps including strong enough water movement.

Where there is hard, igneous rock, but where something is lacking in the environment, corals may attach to the rock and remain there while alive, but the colonies detach and disappear when dead. The reasons remain unknown, but presumably conditions are unfavorable to further limestone cementation. Possibly mechanisms enabling cementation of sand particles are missing, which may be connected with water chemistry or the absence of the microbes that aid in this process. Corals may have been growing on the igneous rock for centuries, but each is eventually lost so there is no overall accretion. In the shallows, large boulders of *Porites* may for a time stay attached on top of one another, but again, this is temporary, and the basement, non-limestone rock remains visible. Where there is an old lava flow into the Red Sea, for example, there is no or minimal coral growth at all, suggesting that a constituent of the lava may itself be responsible. The effect is common, too, in areas of raised nutrients.

Where ocean conditions are marginal, corals can form dense single-species fields covering several square kilometers. Oman has several of these: unconsolidated stands of the branching *Pocillopora* extend over huge areas, where it seems only their interlocking branches hold them in place, while farther south, equally large expanses of a leafy *Montipora* do the same. Their accumulated depth now extends several meters, and often very few other species grow with them. The colonies remain in place, but they are loose and not cemented, and could not survive away from very sheltered conditions behind islands or in bays.

RIGHT| At 32 degrees south off Western Australia, corals are occasionally abundant on older, non-reefal rocks. Corals form a veneer of newer limestone but do not build reefs, likely due to cooler temperatures, slower growth rates, and proximity to land from which there is run-off. This small "reef" is Hall Reef, near Fremantle.



ABOVE | At the northern end of the Ningaloo reef in western Australia, corals can be abundant, but they grow mainly on much older reef that grew millennia ago.

LEFT | Around the Daymaniyat Islands in Oman are massive accumulations of the branching coral *Pocillopora*. However, they remain loosely attached to the older substrate and have not developed substantive reef.

DEEP- AND COLD-WATER CORALS

Although corals are usually associated with reefs, about half or more of the known coral species are found in deeper water below around 195 ft (60 m), mostly between about 650 ft (200 m) to over ⅔ mile (1 km) deep. At these depths, temperatures are cold, from about 40 °F (4 °C) to no more than perhaps 50–54 °F (10–12 °C). Associated with these corals are many other relatives of corals, including black corals and gorgonians.

Most are small but some form huge aggregations, which are found when trawlers fishing in ever-deeper waters started to bring up large tangles of corals, even losing their nets when they became snagged in these large accretions. Later, oil prospecting in even deeper water added to the discovery of deeper and larger patches of deep-water corals.

Several species, most notably the coral *Lophelia pertusa*, are branching, and over thousands of years these and others have slowly formed enormous mounds, termed "reefs" by some. They are not wave resistant and would quickly disappear if exposed to wave action. These coral mounds are found all around the world. They are shaped by ocean currents on the seabed which bring them particulate food; the corals live in cold, dark water where no photosynthesis can take place and so these species do not contain the symbiotic algae that shallow water corals have,

and they grow slowly. Their branching structures trap sediment, so that over thousands of years they build upward, at 1 mm per year. The largest reefs known so far are off Norway and north of the United Kingdom; they are about 115 ft (35 m) high, and extend over a few tens of square kilometers.

These deep, dark reefs are rich in marine life, most being filter feeders, dependent on plankton brought to them by the deep currents. The diversity and concentration of life found in these reefs, such as bryozoans, sponges, and other hydrozoans, is several times greater than on the muddy seabed surrounding these deep reefs.

The reefs have been listed by various bodies as being in need of protection, and many are now endangered. Trawling is fairly indiscriminate and threats from trawls remain severe. Deep-water trawls in particular are very heavy, and easily crush and destroy the reefs when they pass over them while targeting various fish species. Some areas have now fortunately been closed to bottom trawling.

OPPOSITE | Cold-water coral reef framework at 2,000 ft (600 m) depth made by *Lophelia pertusa* on the Logachev cold-water coral carbonate mounds on Rockall Bank (Northeast Atlantic). The fish is a Greater Forkbeard (*Phycis blennoides*).

BELOW | Close-up of a *Lophelia* colony.

ANCIENT REEF BUILDERS

Corals are not the only organisms to have constructed "reefs" over geological time. Completely different groups of animals, microbes, and plants have shared an ability to extract calcium carbonate from seawater and deposit it beneath or around them to build their own foundations. Most of these groups are now long extinct, though some still exist in amounts far too small to form significant reefs. Sometimes the limestone they deposited was in the form of aragonite, like with present corals, or as calcite or another form called high-magnesium calcite.

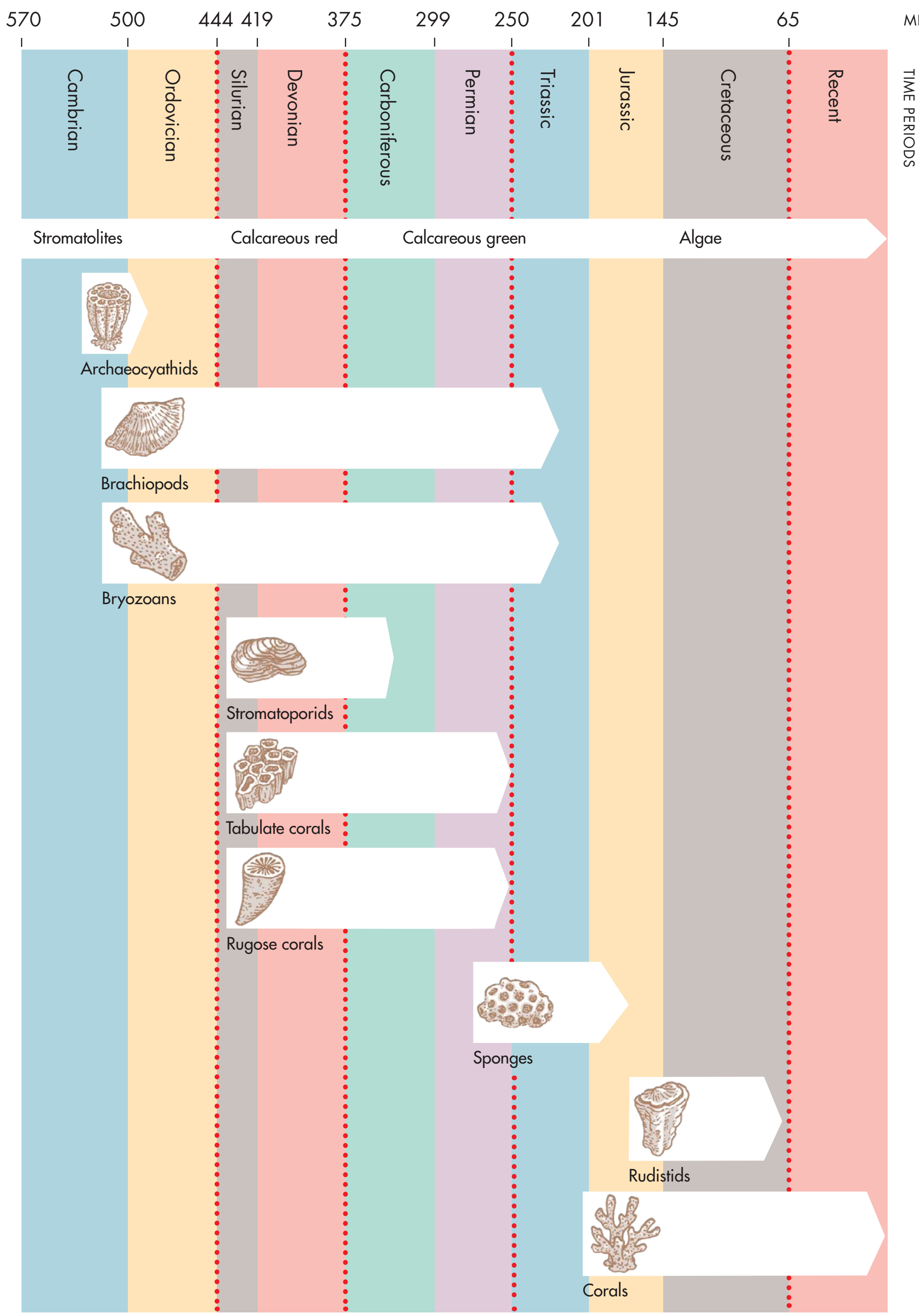
Stromatolites, assemblages of algae and bacteria, are the first known, and these formed abundant reefs in Precambrian times over 550 million years ago. In a much reduced form, stromatolites still exist in parts of the Caribbean and especially in Shark Bay, Western Australia, where salinities and water temperatures are high enough to prevent significant numbers of grazing organisms from entering the bays. Later, in Cambrian times, some forms of stony algae built reefs, as they do today along the most wave-exposed coral reefs.

Later in the Cambrian, sponge-like archaeocyathids formed reefs for tens of millions of years before going extinct. Next were shelled animals called brachiopods, hinged bivalve animals resembling today's mollusks to some extent, and some descendants of these shelled animals still exist today, in much reduced numbers.

During the following Ordovician to the Permian period, reefs were made by bryozoans, primitive animals that are still fairly common today, as well as sponge-like stromatopods, sponges, and two kinds of corals, the tabulate and rugose corals. These two corals were cnidarians, but with significant differences from corals of today. Most of these species disappeared at the great extinction at the end of the Permian period. Later, large shelled animals called rudists formed reefs and then became extinct, and finally today's stony corals came to dominate shallow tropical seas.

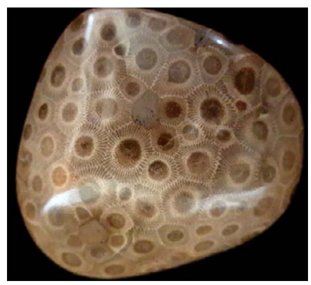
The remains of all these organisms can often be seen on land today, commonly far inland where some form cliffs and low hills. Each kind was associated with a high diversity of other forms of life. The causes of their extinctions may have included a meteorite impact in one case and massive volcanism in others, and were accompanied by raised acidity of the seawater which inhibited reef development for one or several million years. This is a subject now researched intensively in today's environment of human-caused acidification of the oceans.

RIGHT | Modern-day stromatolites at Hamelin Pool, in Shark Bay, Western Australia. The living parts are made from a complex mixture of algae, cyanophytes (a primitive kind of life), and bacteria.



LEFT | The different groups of principal reef builders over time. The vertical dotted red lines show the four largest global extinctions that have removed very high proportions of life in the oceans.

BELOW | Polished rugose coral *Hexagonaria percarinata* from the Devonian period. This lineage became extinct at the end of the Permian. It is the state stone of Michigan, USA, where it is also called a Petoskey stone.



CHAPTER 3

HOW A CORAL REEF WORKS

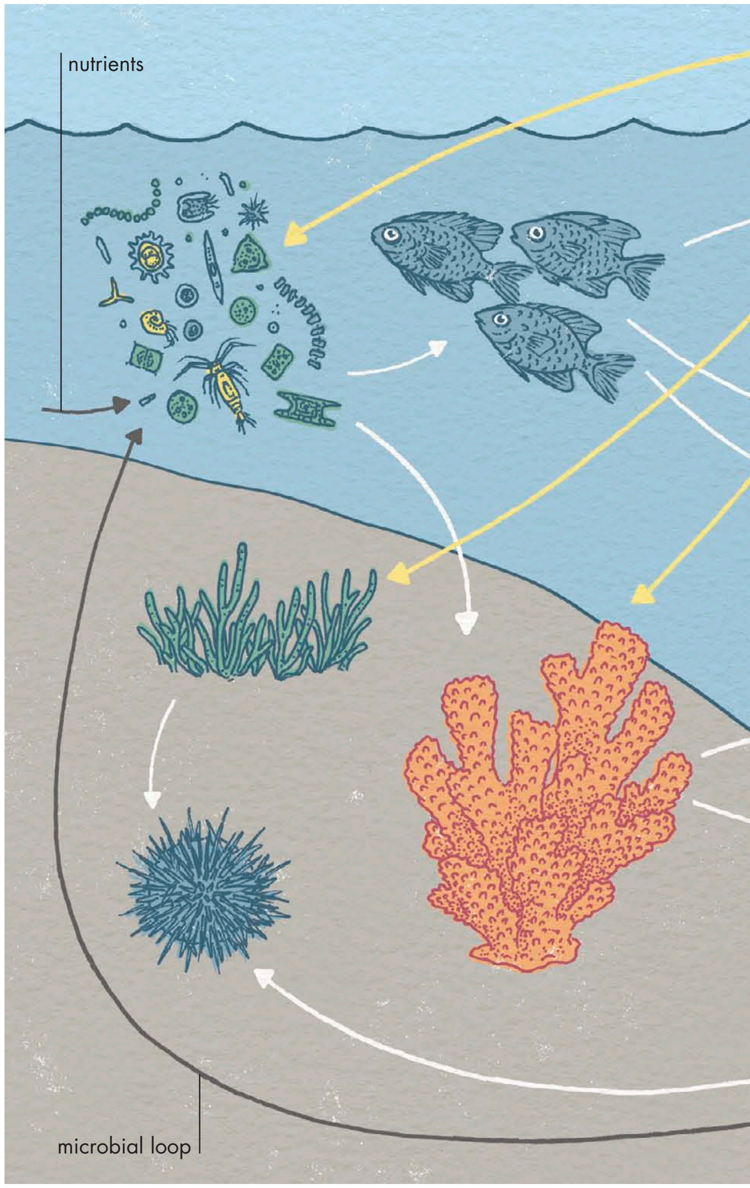
THE INTEGRATED REEF SYSTEM

On and around a reef is the richest assemblage of species found in the sea. In this chapter, key examples are shown of how the whole reef works in an integrated way.

A reef is a mixture of biological and physical integration, making a complex three-dimensional habitat that is likened to a forest that attracts other species, which is why reefs are so rich in life. Predators use this to lie in wait and ambush prey; many more organisms use it for shelter. Some strange associations have evolved in which species share food or space with quite unrelated species. These associations are often symbiotic, meaning both parties gain benefit from the relationship. When the benefit is one way and also harmful to the other then it becomes parasitism. A fundamental character of a reef ecosystem is the high incidence of symbiosis and other close associations between species—reefs are like ecological machines with many closely interlocking parts.

Many fish above the reef are carnivorous, so, unsurprisingly, many other species spend most of their lives hidden or near a refuge provided by corals, benefiting from the reef's three-dimensional structure. Most branching corals are home to schools of tiny, brightly colored fish which withdraw into safety as soon as larger fish approach.

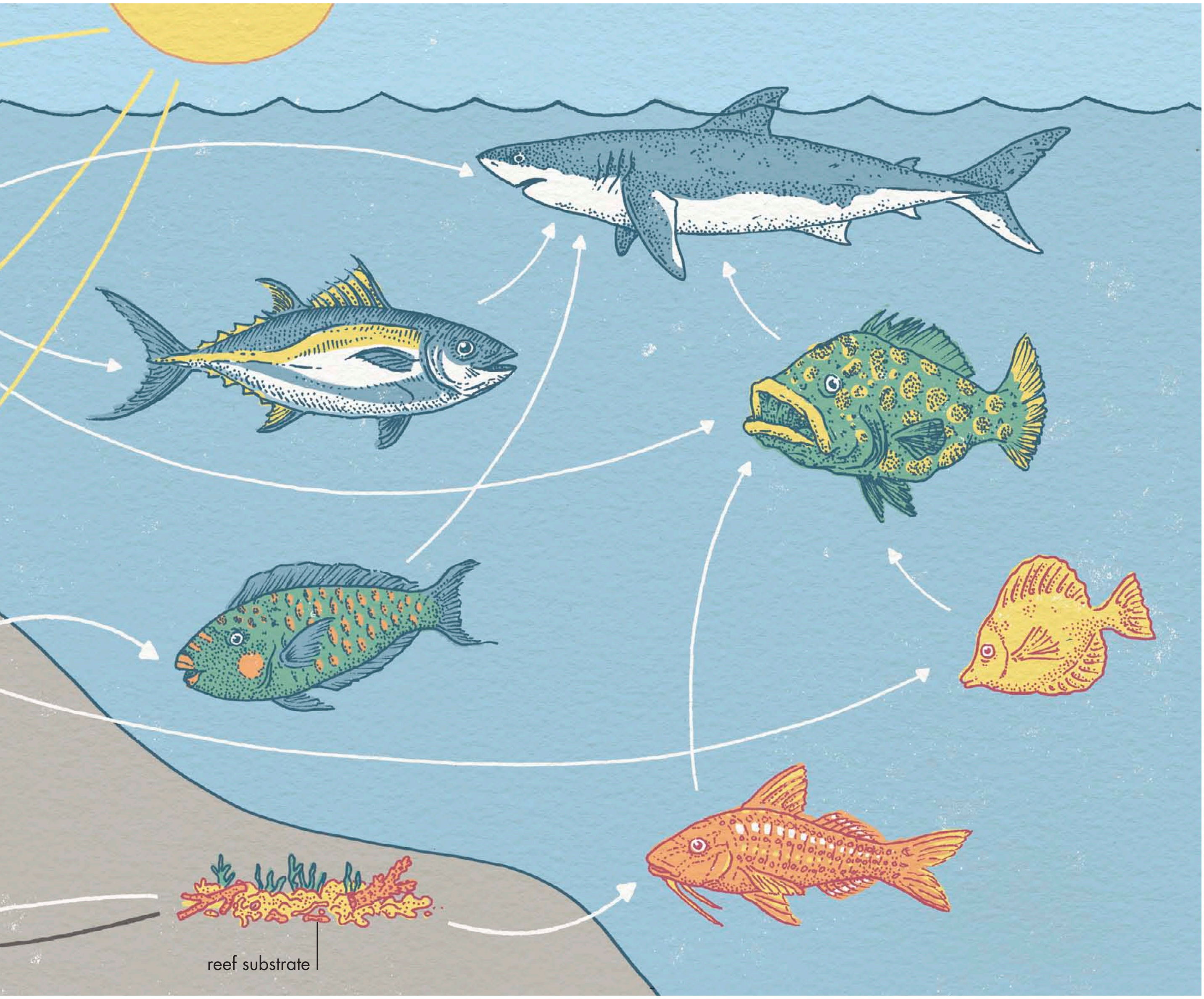
One important aspect of a coral is that it dies and its skeleton is reduced to sand, which later becomes consolidated to produce the reefs of the future. Reef sand and rubble are created by boring and tunneling animals and plants, storms, and grazing animals that scrape their seaweed food from the reef surface. Their rasping creates bare areas for future coral settlement and growth, in an eternal cycle.



Much debate once circled around whether reefs are fragile or robust, but the answer is both, under different conditions. Elimination of one species may be critically important if there are no others to adequately fill the role it once played, while loss of another may have little impact when others fill its ecological role right away.

When a reef is destroyed, as is now happening in much of the world, the loss of this structure causes the loss of biological richness; and the loss of the richness from pollution or from overfishing one or more of its species can lead to a disruption of the pattern in a vicious cycle. Unfortunately, many of today's impacts are overwhelming reefs.

THE MAIN PATHS OF ENERGY AND FOOD FLOW AROUND A REEF



ABOVE | The main, simplified, components of a coral reef. Yellow arrows show sunlight providing energy for plankton, corals, and algae; white arrows represent food and nutrient flows; black arrows indicate the nutrient inputs and "microbial loop" (the conversion of breakdown products back to nutrients and plankton). The "reef substrate" is composed of the algae and corals, plus numerous other components such as detritus and other microbial life.

ZOOPLANKTON FOOD

Polyps of reef-building corals and soft corals feed on zooplankton—tiny, microscopic animals in the water. Some zooplankton are permanently planktonic while others are temporary, larval stages of other animals. Corals will also ingest symbiotic zooxanthellae, which are plant plankton (phytoplankton), when they need to, but they do not feed on them. Corals themselves have a temporary planktonic larval stage so are part of the plankton at this stage of their lives.

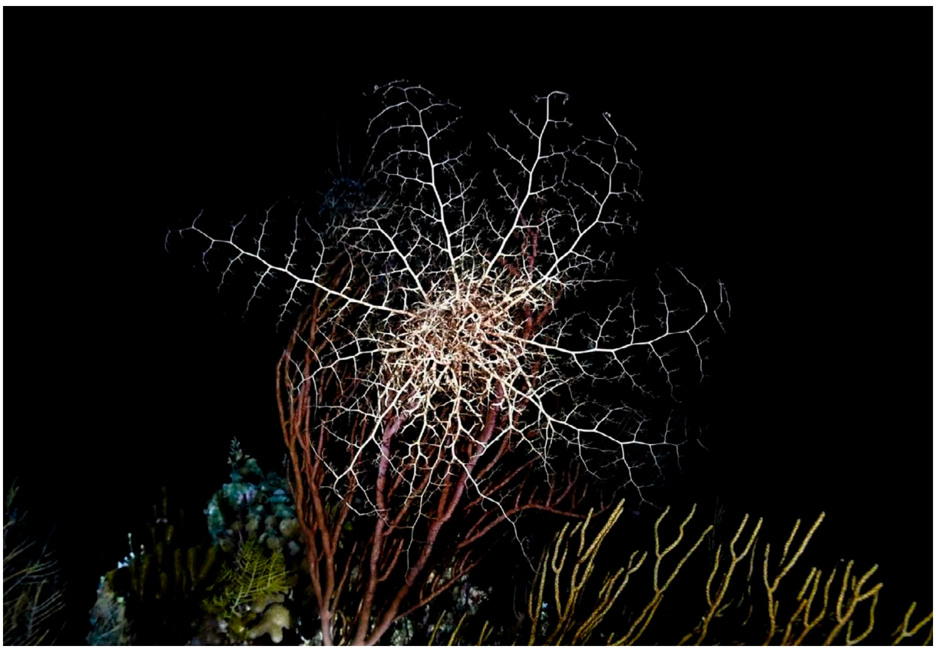
A major group of the permanent plankton are demersal and have a daily rhythm of activity, living in the substrate during the day among the grains of coarse sand and rubble, rising to the surface layers of the water at dusk, and settling down again near dawn. They are usually mysids (small, shrimp-like animals), very small nematode and polychaete worms, and a wide range of tiny crustaceans. Though small, they are among the largest zooplankton, and are an important source of food for both corals and fish.

The densities of demersal zooplankton can be substantial, with many thousands in each square meter of rubble at the foot of a reef. A large proportion of the life attached to the reef is dependent on them for food. Many animals, such as crinoids and basket stars, emerge and unfurl long arms from within reef crevices only at dusk to feed on them. Most corals also extend their tentacles only when dusk comes. The emergence of the zooplankton to rise in the water is very precisely timed. In the Red Sea, they emerge at sunset to within four minutes, and return 82 minutes (plus or minus five minutes) before sunrise. It is assumed that this swamps the predators, as well as avoiding any conditions of lower oxygen in the bottom of the water during the night. When they emerge and rise to the surface layers they have to run a gauntlet of stinging tentacles from corals and the waving branches of crinoids and basket stars, repeating this in the morning when they settle back down.

The zooplankton are attracted to light from a flashlight, and if one is placed next to a coral, the attracted plankton touches a tentacle and their paralysis or death is almost instant, showing the potency of the coral's nematocysts.

RIGHT | Not all tiny animals in coral tentacles are food. Some, like this shrimp, live commensally in the tentacles of corals.

FAR RIGHT | A tiny crustacean, one of billions that form part of the zooplankton, and a rich source of food for corals and their relatives.



ABOVE | A featherstar (in the class Crinoidea) in the phylum echinoderms. The feathery arms trap zooplankton and pass it to the upward-facing mouth. The "legs" attaching it to a coral are cirri. Most species can swim short distances.

LEFT | Another echinoderm, with more complex arms, is the basketstar. Many only come out at night. This deep-water species has slender, branched arms to trap zooplankton.

STONY ALGAE, AND SPURS AND GROOVES

In the shallowest part of many reefs that are exposed to strong wave action and storms, there is commonly a pinkish ridge along the edge of the reef flat, where the waves break. This is the part of any reef that receives the greatest wave energy. The force from huge waves that have traveled oceanic distances, commonly driven by storms, has enormous energy: a 6 ft (2 m) high wave expends tens of kilowatts of energy along each kilometer of reef edge.

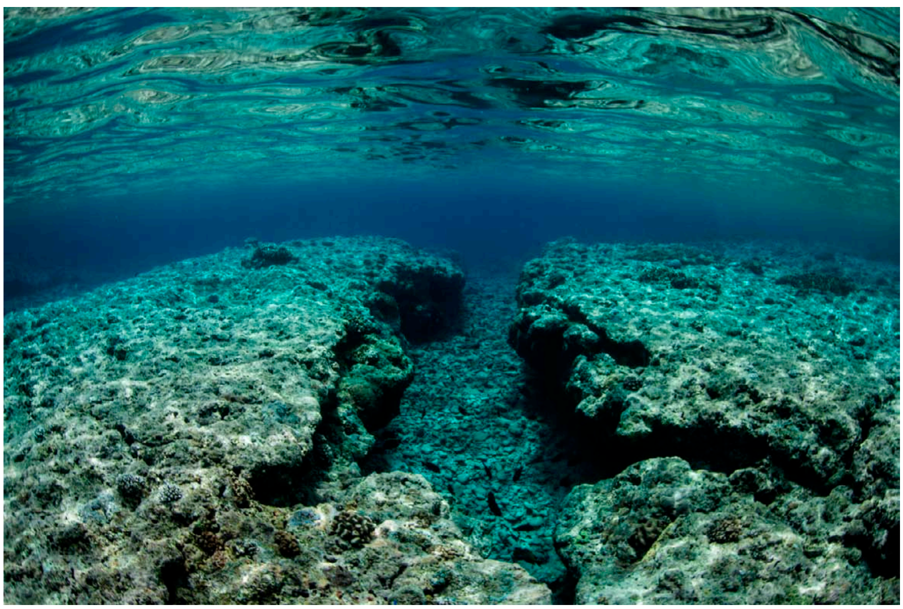
Few kinds of life can live along this turbulent stretch. One that does is a group of stony red algae, commonly called crustose coralline algae. These pink algae deposit strong limestone, usually with a high magnesium content. The reef crest of oceanic atolls can be almost entirely made of them.

The crustose coralline algae not only tolerate high energy but seem to require it to thrive. They may form a ridge—the "algal ridge"—along the outer reef edge, which grows to about 20 in (50 cm) above the height of the reef flat. They also grow seaward from the ridge in a series of spurs, each spur progressing down the reef slope to a depth of a few meters, where it tails off.

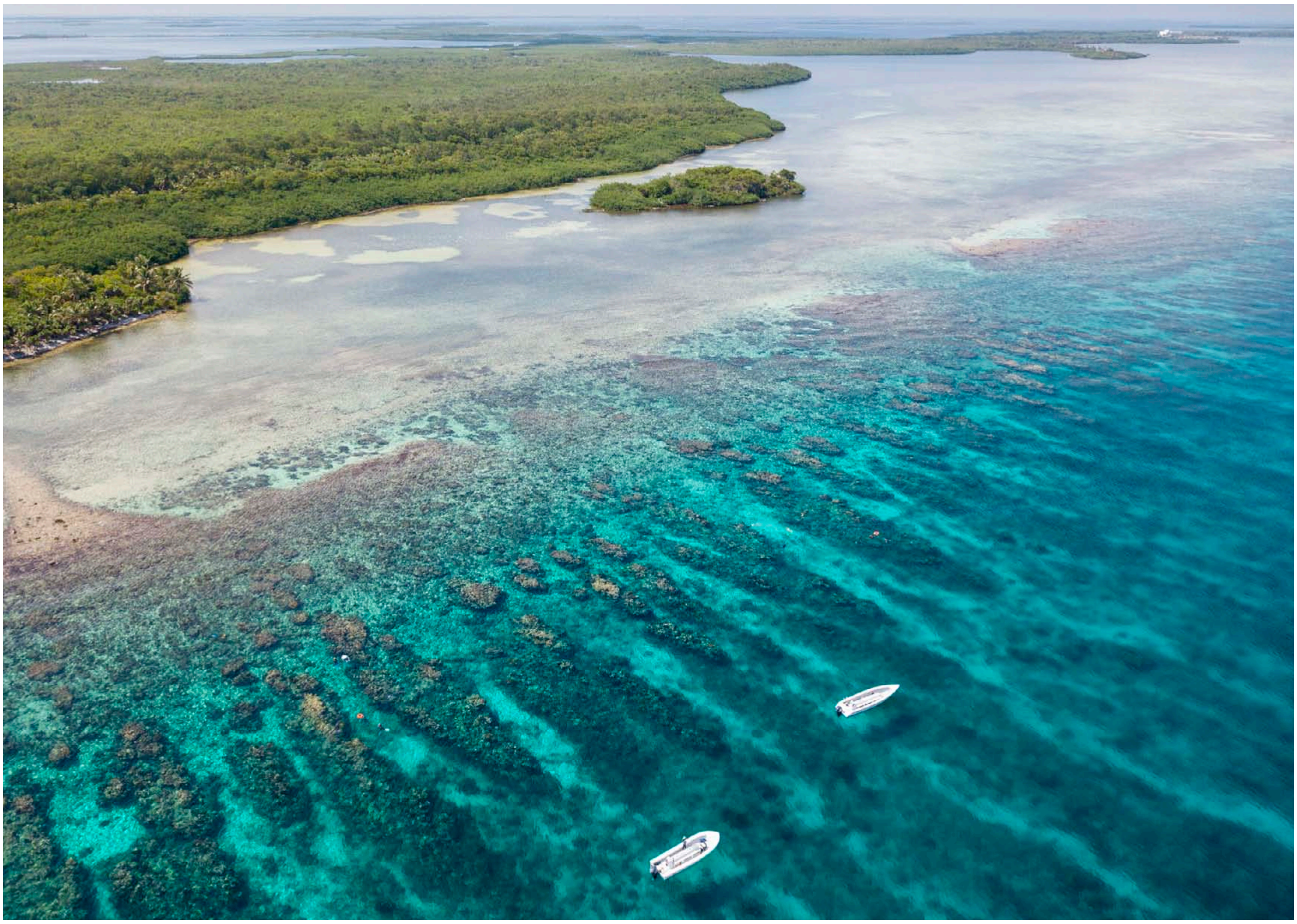
The grooves that separate the spurs have a remarkably uniform spacing on any one reef. The higher the wave energy that the reef experiences, the larger the algal ridges and spurs, the wider the spacing between spurs, and the deeper they extend. Their spacing reflects a complicated harmonic of the average wavelength of the incoming waves.

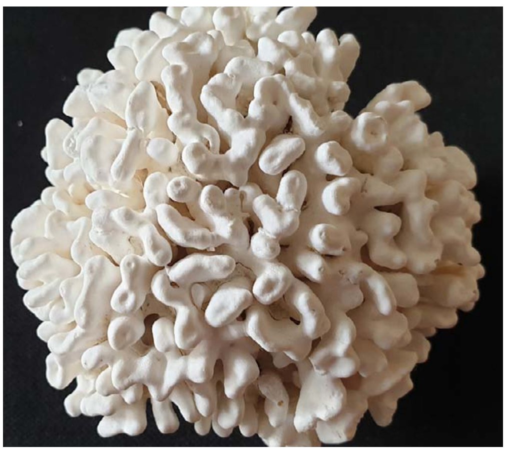
In this remarkable arrangement, each new, surging incoming wave meets and is partly cancelled out by the retreating backwash of the previous wave as it flows off the reef and out to sea, in a way that greatly reduces the overall energy remaining to strike the shore. This is most clearly seen where the clash of opposing water bodies meet in the grooves.

There are a few genera of algae that form spurs and grooves, *Lithophyllum* and *Porolithon* being two common ones. Part of both names—"litho"—appropriately means "stone." They grow slowly, mostly in nodules. It is these that are to a great extent the reason why coral reefs can survive at all, and indeed thrive, in the most turbulent areas.



RIGHT | A reef experiencing less severe exposure has smaller spurs, sometimes arranged in a less ordered pattern. At almost any site, they can reduce the wave energy that strikes the shore by as much as 50 percent.





ABOVE | Large spur system extending seaward from an algal ridge. The breaking waves at the edge of the reef are met with the backwash from the last wave, greatly reducing the energy that will reach the shore. The algal ridge and spurs are made of stony red algae and support few corals.

LEFT | The calcareous red algae, here cleaned and bleached, grow mainly in nodules at their surfaces, though underneath these are layers of limestone that some have determined to be stronger than concrete.

CORAL REEF SPONGES

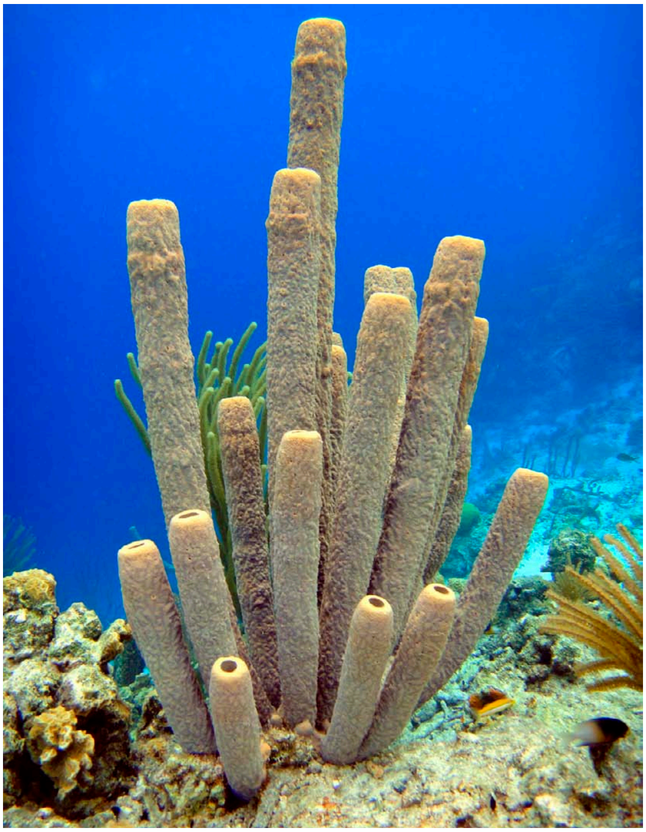
Sponges occur on every coral reef and can be especially dominant in the Caribbean. They are the most primitive of all multicellular animals, and they formed entire reefs long before corals evolved. They are enormously varied in shape and size. In the Caribbean, especially, some form huge vases, while others form tangles of rope-like colonies, or consist of series of pipes of many colors, outnumbering corals in terms of both abundance and the area of reef they occupy. Some species are just a few millimeters across, while others are over 3 ft (1 m).

There are two main groups of sponges, with either tiny calcareous or siliceous skeletal elements in their "body." Most sponges, if not all, house vast numbers of symbiotic bacteria, involved, for example, in the nitrogen, phosphate, and carbon cycling of the sponge, and even with photosynthesis. Sponges have no true organs or tissues, and indeed several species can be passed through a sieve with each tiny fragment then capable of growing into a new, entire colony.

Sponges are important biologically on reefs as filter feeders. Their surface is covered with numerous small inhalant pores and a much smaller number of larger exhalant pores. Water is pumped through their bodies by special cells with beating cilia that line their networks of canals, while other cells filter out food particles in the water. Much of a sponge's diet consists of very small plankton and bacteria, and so efficient are they at water filtration that some species can remove most of the particulate matter in the water column above them every day. Diverse sponge communities filter the entire water column above them every day. This is a key feature, because it connects life in the water column (pelagic life) with that on the seabed (benthic life), thus ultimately capturing and channeling particulate nutrients to higher organisms further up the food chain.

BELOW LEFT | Sponges typically have many tiny inhalant pores and one or more larger exhalant pores. A network of tunnels passes from the inhalant to the exhalant pores, lined with cells that extract oxygen and plankton for food.

BELOW | Hawksbill turtles are voracious sponge feeders. Their diet includes sponges that burrow and tunnel into coral rock.



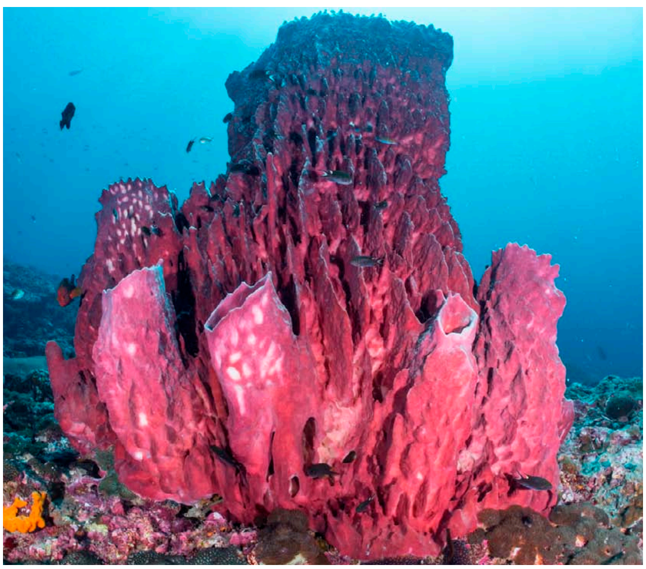
Sponges play key geological roles too. Several are major bioeroders of coral rock (see page 126), and these bore into reef limestone using chemicals produced by specialized cells. Skeletons of dead corals can be reduced to rubble, sand, and clay-sized particles within weeks. Some encrusting sponges, in contrast, grow over and immobilize sediment in crevices, which slowly transforms into solid reef rock.

Various nudibranch mollusks feed on sponges, as do some crustaceans and even fish. The Hawksbill Turtle is a conspicuous predator, and a large sponge may be seen to be covered with Hawksbill bite marks.

LEFT | A colony of Caribbean sponge, whose exhalant pores are located at the ends of each tube. The relatively tiny inhalant pores are located along each tube.

BELOW LEFT | The huge sponge *Xestospongia* can reach the size of a barrel. Usually seen as a large single cylinder, this one has numerous smaller ones developing from the same stem. Different species are found across the Caribbean, Indian, and Pacific oceans.

BELOW | One of the Caribbean "rope sponges" (*Aplysina*) forming a tangle of tubes. Each "rope" contains numerous inhalant pores near each exhalant pore.



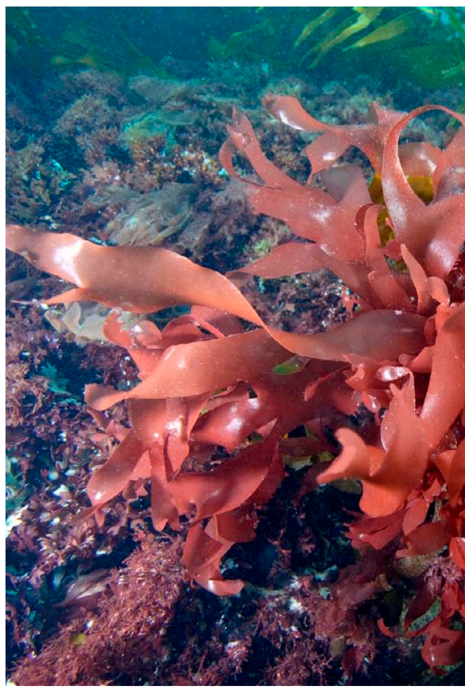
SEAWEEDS ON REEFS

Seaweed, or algae, is the term used for a varied collection of photosynthetic marine organisms, including those found on reefs. There are three major groups: red algae, which are the most diverse, followed by green algae and brown algae. Other groups exist, mostly minute, but the reds, greens, and browns are the seaweeds seen on a reef. All photosynthesize, but all lack many structures that are found in higher plants, such as systems needed to transport water from roots to leaves. In fact, algae do not have roots but rather have root-shaped "holdfasts" that attach the plant to rock.

These three kinds of algae do not have a common ancestor, and indeed it has been said that red algae are more distantly related to green algae than green algae are to mammals! Land plants evolved from green algae.

On a healthy reef, large algae are mostly absent. Algae are cropped heavily by grazing fish and urchins, and are visible mainly as algal turf, a fine fuzz carpeting the rock between corals and sponges. If a patch of turf is covered by a cage that keeps out grazers, within a couple of weeks the seaweed growth all but fills the cage, testament to the amount of grazing pressure and rapid turnover that exists. There are exceptions, however: in areas such as the Arabian Gulf and southern Red Sea there are extensive beds of large brown algae which are relatively indigestible to fish.

There are two additional important groups. One is the crustose coralline algae (see page 102). The other includes stony green algae of the genus *Halimeda*. Each *Halimeda* produces chains of small disks, which are mostly limestone. Each chain can extend by a stony disk every day, so around and beneath patches of this plant, huge mounds of dead *Halimeda* disks can accumulate. Enormous mounds of these are found in and behind the Great Barrier Reef, and the Bahamas Banks have been constructed mostly from *Halimeda* rather than from coral sand. They are enormously important.

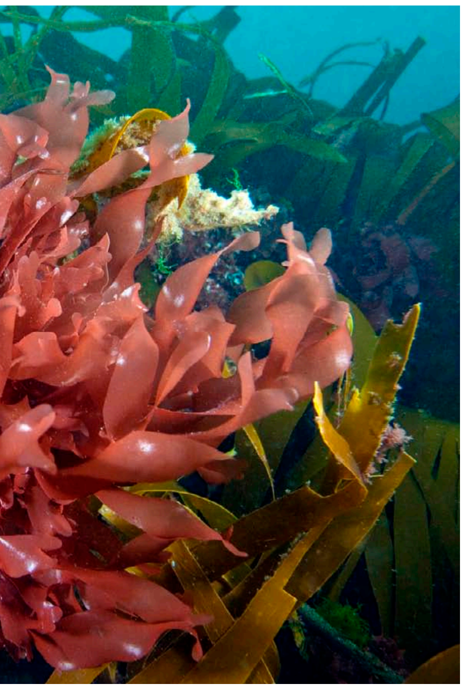


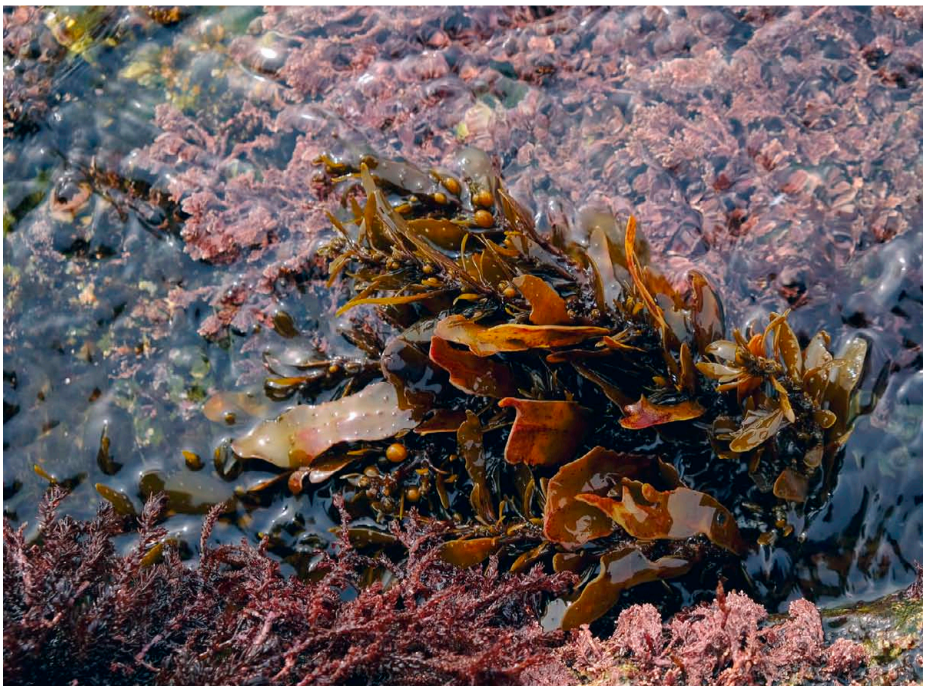
However, although diverse, large seaweeds are usually conspicuous only on disturbed reefs. Green algae especially multiply rapidly where there is nutrient pollution, and usually the presence of a lot of seaweed on a reef indicates pollution, removal of grazers, or other severe disturbances from which reefs find it difficult or impossible to recover.

BELOW LEFT | The calcareous green algae *Halimeda*. Each frond is mostly internal limestone, and can grow one new disk per day. Much of the sand in many reef areas is composed of the dead limestone disks.

BELOW CENTER | Red algae have an ancient lineage, with a rather different cell chemistry to all others. They are diverse, but most reef species are relatively small.

BELOW RIGHT | Brown algae are the third major group of large algae. Larger types mostly like temperate waters though some, like *Sargassum*, are found on reefs, where most examples of this group are fairly small.





REEF FISH

DIVERSITY AND ABUNDANCE OF REEF FISH

A kaleidoscope of thousands of colorful fish is probably the first thing that strikes any observer on a coral reef. Schools of jacks, fusiliers, and even barracuda swarm over it; schools of parrotfish and snappers, sometimes hundreds strong, graze, browse, and hunt over the surface of the coral; butterflyfish and angelfish dart in pairs; and close-up, myriads of small, colorful fish hover close to the surface and disappear into refuges or branching corals if they feel threatened. This riot of color and movement is overwhelming.

There are an estimated 6,000 to 8,000 coral reef fish species, about a tenth being in the Caribbean, with the remainder in the Indo-Pacific. Globally, diversity patterns are similar to those of corals, being highest in the Southeast Asian region. On any one reef or set of reefs, however, less diversity will be found: the Great Barrier Reef has a total of about 1,500 species and some remote atoll systems have far fewer. Some species occur over huge ranges, from Africa through the Asian archipelagos and most of the way across the Pacific, while others are much more restricted, perhaps to a few adjacent atolls. Like with corals, the diversity of reef fish diminishes in higher latitudes.

On a single reef, fish species are distributed according to the strength of the light, depth, and the strength of the wave

action, so that distinct zones appear, usually with the highest diversity in bright water on reef slopes. Some species live over a broad depth range while others are more specific in their requirements.

Fish are key to the working of a reef. By their predation, grazing, browsing, or scraping of rock with hardened mouthparts they keep down seaweed, which would otherwise outcompete coral, and recycle nutrients, all of which helps maintain the growth of the reef itself. The trophic level of fish (their position in the food chain) is important. For example, algae are at the bottom of the food chain (level 1); grazers of algae have a trophic level of 2; primary carnivores eat the grazers (level 3); and second-level carnivores eat the first-level carnivores (level 4); and so on. The trophic structure of fish tells us a lot about the reef. For example, on a fished coral reef, top predators are commonly the first group to disappear.

OPPOSITE AND BELOW | The tremendous variety of colors, shapes, and sizes of fish on coral reefs reflects, in part, their diversity and sometimes their range of food sources, which includes some highly specialized diets. Color can be used for camouflage, signaling, and warnings. Reefs offer a large variety of niches and shelter, providing a range of habitats for different types of fish with varying lifestyles.

FEEDING METHODS OF REEF FISH

Fish are vital to the working of coral reefs because they ensure that both energy and biomass are transferred through the system in a balanced manner. From the grazers at the start of the food chain to the carnivores and higher carnivores, there are numerous feeding modes and specialized shapes of fish, especially of their mouthparts, to enable their many and varied methods of feeding.

Always abundant on a reef are the algal turfs (see page 106). These turfs trap organic material from bacteria, minute animals, plankton, and detritus such as fish feces, which together can contribute more organic matter than the algae themselves. Fish that feed over turf might be either herbivores or detritivores, the latter focusing on the energy-rich detritus, some using comb-like mouthparts to extract it.

Herbivores are one of the most abundant groups, especially in shallow water where light is bright so plants grow fast. Different species crop algae, scrape it off rocks, or even excavate the rock. Some leave a fragment from which more algae can grow, while others remove it completely. Many parrotfish excavate quite deeply using their strong beaks, and some individuals of larger species can grind up one ton of limestone each year, which they then defecate as sand, making this a major source of sand on a reef (see page 124).

Many fish low in the food chain feed on plankton, including both phytoplankton and zooplankton. These include small fish, the "plankton pickers," and some of the largest fish, such as Whale Sharks. The larger species can feed during the day, but many smaller species feed only at night to avoid predation. Other species are corallivores (coral feeders), about half of which are butterflyfish. Some eat only coral, sometimes specializing in just one or two species, while others may feed on other invertebrates too. Invertebrate feeders either forage over patches of sand, which they excavate for worms or mollusks, or hunt over coral rock.

Finally, at the top of the food chain are the piscivores, which consume other fish. They may feed on fish from any other trophic group, including other carnivores, so here the food web becomes complex. Some will actively hunt, singly or in schools, or they may be ambush predators that sit and wait before pouncing. Others may stalk their prey.

Many fish species cannot be exclusively placed in any one of these categories as they have a wide diet.

ABOVE | The large manta rays have enormous mouths, designed to scoop in huge quantities of water as they swim along, from which they sieve planktonic food. Several different species are found on coral reefs.

TOP RIGHT | Paddle-tail snappers (*Lutjanus gibbus*) occur in schools of several hundred or more. They are mainly carnivores, feeding on invertebrates on the reef.

RIGHT | Barracuda are top carnivores, like sharks. Some are commonly solitary, though several swim in large schools.

FUNCTIONS AND DIVERSITY OF REEF FISH

Fish perform numerous different roles on a coral reef, which are key to the reef system remaining highly diverse and productive. For example, the cropping of algae that many herbivorous fish do is vital (see page 110); parrotfish are key to this. Different species of parrotfish live on and influence different parts of the reef.

Many connections are more complicated. In general, removal of a predator permits large increases in its prey. For example, many triggerfish feed on sea urchins, and if the triggerfish are removed by fishing pressure it will cause a "predator release" on the urchins, which can then explode in numbers. When this happens, their increased rasping increases reef erosion. Other triggerfish feed on the Crown of Thorns starfish, which is a major coral predator.

Different groups of herbivores, such as some rabbitfish and surgeonfish, feed on mature, large algae and are essential in reducing it when seaweeds are abundant. Generally, overfishing of herbivores can shift entire reefs toward alternative states dominated by seaweeds. Conversely, if too many carnivorous fish are removed then herbivores increase, leading to too much cropping and erosion.

Several butterflyfish and others are specialist coral feeders. They have elongated mouths that enable them to crop single polyps one at a time. Some rabbitfish have elongated mouths that allow them to feed on seaweed in crevices where others cannot reach. Other species require sheltered water to feed, whereas the better swimmers can feed where currents are stronger.

The total suite of species, from predators that hunt to those that sift minute food from sediments, maintains reef diversity. Most species may be fairly redundant, in that when removed, other species take their place, but others, such as Caribbean parrotfish, have no apparent replacement.

Today, with so much damage to reefs from overfishing and pollution, all these many different kinds of fish are needed if the reef is to recover. Where functions are performed by a single species, the reef will be more vulnerable to degradation, so in general, maintaining the high diversity on a reef is essential for its continued existence or recovery after damage. With warming that kills corals there is an accompanying loss of fish habitat, which leads to undesirable feedbacks for those fish.

BELOW LEFT | Many parrotfish scrape the surface of corals and rock to get at the algae, leaving scars. They ingest particles of rock and defecate these as clean sand.

BELOW | Surgeonfish are mainly herbivorous but will eat animal protein in aquaria, where they are a popular choice for tanks.

RIGHT | The butterflyfish *Chaetodon semilarvatus* is found on reefs in the western part of the Indian Ocean. It eats invertebrates, including corals.

REEF FISH

FISH COLORS AND CAMOUFLAGE

Many coral reef fish are very brightly colored, more so than fish in cold-water communities, so it can be assumed that this has some advantage to them. Many species can see in color, and this often provides a direct signal to, for example, potential mates. As the water becomes deeper colors with longer wavelengths, particularly red and orange, disappear, which might lead to some of the depth zoning seen with different fish species. Several fish have eyes with different kinds of photoreceptors from humans and can see ultraviolet as well; some can also reflect ultraviolet, so may appear bright in this color.

Some species have entirely different patterns when they are juvenile, so can sometimes be mistaken as different species. Others, such as parrotfish, can change sex, and become more brightly colored as they do so. The use of patterning to confuse predators is common, and many fish use disruptive patterns including bold spots or bands, or even eye-shaped patterns near their tails. These make the fish look larger than it really is and suggest it is facing in the opposite direction, to provide a false target and an increased possibility of escaping.

Many species that are poisonous to eat are brightly colored to serve as a warning. This is widespread among invertebrates, too. Other fish are mimics so that, while they themselves are not poisonous, they evidently fool the predator into thinking they are so are similarly avoided. Venomous fish are also commonly highly colored, with lionfish being the best example (see page 160). These are hunters and presumably their colors deter larger predators from eating them. Other highly venomous fish like stonefish and scorpionfish are, in contrast, very well camouflaged and lie in ambush, well concealed on the seabed. Stonefish are the world's most venomous fish and their mottled coloration is particularly effective, added to which algae grows on their skin to increase their disguise.

Yet other species use bright and varied patterning to conceal themselves among the colorful backgrounds of the reef, which confuses predators. Several change their coloration to match different backgrounds, both as a disguise from predators and to aid their own concealment when they are hunting or stalking prey. Flatfish are particularly adept at this and can take up a coloration and patterning remarkably similar to the sand or rubble on which they are lying.

LEFT | Trumpetfish are ambush predators that hover almost motionless and creep toward their prey. They can conceal themselves in branches of soft corals.

BELOW LEFT | The broadhead flathead lives on sediments and gravel areas of reefs. Usually solitary, it lives partially buried for concealment and takes on the color of its background. It feeds at night on invertebrates and fish.

BELOW CENTER | The stonefish is conidered the world's most venomous fish. It is highly camouflaged against rock and moves by "walking" across the bottom.

BELOW RIGHT | A frogfish of the genus *Antennarius*. Frogfish, camouflaged to resemble sponges, sit on the bottom where they are ambush predators.

LEFT | Frogfish are well camouflaged to blend into their background. Their skin can take on lumpy, warty projections and even algae.

RIGHT | Porcupinefishes, like pufferfishes, can inflate their bodies to many times their usual size, in order to deter predators. They do this by drawing in water. The inflation also makes their spines protrude a little more.

REEF FISH
SHARKS AND RAYS

Sharks and rays have an ancient ancestry, dating back 450 million years. The earliest sharks, perhaps surprisingly, probably had no teeth! The characteristic of this group is that their skeletons are cartilaginous, not bony. Shark teeth are composed of hard dentine, and the oldest teeth from shark ancestors are about 410 million years old. The first predators that we would today recognize as being sharks developed shortly after that and were sleek with forked tails, suggesting they were active hunters. Sharks developed flexible jaws, allowing them to eat large prey, and they grow new teeth continuously to replace older ones, shedding and growing around 30,000 teeth over a lifetime.

Rays are a lineage that became flattened over time with their left and right sides symmetrical; this differs from bony flatfish, which are best viewed as lying on their sides with one eye migrated around to the top.

There are numerous shapes, sizes, and feeding behaviors in sharks and rays. Hammerheads have electroreceptors on their strange-shaped heads to help them detect prey. The giant Whale Sharks are the largest living fish, and they swim with their jaws open to scoop in vast quantities of zooplankton, like baleen whales. Angel sharks have the appearance of being a ray in front but with a shark-like rear half. Most rays have slender tails and hunt for food along the bottom and in sand, though the largest, the mantas, feed on plankton. However, the best known among the sharks and rays on reefs are the sleek predators. These are usually solitary, though they sometimes congregate in groups for breeding, and many species are territorial.

Unlike bony fish, sharks mate with internal fertilization, producing fewer but larger young. Some species lay large eggs, but in most, eggs develop and hatch inside the mother, so the young are born alive and fully functional. Young sharks are vulnerable to predation by large fish and other sharks, so are often found among mangrove roots in estuaries where they can find shelter.

On a completely unfished reef, dozens of sharks may be seen on one dive and, being voracious carnivores, they are key top predators. However, millions are caught by humans every year so many places are now denuded of them, unbalancing the trophic structure of the reef. The trade in sharks is extremely wasteful: shark fin is valued in Asia, and the large manta rays are also now killed in huge numbers for their gill rakers, which are used in some folk medicines. The rest of these large fish is simply discarded.

ABOVE | Gray reef sharks (*Carcharhinus amblyrhynchos*) commonly occur in small schools in shallow reef areas, where they may be the most common species of shark found. They are important top predators and are generally less than 6 feet (2 m) long.

TOP RIGHT | Eagle rays commonly swim in schools, though they feed on mollusks and crustaceans on the reef. They give birth to live young.

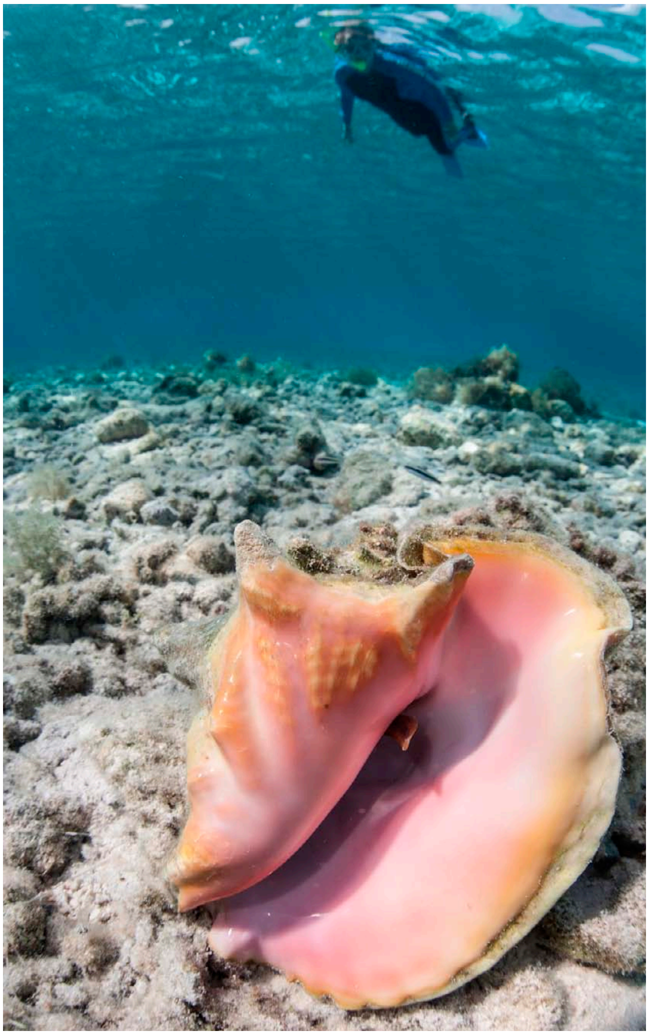
BOTTOM RIGHT | Both blacktip and whitetip sharks are common on coral reefs. They are named for the color of the tip of their dorsal fin.

COMPETITION ON REEFS: THE RED QUEEN HYPOTHESIS

The Red Queen said to Alice (in *Through the Looking-Glass*): "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!" The so-called Red Queen hypothesis is all-pervasive in any branch of ecology. Take a simple example of predator and prey: to try and avoid being eaten, the prey species evolves through natural selection to develop a thicker and harder shell. Its predator, meanwhile, if it is going to survive, develops stronger and stronger jaws capable of crushing the shell to obtain its food. Species that survive the longest are those most capable of responding to changes in the environment, in particular pressures from other species.

All organisms are subject to this pressure. From camouflage and the ability to see through it, to the speed of hunting and avoiding becoming prey, or producing more eggs to outcompete a rival species, all evolve characteristics that give them an edge over others. The results have led to the huge variety of life history traits and body forms seen in any ecosystem, not just coral reefs.

On reefs, fish show this in abundance. Long, thin needlefish hang upside down among coral branches; some fish can become almost indistinguishable from seaweed; and others are extraordinarily fast or agile. The highly venomous stonefish and scorpionfish have become extremely difficult to spot on a reef, while the equally venomous lionfish, in contrast, have moved toward being highly conspicuous, and so avoided by predators. Several species have evolved to look much larger than they really are, with a very large and striking eye-like spot near their tail, to deter a predator. On the predator side, many hunters merely lie motionless in wait, so that when a prey species



passes close by, they suddenly open their large mouth to create a water vortex that sucks the prey into the mouth.

Development of armor has commonly increased to apparently absurd scales. Crustaceans have external skeletons anyway, and these have increased and hardened in several crabs and other groups. Many mollusks have developed very thick shells, necessary to deter predators even though they take considerable energy to create. Many, though, are still vulnerable to some starfish that can pull bivalve shells apart using large and sustained force.

As a prey species develops a more extreme characteristic, so its predators evolve to overcome the defense. If either case is not good enough, the species will simply join the much greater number of species that have become extinct over time.

LEFT | Reef lobsters are large crustaceans that live in overhangs on the reef and in caves. They can be common but are commonly overfished. They have two long antennae and only small claws, unlike some cooler-water relatives.

ABOVE | The Caribbean conch is a widely sought-after food and has an extremely hard, thick shell.

ABOVE RIGHT | Razorfish, sometimes called shrimpfish, swim vertically in schools. They are commonly found suspended among the spines of the Long-spined Sea Urchin or branches of *Acropora* corals. They feed on tiny crustaceans, including those in plankton.

SYMBIOSES AND COMMENSALISM ON REEFS

Numerous symbioses exist on coral reefs, where two or more species live in very close association with each other. In addition to the coral–algal and sponge–bacteria ones (see pages 18 and 104), many examples exist between fish and invertebrates.

Many eel-like fish, including the small pearlfish, live inside echinoderms such as sea cucumbers, where they may feed on the host's tissues, making the relationship parasitic, or simply use the sea cucumber for shelter after feeding outside, in which case the relationship is more commensal —an association where one species benefits and the other neither benefits nor suffers. Many goby fish live in close association with shrimps in burrows, where the shrimp digs the communal home while the fish stands guard. Several gobies live on specific corals or sea fans, or even a particular color of coral species.

A well-known relationship between a fish and an invertebrate form of life is that between the colorful clownfish, also called anemonefish, with sea anemones (the anemones are themselves symbiotic with algae). Some clownfish live among the tentacles of all ten anemone species known to form this association, while others are specific to one anemone species. The fish receives protection by living among the stinging tentacles, while the host anemone is protected too when the fish deters predators. The fish also drops food and its feces onto the anemone, which enhances the sea anemone's growth as well as that of its symbiotic algae.

Many shrimps live on and among the tentacles of those coral species that have tentacles expanded in the daytime. In these cases, as with anemonefish, the animal does not trigger its host's stinging mechanism, perhaps using a chemical

recognition system. Anemonefish are commonly seen rubbing against the anemone's tentacles, perhaps using its mucus as a recognition signal.

Symbioses between fish include examples of cooperative hunting, as seen between eels and larger predatory fish where the eel flushes prey from small crevices to be killed by the larger fish. Another well-known example is that between cleaner fish and many other species which wait passively at cleaner stations to have parasites removed, including from inside their mouths. This, however, is exploited spectacularly by a mimic, the False Cleanerfish, which looks similar to the cleaner fish but which takes bites from the fish being cleaned. There can never be too many of these or the cleaner station system would collapse, so, like with most biological interactions, an equilibrium is achieved.

BELOW LEFT | Clownfish live in the protective tentacles of sea anemones, to their mutual benefit.

BELOW CENTER | Some species of shrimp and gobies live in the same burrow. The shrimp busily excavates while the fish stand guard to provide warnings.

BELOW RIGHT | Cleaner wrasse pick parasites off larger fish at cleaning stations.

KEY ORGANISMS THAT ERODE A REEF

From the moment a coral starts growing, it is bitten or scraped by several conspicuous groups of animals, including fish and urchins, which reduce its skeleton to sand.

The most important in this respect are several species of parrotfish, named because of their powerful beak-like mouths. Usually seen in schools, they will swarm over a reef, scraping the surface of corals in order to ingest the living coral and algae on them. They grind the material up and swallow it, their digestive systems extract the nourishment from the mix, and then the parrotfish defecates the remaining sand. It is common to observe several fish defecating clouds of sand in a school, and it has been estimated that parrotfish feces is one of the major producers of sand on coral reefs—and on beaches where people lie on vacation. One of the consequences of overfishing parrotfish, which is all too common an occurrence, is that algae grow more abundantly and outcompete the corals, the net result being a drop in reef growth, causing a shift in the reef's ecology.

Sea urchins are another crucial bioeroding group. Numerous urchins dig hollows in the soft coral rock in which to shelter during the daytime, to emerge at night to forage. They also scrape rock to feed, and in the Caribbean especially the Long-spined Sea Urchin (*Diadema antillarum*) has achieved a particular importance. A disease rapidly killed over 95 percent of this urchin on Caribbean reefs in 1983, which resulted in a great increase in abundance and cover of their algal diet. This widespread increase in algae inhibited coral settlement and growth, leading to further reef degradation. The 1980s also saw the demise of most of the large Elkhorn Coral (*Acropora palmata*), again from disease. The vast Elkhorn forests of the shallows turned to rubble, which led to marked reef and shoreline erosion.

Similarly to urchins, many species of gastropod mollusks are grazers, and their hard mouthparts are like rasps which scrape the reef surface as they feed.

These important organisms feed from above; the next section describes some that burrow into the rock. The two mechanisms, erosion from above and tunneling from below, act together to ensure that in some areas, reef loss can amount to several kilograms on every square meter per year.

RIGHT | Many urchins scrape algae off rock with their mouth parts, eroding the soft limestone rock at the same time.

LEFT | Scrape marks on a living coral show that a school of parrotfish has recently passed by. The scrape of limestone skeleton ingested by the fish along with the living surface material is needed to aid digestion, and is then excreted. A significant amount of the sand on reefs and beaches is made up of this excreted limestone.

BELOW | Parrotfish school swimming over a reef and feeding on it by scraping the surfaces of the corals to obtain food.

REEF BORERS

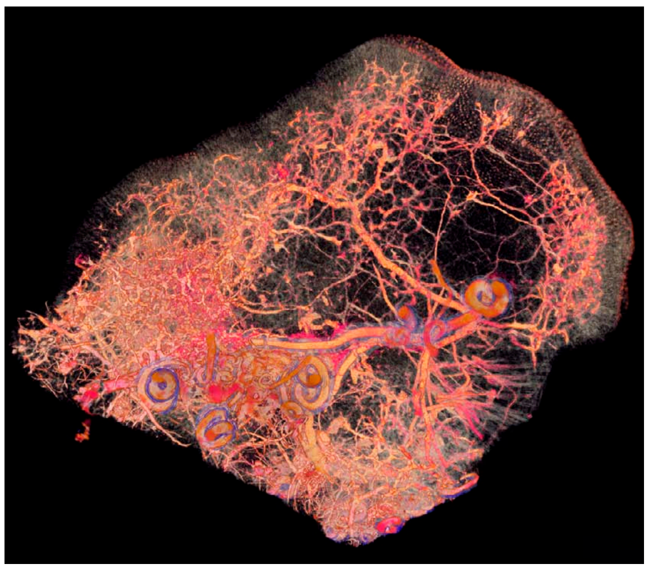
The mechanisms used by both plants and animals to bore into coral rock have similarities. Reef limestone is aragonite, a form of limestone which is not only relatively soft but also basic, or alkaline, meaning acids readily etch it. Secretion of acids by boring organisms is a common means of rock tunneling.

It takes an X-ray to look inside pieces of coral rock and see the extent of their internal dissolution. The end result can be a total disintegration of the skeleton into rubble, sand, and silt grains, and finally, for some of it, to dissolve back into solution in the seawater again.

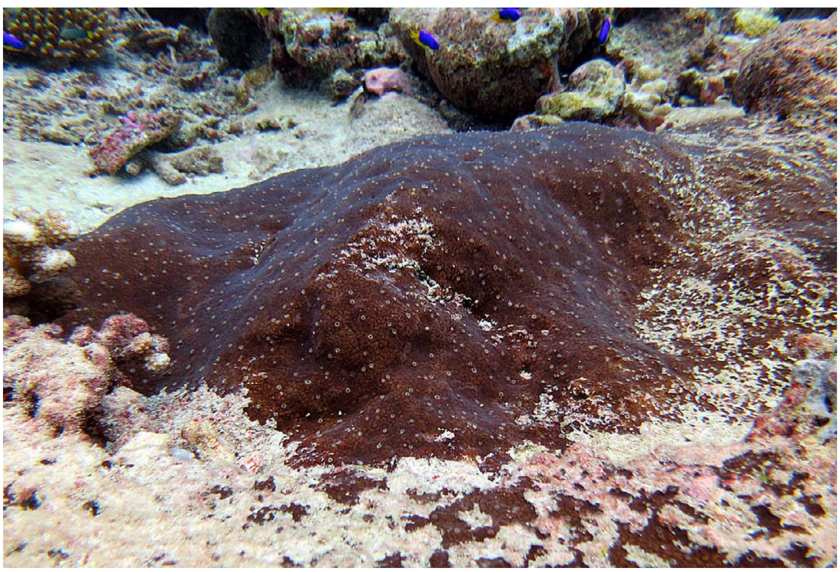
Firstly, though, the larva or spore of the boring organism has to settle on a bare patch of rock. Larvae that land on a coral or soft coral will simply be eaten. After settlement, boring can commence. One of the commonest boring organisms that can be easily seen is *Cliona*, a sponge that occurs throughout the tropical world, visible by the presence of sheets of colored tissue on the rock surface. Important species are brown in the Indo-Pacific, while in the Caribbean a common one is orange. Each thin sheet can cover a square meter or more, and visible on its surface are a series of pores through which it pumps water. However, most of the mass of the sponge lies beneath, in the top few millimeters or centimeters. In the Caribbean, boring species of *Cliona* can erode up to 5 lb of rock per sq ft (24 kg per sq m) per year.

Other species actively drill into the rock; many bivalve mollusks have hinged shells which scrape their way in. Several groups of worms also bore, but even the drillers commonly secrete acids to aid entry.

Several algae can also bore. These are mostly very small kinds, and limit their penetration to just a few millimeters deep because they still need light to photosynthesize; coral rock is translucent, allowing light penetration to a few millimeters, but no deeper. One common type of alga is *Ostreobium*, which can be seen as a dark green band just beneath the surface in a collected lump of coral. Fungi commonly accompany the *Ostreobium*. These are microscopic, and it has been estimated that there can be nearly 200 filaments per square millimeter tunneling into a *Porites* skeleton. They may be tiny, but collectively they have a massive effect.



RIGHT | A CT scan of a bored coral. The round disks are coiled tube worms near the surface. All other patterns are tubes made by several animals and plants.



ABOVE | The Caribbean sponge *Cliona delitrix*. The two sizes of pores can be seen, many small inhalant pores and fewer larger, prominent exhalant pores.

LEFT | The Indo-Pacific boring sponges in the genus *Cliona* can reach a square meter in area. Most of this very destructive sponge lies inside the rock, which it is gradually etching away.

SAND CYCLES

From the moment they settle and commence growth, corals everywhere are ground down into sand by waves and hollowed out from the inside by animals and plants that bore into their soft limestone skeletons. Other sand comes from mollusk shells, urchin spines, some plants, and the large group of protozoans called foraminiferans. Much more is generated by parrotfish and urchins that rasp the corals. Sand finds its way into cracks and crevices on the reef, much is carried off by currents to lagoons or low-energy areas where sand patches are found, or, if the reefs abuts land, it is thrown up by waves onto the beach.

In crevices in the reef, this sand and limestone dust produced by the action of borers like sponges and algae can remain for years. With chemical, algal, and microbial action it becomes consolidated and recemented into the reef matrix, usually becoming more solid than the original coral. Bacterial films on the particles can change the pH in the immediate layer of water, which cements particles back together into rock.

In some parts of the world much sand is made by the green seaweed *Halimeda* and a few other green algae (see page 106). Ground-up urchin spines and mollusk shells are always noticeable, and one important component is usually foraminifera, or forams, a large class of amoeboid protists, single-celled animals that have a chambered limestone test (shell) around them. These feed on bacteria or other microscopic life forms, and many are symbiotic with several kinds of single-celled algae including dinoflagellates (the coral symbiont group). Several retain chloroplasts—the cell structure containing chlorophyll—from algae they have eaten, which still continues to photosynthesize for the new host.

On reefs near continental land, much sand can come from sediment from weathered rocks washed off the land. This can be excessive and smothering when deforestation has occurred. However, on more distant reefs, especially, most sand comes from corals, and most is carried away from the reef. Sand patches are a major, integrated part of a coral reef's ecology. Usually found in the lee of a reef, sandy areas are typically more extensive than the coral reef which supplies them. As sand is moved by waves it becomes graded by particle size. Coarser pieces and rubble are not moved far and settle out immediately behind the reef, while the finest particles are carried much further. Deeper lagoons well in the lee of the reef contain the finest sands and mud. The proportion that is thrown onto land, if land exists, forms the white sandy beaches familiar from tourist brochures.

TOP LEFT | Close-up of sand, showing grains of forams, broken corals, urchin spines, and *Halimeda* disks.

ABOVE | A beach on a coral island at high tide. The sand is mainly ground-up coral, mixed with fragments of several other types of animals and plants.

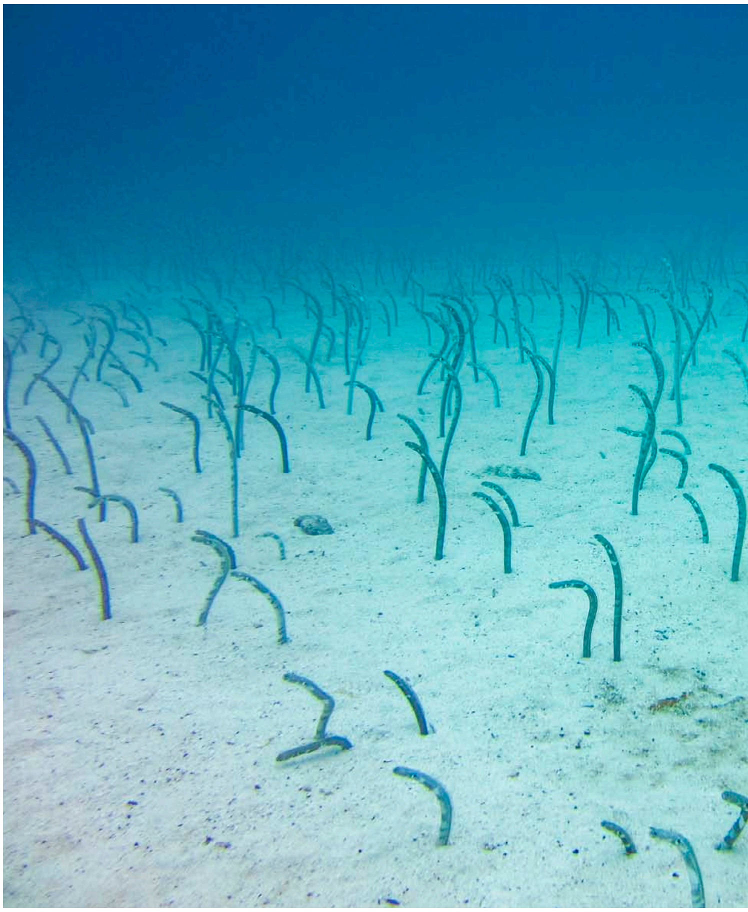
LEFT | A selection of sand grains taken from coral sand, showing a variety of foraminifera, which come in many shapes and sizes. Among these are urchin spine fragments and micro-mollusk shells.

LIFE IN CORAL SAND

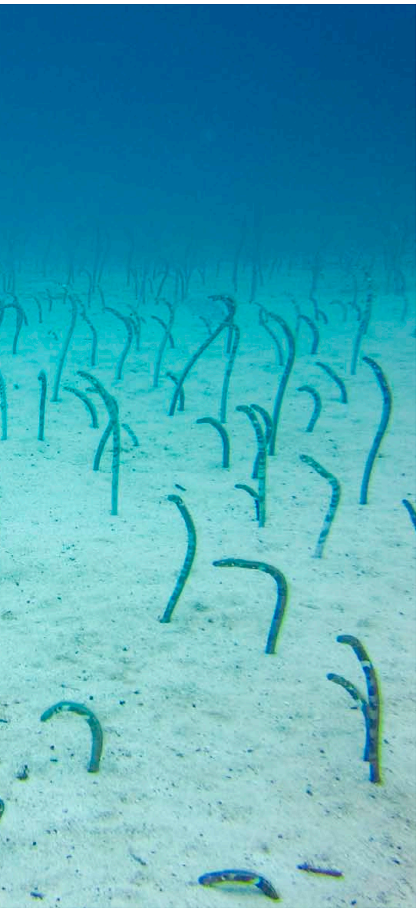
The great expanses of sand behind and among coral reefs are far from lifeless. The quantity of life—the biomass—may be significant, but with conspicuous exceptions, much is very small, mostly buried, and with a fairly rapid turnover.

Sand would be white if it was lifeless, but on the seabed it is usually gray or green-brown, caused by a film of algae and bacteria growing over the surface. This is food for numerous grazers. Most conspicuous of these are sea cucumbers, large echinoderms that ingest large quantities of sand almost continuously, digest the algae, and excrete the rest as pure white sand again.

At night, more activity is visible. Colorful cone shells, volutes, olives, and other mollusks hunt, gliding through the uppermost layer of the sand with only their siphon visible and leaving a visible trail as they go, many using their venomous darts to immobilize prey. A huge group of bivalve mollusks also live under a thin layer of sand, filter feeding, and sand dollar urchins shuffle through the surface layer, browsing on what they can. Then there are the micromollusks, a very diverse group of gastropod mollusks with tiny shells that end up as part of the sand.



BELOW LEFT AND RIGHT | A sea cucumber feeding on and excreting sand.



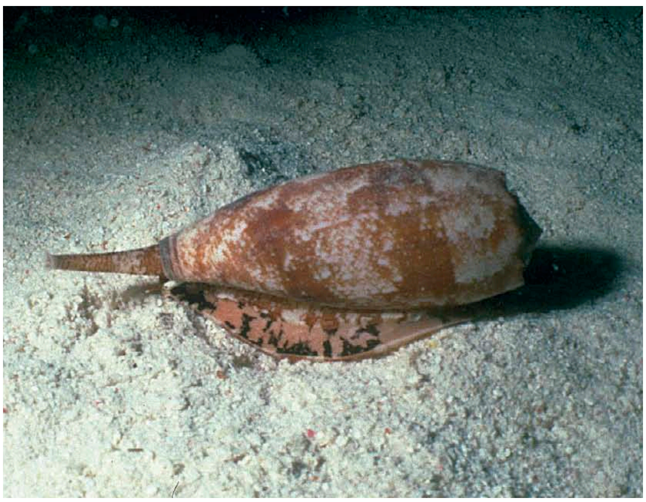
The smallest animals live among and between the grains of sand. Many larger, burrowing animals make their home in it, and puffs of fine sand frequently reveal burrowing activity. Small fish, crabs, and many kinds of worms have tunnels and burrows, excavated and maintained constantly. Large stingrays and other fish constantly wreck the burrows as they forage through, some using feelers to search through the sand, and others using electrical sensors to detect where prey animals are lying concealed. Stingrays themselves, when resting, bury themselves using flips of their wings, to cover themselves. Occasionally a field of garden eels is seen; these are fish in the conger eel family, each very thin but 20 in (50 cm) to over 3 ft (1 m) long, that live in burrows with only their top ends emerged. Very shy, they retract back into their burrows in synchronized waves if a diver approaches them.

Activity is such that there is considerable turnover and aeration of the topmost several centimeters of sand. One experiment covered a patch with a thin film of dark sand, and showed that this had been mostly overturned and churned back only one day later.

LEFT | A large sand patch filled with garden eels, harmless members of the conger eel family. Their heads protrude above to feed, but they are extremely cautious fish and will withdraw with the approach of a diver or predator.

BELOW LEFT | The sand-dwelling geography cone shell emerges from sand at night to feed on fish. It is extremely venomous.

BELOW RIGHT | Stingrays conceal themselves in sand by fanning sand over themselves. This partly remains when they swim to feed on buried organisms.



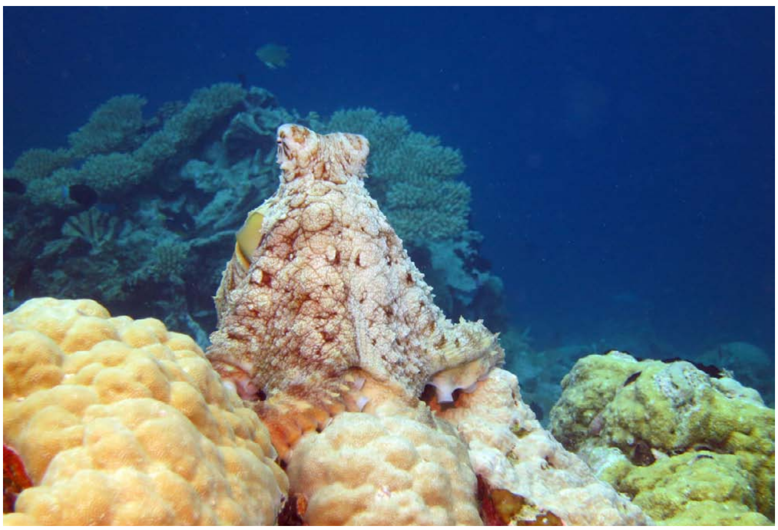
IMPORTANT REEF LIFE: MOLLUSKS

Mollusks are a huge and very varied marine phylum and, partly because of their attractive shells, their taxonomy has been studied in greater detail than that of most groups. Mollusks now comprise a quarter of all described marine species. There are eight or nine classes, containing nearly 50,000 marine species (with more on land and in fresh water). Because of their shells, they have a relatively clear fossil history, and their ancestry has been traced back nearly 500 million years. Mollusks probably have the most varied range of form of any phylum.

Gastropods or sea snails are the most diverse group and include members that are fairly sedentary, such as limpets, and others which can travel quite swiftly, such as the cone shells. Bivalves, with two hinged parts to their shells, are also numerous and form the prey for many other species. Nudibranchs include some of the most exquisite forms; these have lost their shell over evolutionary time and are now entirely soft-bodied. Chitons have multiple plates on their back, and there are other smaller groups too. The octopuses and squid, members of the cephalopod class, are perhaps the most distinctive group in that most are fairly large, and in terms of neurological development they are the most advanced of all invertebrate animals. These mollusks now only have a small, reduced internal shell.

The aeolid group of nudibranchs have remarkable traits. Some graze on hydroids and ingest their stinging cells without triggering them. The stinging cells then migrate to the nudibranch's back, where they form part of the mollusk's defense. Others also ingest the algae of soft corals so the nudibranch can benefit from their photosynthesis.

Their sheer abundance and variety make mollusks an important group of coral reef animals. Shells of gastropods in particular have been heavily sought-after, and the removal of far too many, such as of the Giant Triton in the Indo-Pacific and the Queen Conch in the Caribbean, has led to ecological problems. Bivalves, especially mussels, scallops, and clams, are an important source of food for people, and many are cultivated for food and, in the case of oysters, for pearls. Some have toxins that are dangerous to people, and these are used for pharmaceutical purposes.

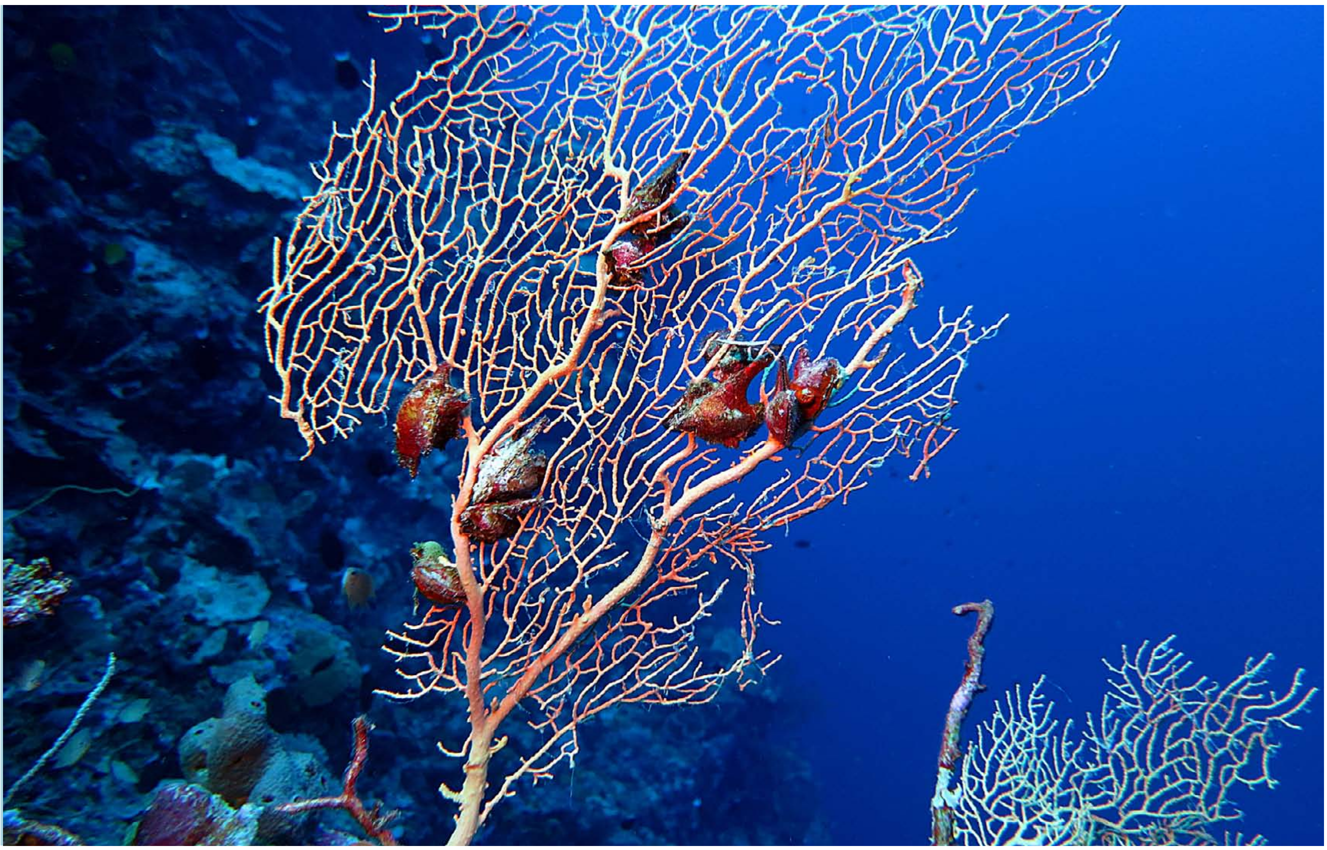


LEFT | Octopus and squid are advanced mollusks, that have been shown to be relatively intelligent. This one is waiting prominently on a coral for a mate.

OPPOSITE TOP LEFT | Giant clams are members of the *Tridacna* genus. They have colorful tissue filled with symbiotic algae, and light-sensitive "eyes" that detect movement and light differences, which cause the shell to close.

OPPOSITE TOP RIGHT | A flamingo tongue snail *Cyphoma gibbosum*. It is found on several species of gorgonians on which it feeds.

RIGHT | The wing oyster *Pteria colymbus* is commonly seen on Caribbean reefs attached to sea fans. It is a filter feeder, feeding on waterborne plankton.



LEFT | The dorid nudibranch *Hypselodoris* is a group that contains many colorful species. Their diet includes hydroids and sponges, which makes them toxic to other potential predators. Most are solitary, but they can gather in groups to breed, and are found across the world.

RIGHT | The nudibranch (which means "naked gill") mollusk *Goniobranchus geminus*, more commonly known as the gem sea slug, is an Indian Ocean reef species that grows to about 3 in (5 cm) long.

IMPORTANT REEF LIFE: ECHINODERMS

Echinoderms are an entirely marine group with no terrestrial or freshwater species. There are five classes, all of which can be conspicuous on coral reefs: the starfish, brittle stars, and urchins, the feather stars, and sea cucumbers. The main characteristic that unites them all is that they are built with fivefold symmetry, though there are a few species with sixfold or tenfold or more too. Curiously, the larvae of all have the much more common bilateral symmetry, but this changes when the larvae metamorphose to adults. There are about 7,000 species of echinoderms living today, with nearly double this known from the fossil record.

All echinoderms have a skeleton composed of myriad small limestone plates, which may be fused together as in urchins or flexible as in the arms of starfish, brittle stars, and feather stars. The spines of sea urchins are also composed of limestone. The mouthparts of urchins, called "Aristotle's lanterns," are used for grazing and are also made of similar material, as are the stalks of crinoids (feather stars). The animals move using a water-filled system of tubes and canals that is unique to the echinoderms.

Starfish are predators and use their arms to prize open molluskan prey, into which they exude their digestive juices. Sea urchins are mostly grazers, rasping algae from rocks with their hardened mouthparts, though some are scavengers. The crinoids are largely sessile, though most can swim to a limited extent; they raise their many-branching arms into the water mostly at night to trap plankton, which is then passed to the central mouth. Sea cucumbers are important inhabitants of coral reefs, though most species live on adjacent sand (see page 130).

All these animals have a marked capacity to regenerate when an arm or segment is lost to a predator. Some starfish and brittle stars may even deliberately detach an arm when attacked so that they can escape. It is common to see starfish with arms of different sizes because of this.

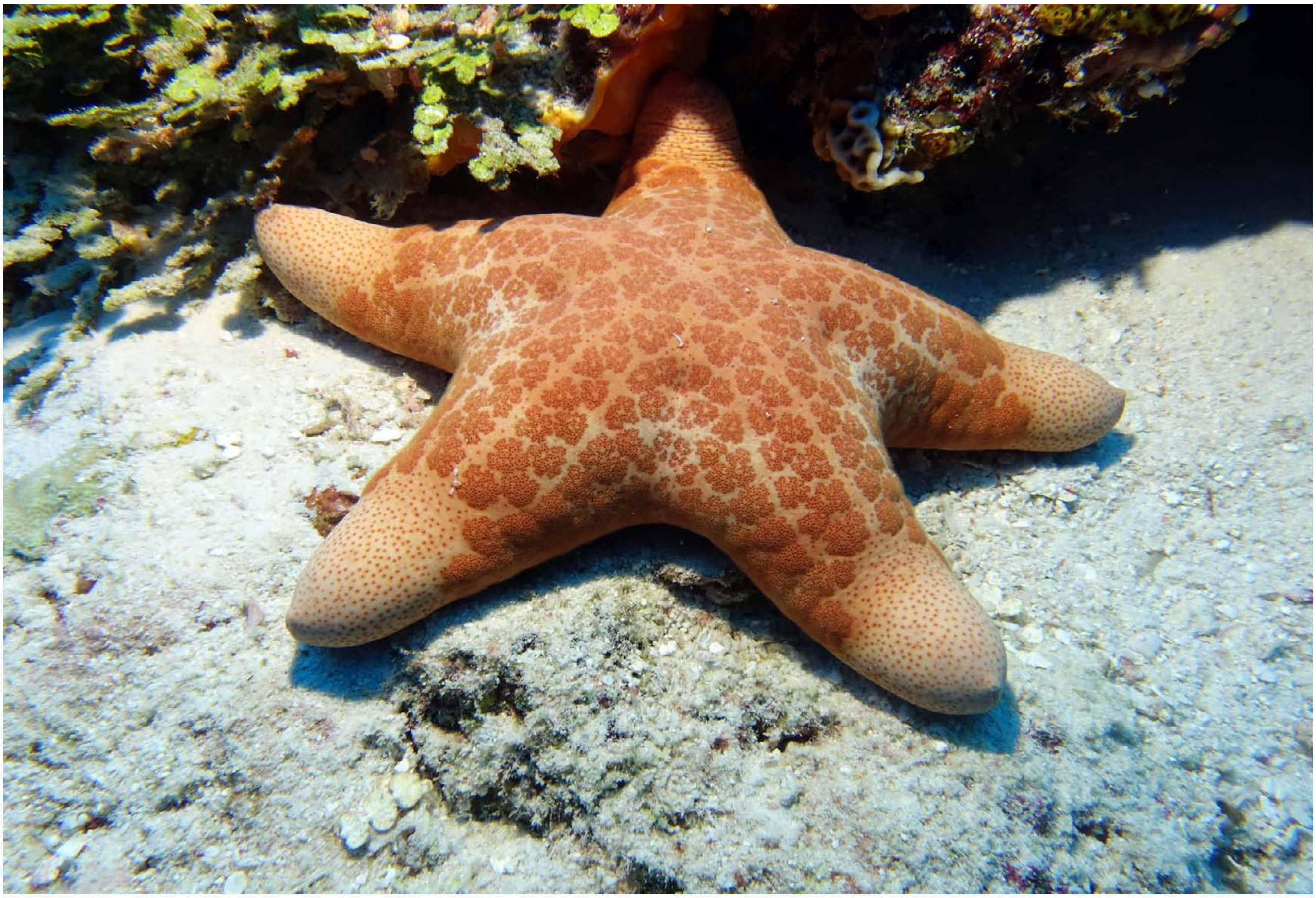
Only sea cucumbers and a few urchins are eaten by humans, and about a dozen species are regarded as delicacies or as an aphrodisiac in some parts of Asia. Unfortunately, collectors may strip the reef of sea cucumbers, causing ecological problems.

LEFT | Sea apples are stumpy sea cucumbers. They feed on plankton using their tentacles, usually at night, and can move along the reef by inflating their bodies to double their usual size, then floating in a current.

OPPOSITE TOP | The granulated sea star, *Choriaster granulatus*, is a starfish common on reefs. It is a carnivore, feeding on small invertebrates and carrion.

OPPOSITE BOTTOM LEFT | Dried sea cucumbers for sale in an Asian market. These are echinoderms too, with a five-fold symmetry, and are important cleaners of organic debris.

OPPOSITE BOTTOM RIGHT | This blue-striped urchin, *Mespilia globulus*, is found on reefs and adjacent rubble areas and seagrass beds. Like all echinoderms, it has a fivefold symmetry.

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LEFT | The Christmas tree worm, *Spirobranchus giganteus*, is a small, very common tube worm. It is usually seen with its tube embedded in a massive coral. Its double whorls of tentacles are both gills and organs for trapping plankton. They flick back into their buried tube if disturbed.

RIGHT | The mantis shrimp, of which there are several reef species, is a colorful crustacean and a powerful predator. It kills prey with its highly adapted claws by smashing or spearing its quarry, or by creating a significant shock wave by flicking the claws with massive acceleration. This causes cavitation bubbles that administer a second stunning blow. The mantis shrimp's eyes are the most complex known, containing many more types of photoreceptor than human eyes.

SEAGRASSES AND MANGROVES

Seagrasses and mangroves, which are both flowering plants (angiosperms), are associated closely with coral reefs and are integral to them in several ways. Many reef animals spend part of their life in one or other of these adjacent habitats, and indeed some fish migrate between reefs and one or other of these habitats every day.

Seagrasses have roots and flowers and, while most live in calm sandy patches behind reefs, one or two grow on the reef itself in close association with corals. Seagrass beds may cover many hectares behind reefs and provide sheltered breeding and nursery grounds for many reef species. Few animals feed directly on the grasses, though conspicuous exceptions are green turtles and dugongs, a sea mammal.

The importance of seagrasses comes partly because of their extensive root systems, which stabilize sand. The leaves provide a surface on which many sessile organisms attach, and they house a huge abundance of mobile animals including worms, mollusks, and crustaceans. When seagrass leaves die they are decomposed by microbial activity, so their high productivity enters the food web via particles consumed initially by plankton- and filter-feeding organisms and detritivores. When seagrass is extensively killed, such as through anchoring or pollution (see Chapter 4), their stabilizing effect is lost and erosion sets in.

Mangroves are trees that can live in salt water. As with seagrasses, their root systems stabilize otherwise mobile

sandy or muddy substrates. However, being true trees, their canopies are entirely above water. On many islands far from shore, especially in Southeast Asia, the Pacific, and Australia, the trees may be the only part of the reef system visible above water. Or, they may occupy the strip between land and a fringing reef farther out to sea. Their networks of roots provide shelter for juveniles of several species of fish, keeping larger predatory animals out.

Reefs, seagrasses, and mangroves can form an integral system: reefs take the force of ocean waves to provide conditions suitable for mangroves and seagrasses, and conversely mangroves and seagrasses trap sediment running off the land which might otherwise smother the reef. Their importance becomes evident when one or the other is removed during shoreline construction, which leads to the other habitats soon disappearing as well.

OPPOSITE | A few seagrasses, such as *Thalassodendron ciliatum*, grow on coral reefs as well as developing expansive beds in sand behind reefs. The roots of these can establish in very shallow and coarse sand and rubble beds.

BELOW | Mangrove trees have elaborate prop root systems to stabilize the trees in mobile sediments. These act like the bars of a child's cot, preventing larger fish from entering so that juvenile species are safe from larger predators. Many reef species move between the reef and adjacent mangroves.

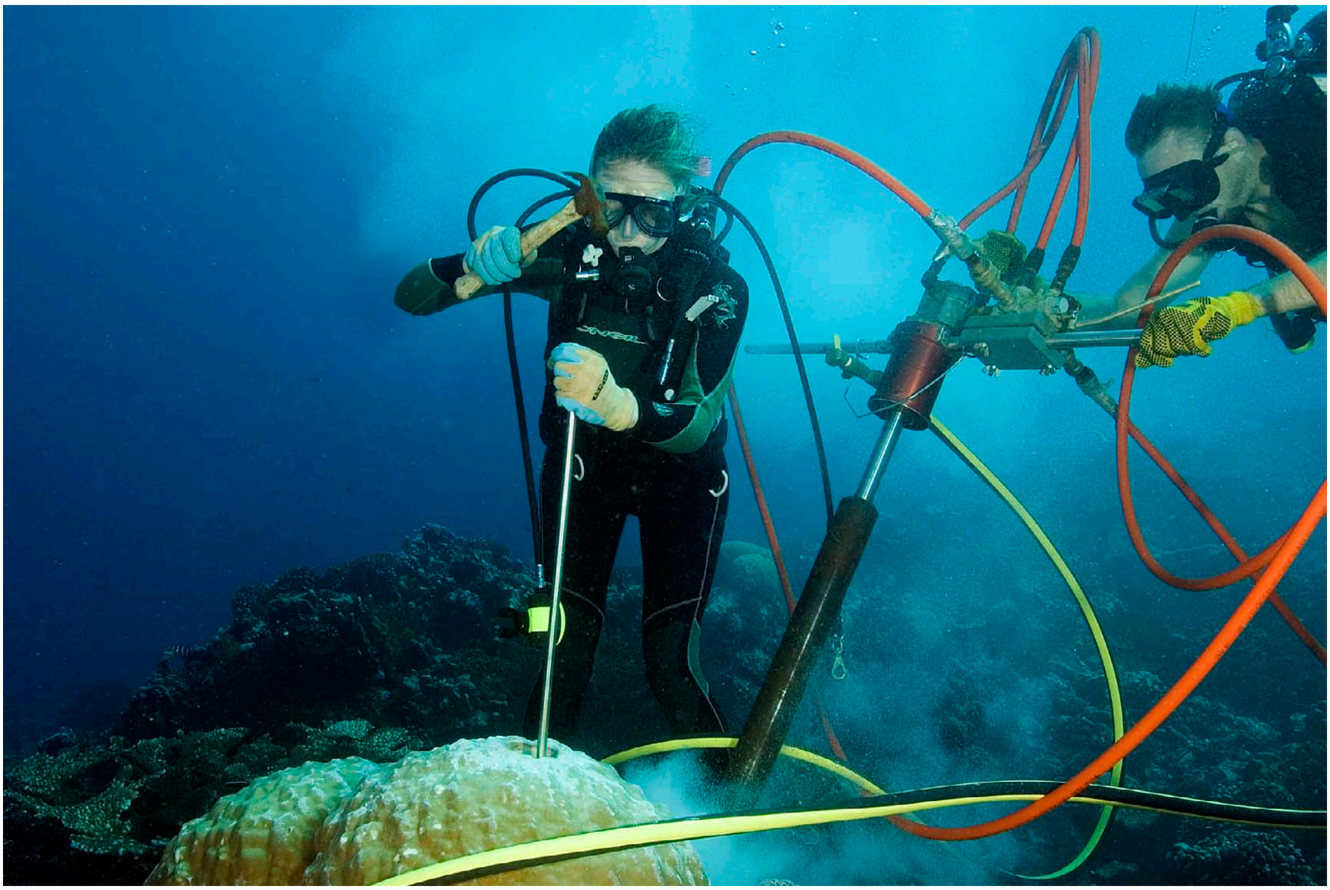
MEASURING THE PAST

The giant members of the coral genus *Porites* can be cored with a drill to obtain information about past climate. The drills are usually powered by compressed air, supplied from the surface or from cylinders, and can extract a tube of skeleton a few centimeters wide.

Porites grow about ⅓ in (1 cm) per year, but the rate can vary with different seasons, so a coral core will contain a series of bands, much like tree rings. Therefore, a sample from 50 bands down the core was laid 50 years ago. The physics and chemistry of that slice reveal a lot about the climate at that time.

A common technique to study this is to measure the ratio of two different stable isotopes (forms) of oxygen, ^{16}O and ^{18}O, in the coral skeleton. This is related to the water temperature at the time the coral grew. It can also be used to determine the pattern of rainfall. Rainwater in the tropics is richer in the lighter isotope ^{16}O because the lighter water evaporates more readily than the heavier one. This enriches its proportion in rain, and this becomes reflected in the oxygen component of the calcium carbonate of the coral skeleton.

Another technique is to deduce the relative strength of the climatically important annual monsoons by looking at the amount of several trace elements embedded in the skeleton, because these levels change according to how much terrestrial dust is washed into the ocean with rain.



In a similar manner, relative changes in water pollution can be measured by the amounts of elements such as lead or cadmium deposited in each layer of the coral core.

Other isotopes are measured as well. The strontium/calcium ratio can be used for measuring temperature trends because when waters are cooler corals deposit more strontium compared to calcium. These trends can be extended backward using fossil corals.

An older fossil coral's age can be determined by the ratio of uranium and thorium in the sample—that is, how much uranium has, through radioactive decay, turned into thorium. These techniques can be used to obtain information about the climate many thousands of years ago.

Usually, after a core has been extracted, the hole is plugged with concrete, which will be grown over in two or three years by new polyps. This conceals the hole and prevents bioeroding organisms from entering and starting to hollow out and destroy the coral.

OPPOSITE | Large massive corals usually lay down annual bands of layers like tree rings. The corals can be cored with drills, then sliced and X-rayed to see the rings.

BELOW | Old buildings in now abandoned coconut plantations were commonly built from coral rocks 200 years ago. These rocks can be cored just like living corals, and will extend the time series of climate data back 200 years, providing valuable information on past environments.

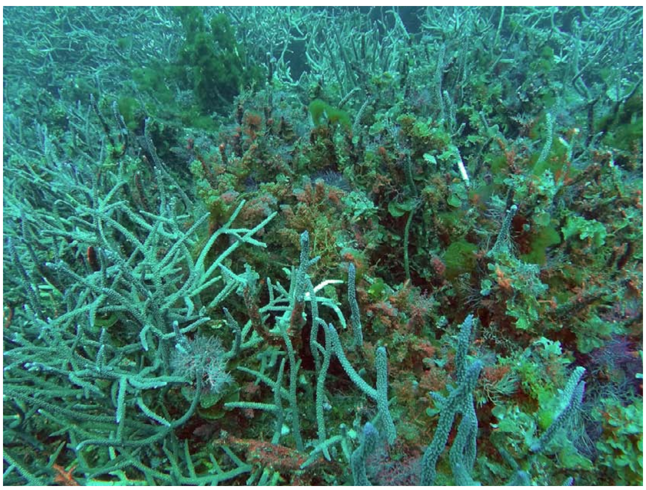
WHERE REEFS GRADE TO COLDER WATERS

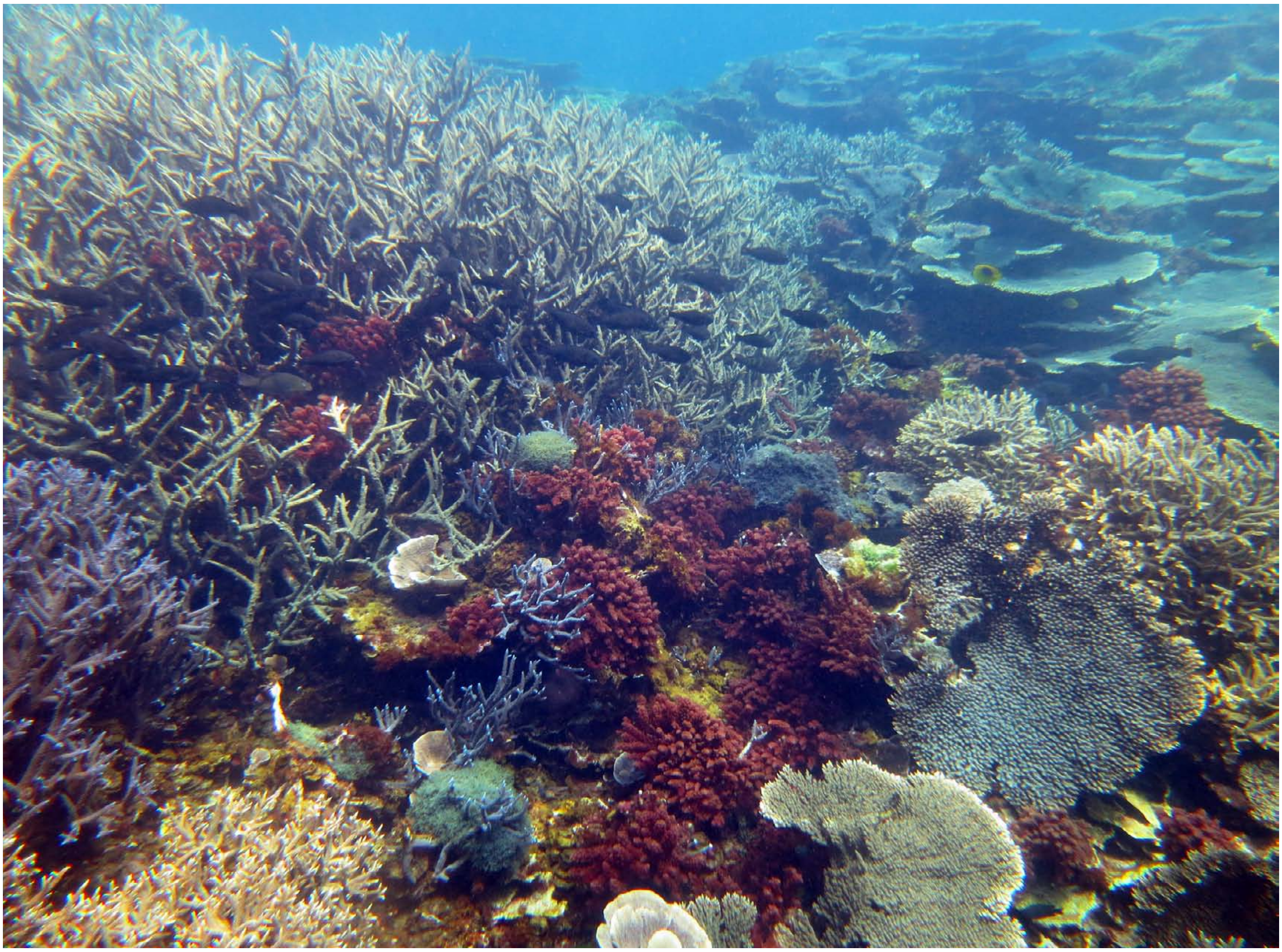
Tropical coral reefs are confined to warm water only. Higher latitudes, meaning places nearer the poles, are the domain of large seaweeds such as kelps, though they do have species of cold-water corals, usually small, that do not build reefs. Higher latitudes have cooler waters and more dissolved nutrients, both factors that are hostile to reef-building coral polyps. Most species anywhere in the world have their preferred zones, and reef-building corals are no exception.

However, the world of corals does not end abruptly, but tends to grade fairly gradually into the ecosystems of temperate, cooler waters. First, consolidated reef growth will cease, even before many of the reef-building corals disappear. There are several areas where this is especially noticeable: along both coasts of Australia, the Atlantic coast of South America, and northward in Asia through the southern Japanese islands. In the USA, Florida sees the end of Caribbean reefs, and the offshore island of Bermuda is the northernmost outpost for Caribbean corals and reefs. As well as falling temperatures and rising nutrients, a change from suitable rocky surfaces to a sandy seabed sometimes inhibits and eventually limits the corals from growing.

With increasing latitude, coral diversity also tails off, though this need not be very marked. A good example is the reduction in coral diversity down the length of the Great Barrier Reef of Australia, and there is also a corresponding decline in their growth rate toward the south and cooler waters. However, with both numbers and growth rates, the great width and complexity of its numerous component reefs complicates the pattern. In some cases, such as with the tailing off of Caribbean species farther south down Brazil's coast, there are changes in the types of corals, too, in this case made more marked by the present isolation of this area from the main body of the Caribbean by the Amazon and Orinoco rivers, whose fresh water provides a barrier which has isolated the Brazilian corals for millennia.

As coral richness and growth rates decline toward higher latitudes, large seaweeds increasingly enter the scene. The Houtman Abrolhos Islands in Western Australia show this. Farther south on this Western Australia coast, rocky shores at Rottnest Island near Perth are near the end point of the process, being mostly covered in seaweeds, with just a few scattered corals surviving among them. Oman also shows this pattern clearly, but it does not have a particularly high latitude; instead, it is strong upwelling of cold water that mimics colder latitudes and causes the shift to kelps.





FAR LEFT | Algae coexisting with corals in cool waters. This is in the high-latitude Houtman Abrolhos islands, Western Australia, where branching corals are competing with mostly green seaweeds.

LEFT | In Oman, cold-water upwelling has a similar effect on water temperature, as do higher latitudes, so kelps intermingle with corals on the southern reefs.

ABOVE | In Western Australia on the high-latitude Houtman Abrolhos Islands, algae coexist with staghorn corals. In this scene they are mostly red algae.

ISLAND AND REEF CONNECTIONS

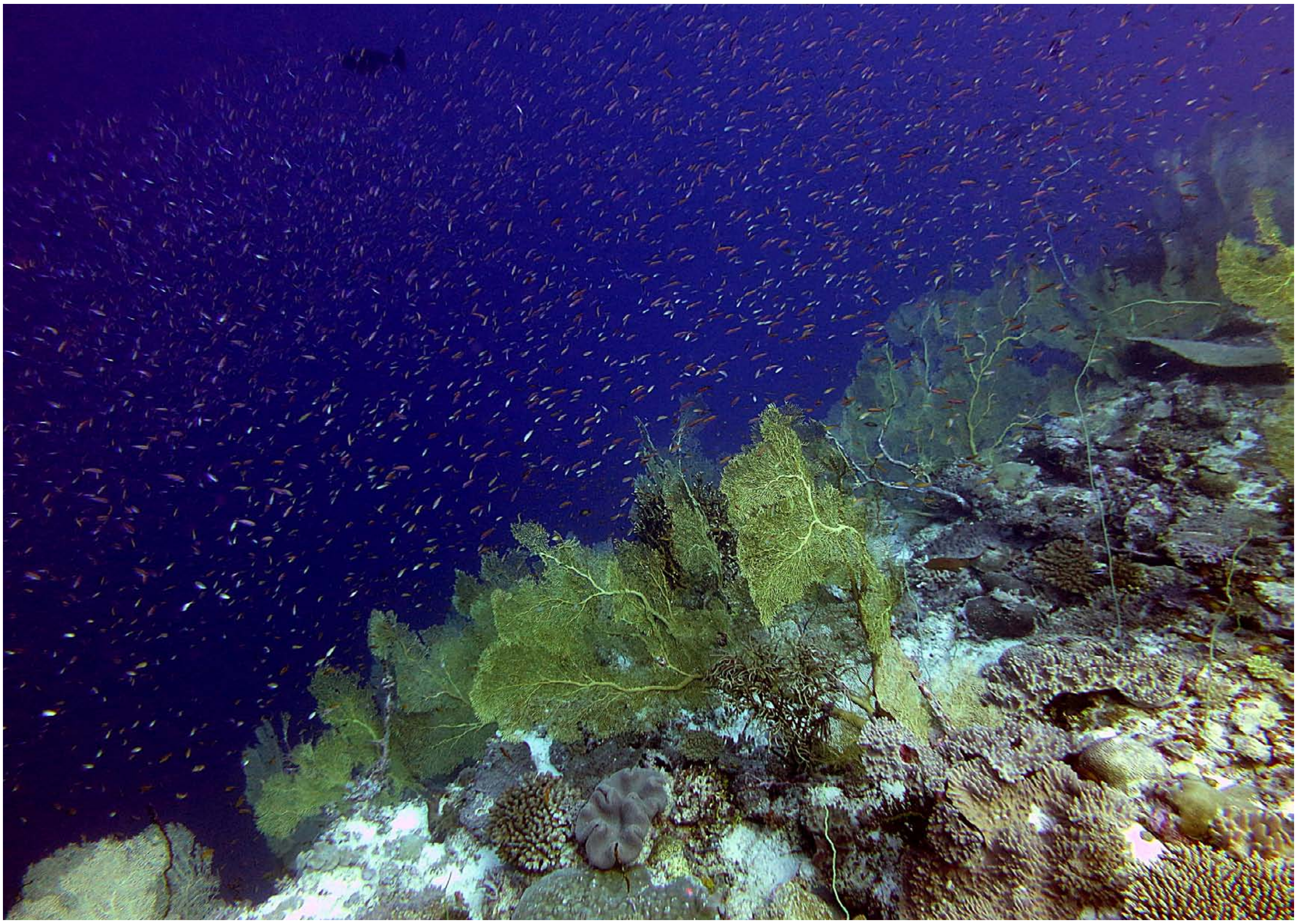
Coral islands are dependent on the reefs upon which they sit for the limestone fabric that makes them, but the connections between island and reef extend much further than that. The difference can be seen in islands which have been vastly altered by people, where native forests and their rich seabird populations have been removed.

Many, perhaps all, uninhabited coral islands will have once contained enormous densities of nesting seabirds, but several kinds of disturbances have caused them to lose most, or even all, of these colonies. A common cause is the conversion of the native trees, whose branch structure was suitable for nests, into monoculture plantations of palms, which are not suitable for nesting. In other cases, construction of villages and direct disturbance from people caused birds to vanish, and guano mining for use as fertilizer—formerly a substantial industry in some places—has also ruined the birds' habitats. A third very important cause has been the introduction of rats. Wherever humans go, they have brought rats, and hungry rats consume small seabirds, their chicks, and eggs, starting with those species that are ground-nesting.

This loss of birds has profound consequences for the reefs that built the island in the first place. The thousands of nesting and roosting seabirds forage over large distances, sometimes well over 100 miles (160 km) over the surrounding ocean, catching fish and bringing much back to their nests to feed their chicks among the island vegetation. All defecate, producing nutrient-rich guano. This fertilizes the plants, and much is washed off onto the surrounding reef. Unlike sewage inputs from villages, which are generally harmful, the run-off from islands with many birds is rich in phosphorus, with a better nitrogen–phosphate balance than human sewage. The result is a level of fertilization which leads to much faster-growing fish with a higher overall biomass. Grazing of algae by fish is essential for maintaining a vigorously growing reef, and is over three times greater where there are many birds than where there are none.

The effect continues up the food chain. The nutrient run-off entering the waters of the reefs around islands with numerous birds fuels a greater abundance of plankton, allowing more zooplankton, which is reflected in higher densities of filter-feeding animals including manta rays.

RIGHT | Large colonies of seabirds nest and roost on suitable coral islands. They deposit their droppings (guano), which fertilize plant growth. Nutrients run off the land after rain and are carried onto the reef, allowing corals and reef fish to grow faster.



ABOVE | There are multiple connections between islands and surrounding reefs. Nutrient transfer from birds is just one. Increased coral growth results in higher sand production and greater reef growth, leading to increased protection from the reef of coral island shorelines.

LEFT | As with corals and fish, manta rays also benefit from increased nutrient run-off from birds on coral islands.

CORAL REEF RESEARCH TODAY

Understanding the key aspects of how a coral reef functions, especially with the problems that reefs face from human pressures, has increasingly been one of the main focuses of research for several decades. Although coral reefs have a high species diversity, most animal species are small and cryptic, spending most of their life well hidden, which is not surprising considering the swarms of hungry predators hovering above. In fact, most of the diversity on a reef occurs in the cryptic spaces. Previously overlooked species have turned out to be crucial. The three-dimensional structure created by corals that is used by many species for shelter and protection is changing and has been one of the most important features to disappear with ocean warming.

The huge number of closely interlocking parts and the interconnection between different species on a reef can make the system fragile in some cases and robust in others. The issue of fragility or robustness of coral reefs is especially important now because of the damage that is being done to them. Sometimes, with so many species around, removal of one or two might have little consequence in cases where another species can readily take their place, and this argues for reefs being robust. Conversely, several species have a key importance that cannot be replaced by others; the Long-spined Sea Urchin (*Diadema antillarum*) and Caribbean parrotfish (see pages 162 and 124) are excellent examples. These have no effective replacements, so their removal collapses the reef system to an algal plain with much lower diversity. A lack of redundancy in this respect argues for the reef being fragile and easily disrupted.

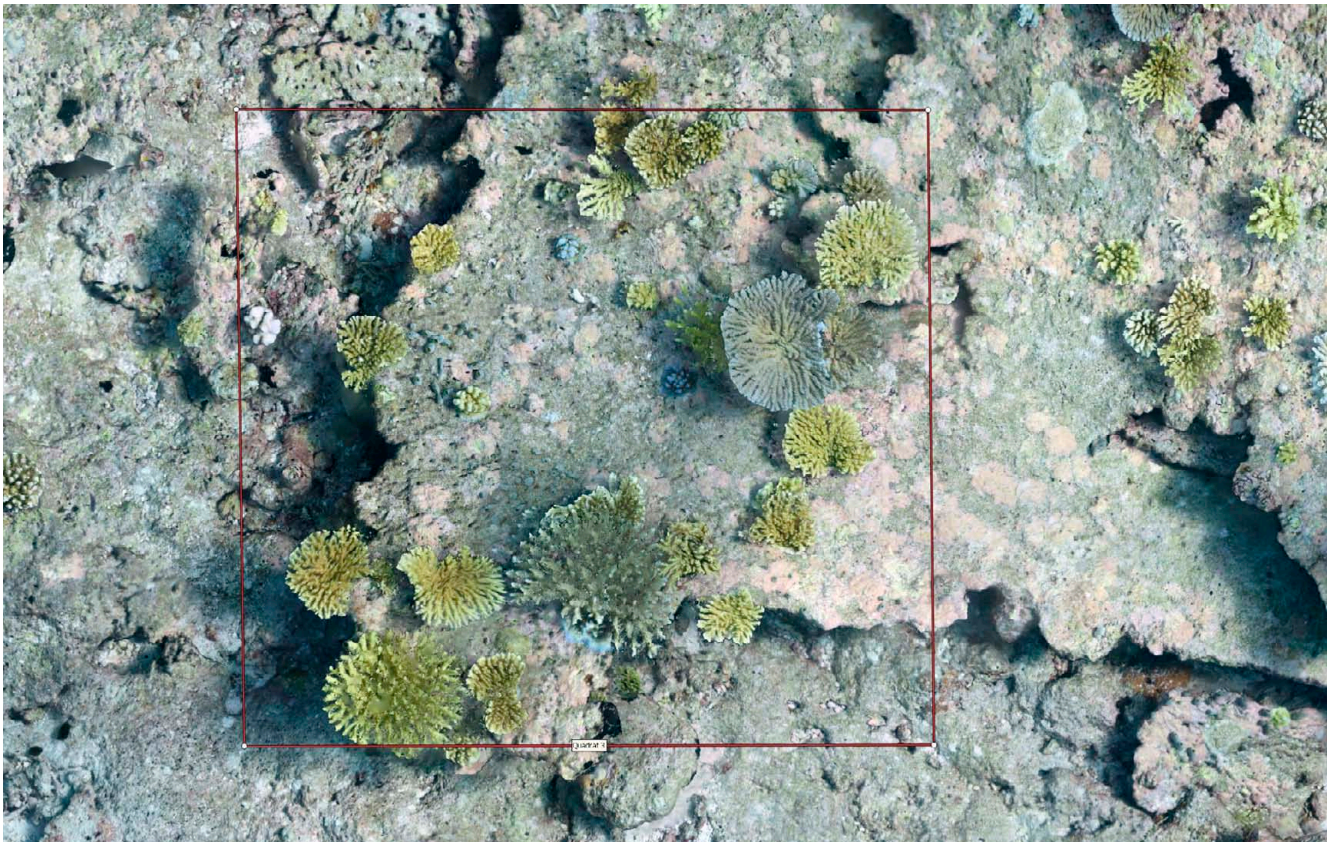
Another important point is the question of scale; something that is crucial on a small scale may not matter to large species, but often small-scale interactions between species can structure habitat at larger, whole-reef scales too. The identity of a dominant coral species determines to a large degree what species of fish are found near it, showing that the fish communities are finely dependent on the identity of the corals on a reef, not only the quantity.

These and other aspects are important to the condition of a reef and, as humans exploit coral reefs, determining these differences becomes ever more important.

ABOVE | The *Diadema* urchin is a major Caribbean grazer, which helps reduce the quantity of seaweeds on reefs.

TOP RIGHT| Some modern survey methods make extensive use of photography, so one hour underwater can be saved for further study. This scene is a mosaic of many photos stitched together, monitoring recovery by juveniles of a heavily killed reef.

BOTTOM RIGHT | The Caribbean stop-light parrotfish, *Sparisoma viride*, is a major reef grazer, which keeps the quantity of algae in check. When fished out for food, seaweeds quickly dominate and reefs deteriorate further in a spiraling decline.



CHAPTER 4

LOCAL AND REGIONAL DISTURBANCES TO REEFS

FISHING AND DESTRUCTIVE FISHING

Maintenance of a healthy reef with high rates of protein production is key to the welfare of a huge number of people. Probably about half a billion to one billion people obtain their protein from coral reefs, so healthy reef systems are critical to humans. Unfortunately, fishing is one of the most ecosystem-disrupting activities of all on a coral reef, and as more and more people place greater and greater demands on reefs they are becoming depleted, so increasingly desperate people are using more and more damaging methods to fish.

Consider, too, that in some Southeast Asian countries, a fisher using dynamite can earn in one year several times more than a professor at the local university. This illustrates how intense the incentive for this destructive and usually illegal method is, so dynamite fishing remains pervasive. Explosive blasting can be felt by a diver more than 330 ft (100 m) away as a kind of dull hammer blow. The blast ruptures fish swim bladders, the organs that give them their buoyancy. Following the blast, killed or injured fish are collected, though many are missed and simply rot. A circle with a radius of several meters is blasted flat; corals are knocked over and destroyed and a colorful reef turns instantly to a flattened field of rubble. Dynamite, commonly purloined from construction projects, is commonly used, as are home-made explosives stuffed into glass bottles, which are also very dangerous for the fishers. Dozens or even hundreds of blasts in one week, progressing relentlessly along the reef, completely wreck it for decades.

Another kind of destructive fishing uses cyanide squirted into crevices. The poisoned fish can recover and those that are desirable for the aquarium trade are usually exported live, though many die later. But corals are killed and disintegrate, with consequences similar to those of explosives.

Traditional methods, too, such as netting, are now intense enough to cause problems. The more sought-after carnivores and large herbivores are exploited relentlessly, and their removal commonly leads to an explosion of seaweed growing on a previously healthy reef, outcompeting corals and reducing the reef to a ghost of its former glory. Too many people are taking too much from the reef and, while fishing for survival is completely understandable, overfishing causes reef decline and the loss of future resources.

OPPOSITE BOTTOM | Destruction of corals by lost and discarded fishing gear is common. Nets break up corals and continuously entangle fish, which are then wasted.

LEFT AND BELOW | Destructive methods of fishing, such as using explosives or poisons like cyanide, are common in some countries. These kill many more fish than are caught for food and destroy the reef for years to come.

SEWAGE, NUTRIENTS, AND REEFS

Nutrients fertilize and, in the correct quantities, encourage plant growth. But on a reef, human sewage, with its particular organic and nutrient mix, commonly has disastrous consequences. In the same way, run-off from agricultural fields after rains can have a similar effect, as it carries with it fertilizer that has been added to crops. Both have substantial, harmful effects on corals and damage reefs.

The fact that coral reefs are found in nutrient-poor seas once puzzled scientists, who wondered for years where the fertilizing base came from to support such rich and teeming, but isolated, ecosystems. They thrived in a nutrient-poor environment because, it was deduced, they had a very tight recycling system. But it was also known that the addition of even moderate quantities of human sewage or run-off could rapidly lead to coral death and collapse of the system.

The truth is that sewage encourages growth of large algae, which grow much faster than corals and outcompete them for space. On an unfished reef with high fish populations, grazers will keep the algae in check, but when overfishing has eliminated them there is little to stop the seaweeds from dominating the reefs to the exclusion of corals. Another key consequence of more seaweed is that when it is not eaten it ends up as dissolved organic carbon in the seawater (see page 156).

Discharge of raw sewage is common in developing countries. However, in many coastal communities near reefs even in the developed world, there is no tertiary sewage treatment—the final and expensive process that removes nutrients from the sewage. Even partial sewage treatment can be insufficient for coral reefs.

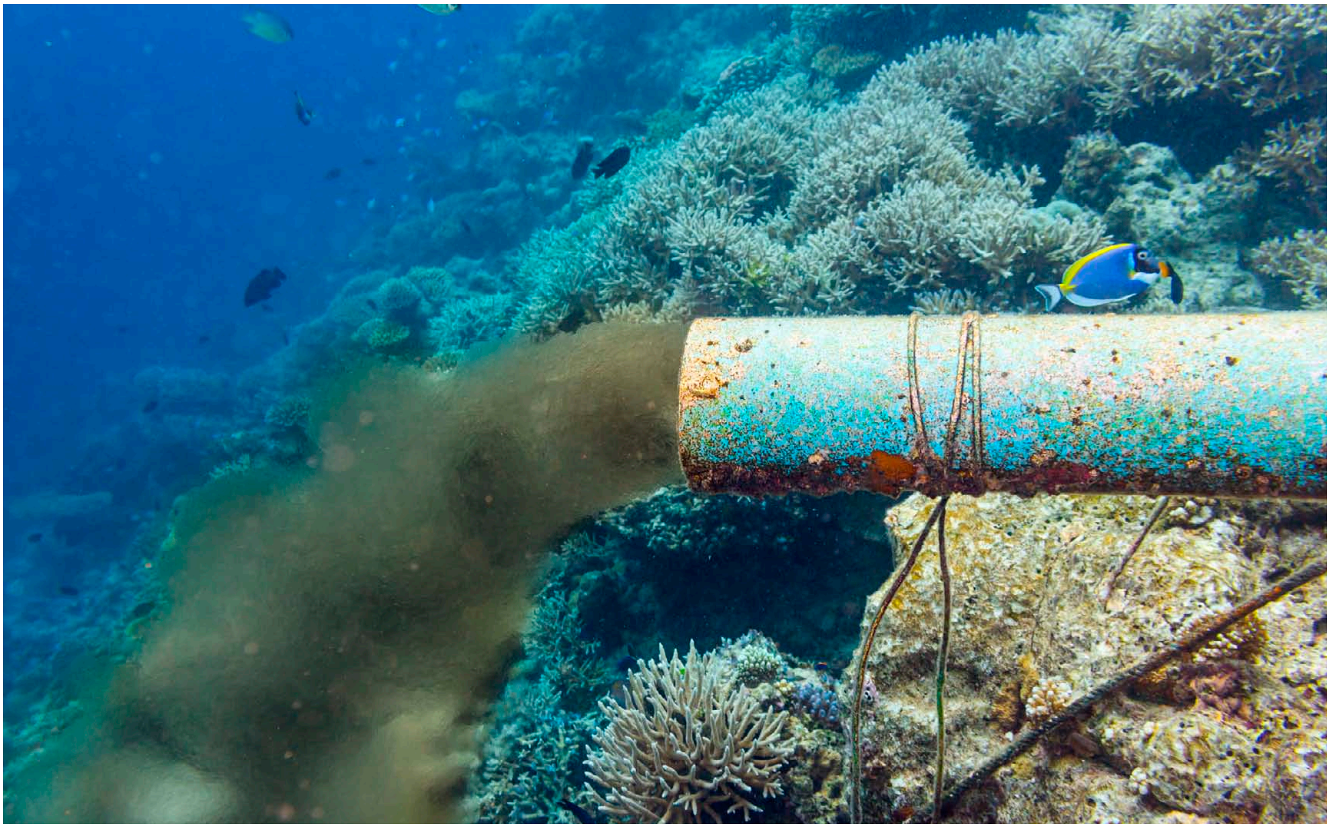
Another consequence of sewage is that it contains numerous human pathogens, such as *Vibrio* and *Rickettsia*, which are not normally familiar to corals, and can sometimes be harmful to them.

Overall, therefore, several factors from sewage combine to cause damage to corals. Firstly, there is a fertilizing effect of sewage that stimulates the growth of algae, which overgrow coral colonies. Also fertilized are the microbes that live naturally on the surface and mucus of the coral, so that the total microbial community is thrown out of balance. Added to this, some of the microbes are new ones that the sewage has introduced (see page 158). The net result of human sewage, therefore, is a combination of harmful effects, and badly affected corals and reefs cannot survive.

ABOVE | One of the *Vibrio* bacteria. *Vibrio* are pathogens from human and farm animal sewage, and several thrive in coral mucus, killing the coral.

TOP RIGHT | More sewage enters the sea through many small pipes than is discharged through better-regulated and treated municipal treatment centers. All add pathogens as well as harmful nutrients, which cause serious problems for corals and other reef organisms.

BOTTOM RIGHT | A sea fan, now killed and festooned with a mixture of fine, filamentous green algae and cyanophytes (strings of filamentous organisms related to the bacteria). This occurs when the nutrient balance of the waters around reefs is grossly disturbed.



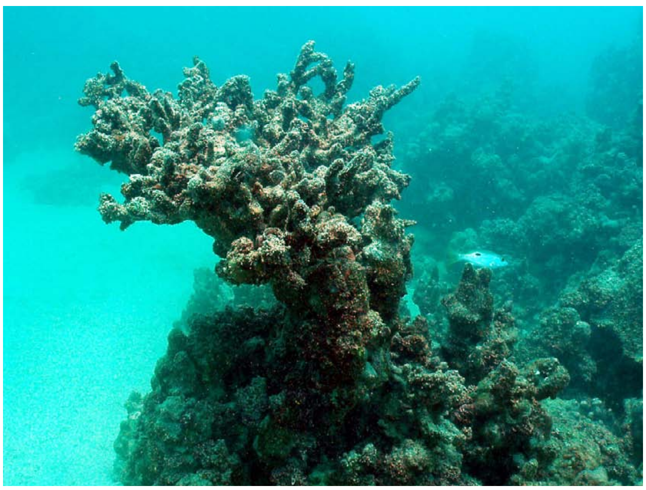
DISSOLVED NUTRIENTS ON REEFS

As previously discussed, one consequence of overfishing is the removal of grazers, resulting in much more seaweed on reefs. Seaweeds usually form the base of food chains, and there is loss of about 90 percent of biomass between each level of a food chain. Thus, roughly, a 100 lb (50 kg) shark or 100 lb (50 kg) barracuda will have been made from 1,000 lb (500 kg) of secondary carnivores, which in turn was made from 10,000 lb (5,000 kg) of herbivorous fish that grazed seaweeds, and that level was formed from 100,000 lb (50,000 kg) of seaweeds. So, 50 tons of algae is used to maintain one 100 lb (50 kg) shark or the equivalent mass of barracuda!

When overfishing has taken place, the algae will end up not as food but as huge quantities of organic material that decomposes and dissolves. This fuels microbes. There is a substantial density of microbes on the surface of corals, especially in the mucus they secrete. With more nutrients, more microbes grow. The addition of dissolved organic carbon exuded by disintegrating seaweeds greatly fertilizes the microbes on coral surfaces so that their numbers can increase tenfold or more. Of those that bloom, some may be directly harmful to the corals. But even harmless microbes are only harmless in "normal" densities. Rapidly growing microbes consume all the oxygen in the layer of water in contact with the coral, and also absorb the oxygen produced by the coral's photosynthesis. In short, the coral suffocates.

Unfortunately, this algal decay material is a mixture of many substances, not only nitrogen and phosphorous compounds, and is, in fact, a much more potent stimulant to microbial growth than nitrates or phosphates on their own.

The effects go on: when the coral dies and its own tissues dissolve away, more bare limestone substrate is created for



more algal growth. This in turn produces more dissolved organic material, and a positive or self-reinforcing feedback develops. Very often it is not a particular pathogen that is killing the corals in such cases, but just far too many microbes of the sort that occur naturally and usually harmlessly on their surfaces; microbes that were a part of the whole, balanced symbiotic system. The natural balance, in other words, has been disturbed.

OPPOSITE | Reefs are killed by too much nutrient in the water, especially sewage or sediment—these being a common combination. This reef, Fasht Adham of Bahrain, once the largest reef in the Arabian Gulf, is now dead and partly buried due to poor water quality and improper development practices.

BELOW | Dead coral skeletons, like this *Acropora* colony, are rapidly covered with small filamentous algae. These algae are grazed and kept under control on healthy reefs. When too much coral is killed and too many grazers are fished out, these algae will increase and swamp the surfaces, preventing new coral growth.

CORAL DISEASES AND SYNDROMES

Increased coral diseases often follow on from increased nutrients. They are complex, and it is difficult to study or cultivate the pathogens. Pollution and warming water can both trigger some microbes into becoming pathogenic; microbes may have lived on coral mucus for generations but in higher numbers they will become virulent, resulting in the coral's death. Generally the term "disease" is used when a pathogen is known, while "syndrome" is used where the causes are unidentified, so syndromes may become diseases when their microbes become identified by further research.

The first known reef disease pandemic was by a fungus in 1938 that killed two-thirds of the sponges in some Caribbean areas. Since then, reports have increased throughout the world linking disease occurrence and virulence to deteriorating water quality. Sewage-derived nitrogen is implicated in many cases, as is warmer water.

Many microbial groups are associated with coral diseases, including bacteria, slime molds, protozoans, blue-green algae (cyanobacteria), and several viruses, but often it is unclear which is the primary pathogen and which organisms just appear later, benefiting from the heavily compromised or dead coral tissue. Some diseases are caused by a combination of microbial types, and almost all are named from their appearance: white band disease, white pox, yellow blotch, purple band, and others. The pathogens may impart the color, but where white is part of the name the color is usually that of the coral skeleton. In white band disease, for example, which famously killed most Elkhorn

Coral (*Acropora palmata*) in the Caribbean, the white band was a strip of bare skeleton that moved along each branch as the disease progressed. Ahead of it, the coral was a brownish yellow, while behind it darker filamentous algae colonized the skeleton, leaving a white band in between.

Some diseases remain of minor importance while others have essentially removed entire reef zones. They are a symptom of reef ecosystem stress. Diseases are clearly increasing in variety and occurrence, as pollution increases and water warms. Disease *occurrence* alone, however, is not a good measure of disease *importance*. In a counterintuitive way, consider that the common cold may have an occurrence in a classroom of ten percent while the terrible medieval Black Death that killed a third of Europeans had an occurrence of less than one percent at its peak, because it was so virulent and quick that victims quickly died and were no longer "an occurrence." Coral disease is difficult to quantify, but is clearly becoming increasingly important.

OPPOSITE | Black band disease presents as an advancing band of black, moving across a coral. It leaves behind the bare, white skeleton. After the skeleton has been exposed for a week or two, it will darken again due to the growth of algae.

BELOW | White pox disease is associated mainly with the large Elkhorn Coral in the Caribbean. Patches of white appear where the coral tissue has been killed. It is distinguished from the similarly common white band disease, which forms a clear band that advances across the coral, rather than appearing in patches.

PROBLEM SPECIES
LIONFISH

Introduced species, meaning species introduced from their native region to another place far away, can sometimes be very problematic and cause expensive and extensive damage. Many familiar terrestrial examples exist, from the rabbit introduced into Australia to numerous weeds introduced across the world. Sometimes these establish but remain scarce or harmless (these are termed “introductions”) while others become invasive; they can spread like a plague, displace local species, and disrupt entire ecosystems. In the ocean, examples are less familiar but equally important: a jellyfish introduced into the Black Sea which has all but eliminated several species of fish; or the Zebra Mussel into North America, where it is choking waterways.

In the oceans generally, species most often become translocated in ballast water from ships, or attached to their hulls, or as escapes from home aquaria or aquaculture facilities. Some have been moved deliberately to introduce a new food source.

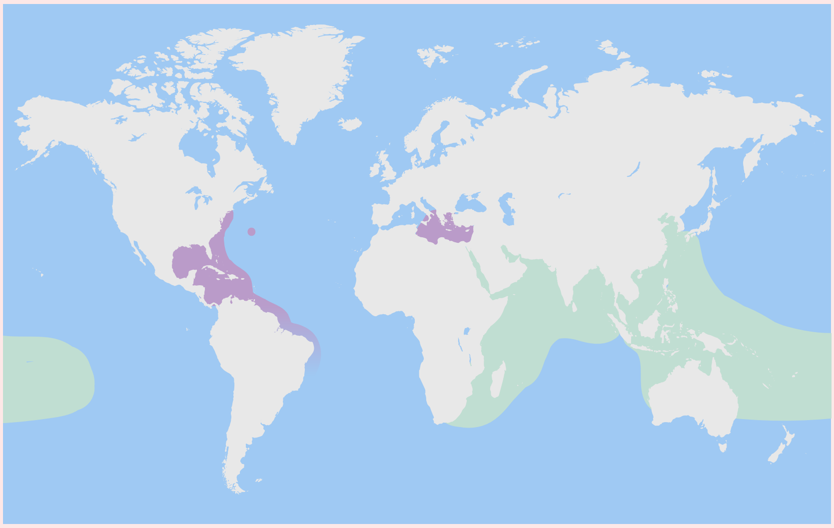
On coral reefs, a notorious example is the lionfish, an Indo-Pacific genus of 15 species, two of which, *Pterois volitans* and *Pterois miles*, now occur throughout the Caribbean, the southeastern seaboard of the USA, and Bermuda, and have reached as far as Brazil and the Mediterranean. These colorful carnivores are voracious predators. They have highly venomous spines in their fins that inject a very painful mix of neurotoxins.

When still small, lionfish are popular aquarium species. It is thought that they were introduced into the Atlantic from Florida in the 1980s, when six or eight were released from an aquarium. Over successive years they were mapped spreading southward through the Caribbean, and their spread did not take long.

Lionfish have few predators, and most native, smaller fish species are naive to them—they do not recognize them as being a predator to avoid. With such an abundant diet, lionfish grow quickly to 12–16 in (30–40 cm) long, and, unusually for fish, many even develop extensive fatty deposits. They reproduce rapidly too.

Attempts have been made to control their spread and abundance by spearing, with spearfishing competitions, leading to the production of recipes for eating them and making jewelry from their spines. These control methods have mostly failed because the fishes’ range extends into much deeper waters than divers can go. While local control efforts might have an impact at some popular diving sites, lionfish are in the Caribbean to stay, and research into their considerable ecological impacts is ongoing.

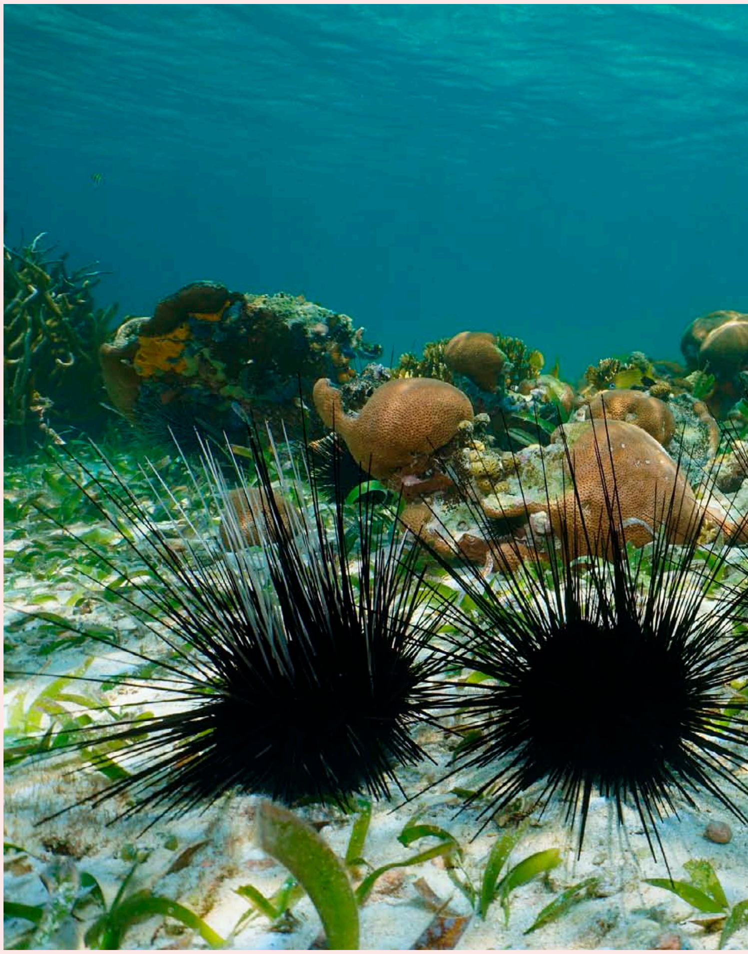
RIGHT | Lionfish spearfishing competitions have developed in an attempt to control the invasive species *Pterois volitans* and *Pterois miles*.



ABOVE | The lionfish *Pterois volitans* is identified by the "sails" on its highly venomous fins. It is a predator, and its bright coloration serves as a warning to larger predators.

LEFT | Map of the natural range of lionfish (green) and the areas in which they are now an invasive species (purple). The Caribbean and, now, the Mediterranean have been invaded.

PROBLEM SPECIES
THE *DIADEMA* DIEBACK



Grazing of algae by herbivores is crucial in the natural maintenance of coral reefs, because by keeping seaweeds closely cropped, the much slower-growing corals can thrive. While herbivorous fish are commonly the main grazers, invertebrate species like sea urchins are important too.

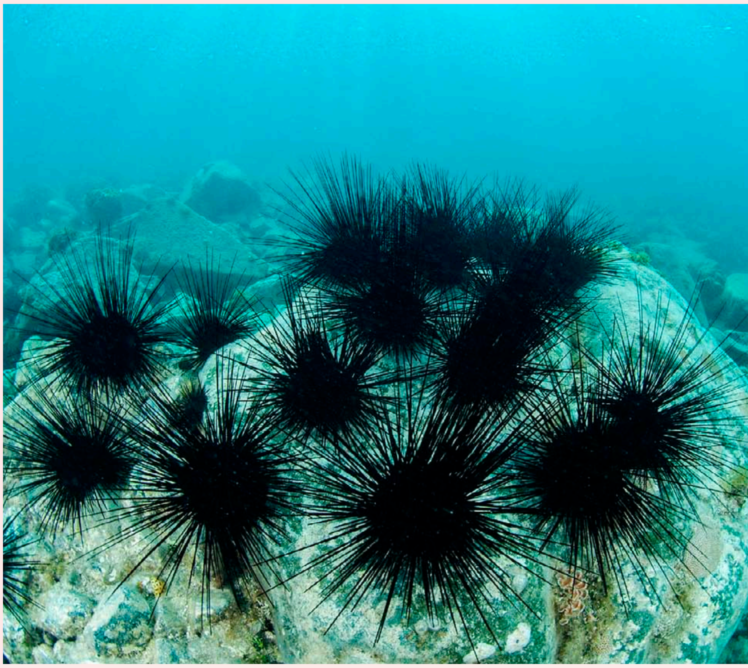
In the Caribbean, the black Long-spined Sea Urchin (*Diadema antillarum*) is very important. For decades, overfishing in the region had removed herbivorous grazers such as parrotfish along with the carnivores, at least 15 species of which fed on the Long-spined Sea Urchin. Without predators and with lots of food, *Diadema* thrived, and by the late 1970s this urchin had become the main or keystone grazer of algae in the Caribbean and became primarily responsible for preventing algae from outcompeting corals.

In the early 1980s, a disease of this urchin appeared in the Caribbean. The urchin had such high densities that the disease spread rapidly. It began near the Panama Canal, suggesting that the pathogen may have been introduced from ships in that region, perhaps through ballast water. In 1983–84 the disease swept through the Caribbean, killing about 97 percent or more of the *Diadema* present. Populations crashed and remained low for decades; although juveniles of this urchin were much less affected by the disease, recovery was almost nonexistent.

With many of the algae-eating fish species already overfished, many Caribbean reefs now had almost no herbivorous organisms at all, so the substrate became rapidly overgrown with leafy and fleshy algae. The obvious consequence was a substantial decline of reef-building corals, accompanied by a corresponding decline in many coral-associated organisms. There was an "ecological phase shift" in the region from coral-dominated to algae-dominated communities.

When populations of the corals were at these low levels, reproduction and repopulation simply did not occur. However, in some places natural reservoirs of urchins remained, and sometimes considerable programs of relocating urchins to badly affected areas has had beneficial effects. For these interventions to work, much laborious and expensive manual removal of mature algae needed to be performed first. When this was done, some recovery of the corals took place.

Today, in the Caribbean as a whole, some recovery has meant that population densities of these urchins have now reached about 12 percent of the numbers before the mortality; it is a low number, but the trend is in the right direction.



ABOVE | *Diadema antillarum* in the Caribbean. Their grazing activity controls algae to the benefit of corals. Many people consider them to be a delicacy.

ABOVE RIGHT | *Diadema* can graze almost all the turf algae from rocky surfaces in a short time. When they suffered mass mortality, the resulting dense algal cover inhibited corals.

PROBLEM SPECIES

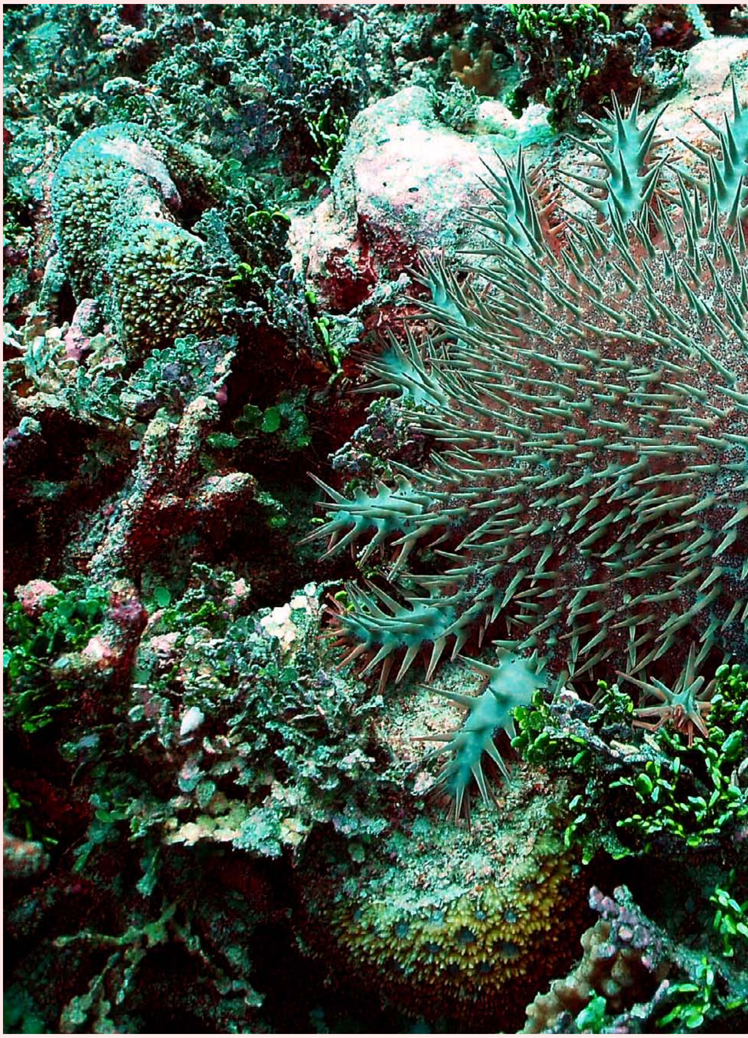
CROWN OF THORNS STARFISH

The predatory Crown of Thorns starfish (*Acanthaster planci*) has become an important cause of coral mortality in several areas across the Indo-Pacific. It is large, and can reach well over a foot long (a third of a meter) across, becoming one of the largest starfish. It has a large central disk and up to 20 arms, each adorned with spines that contain a toxin.

As an adult it preys on coral. It is surprisingly flexible and agile, climbing up branching corals as well as onto massive corals. It feeds by everting its huge stomach outside of its mouth and over the coral, flooding the coral with digestive juices, and then sucking the digested liquid back into its body.

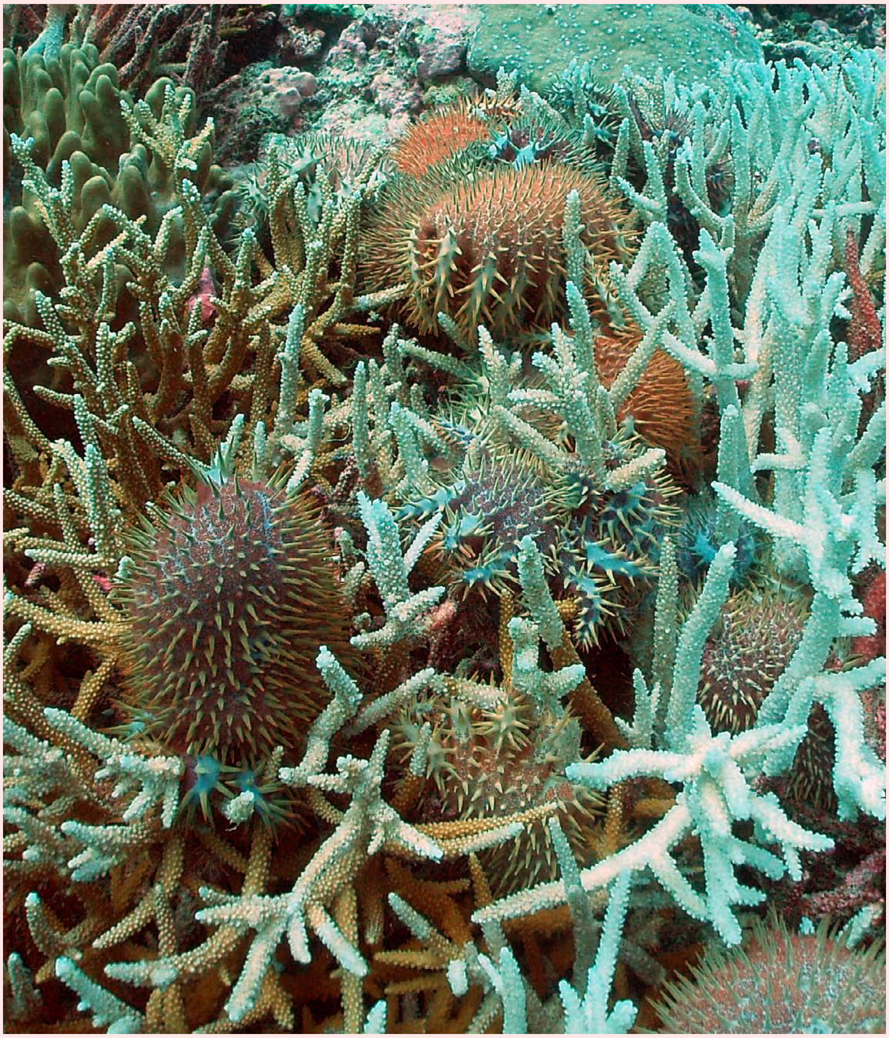
The Crown of Thorns starfish is a normal component of many reefs, where it can be spotted in very low numbers. However, it becomes very destructive when it occasionally appears in plague densities of up to a dozen per square meter over many hectares. A reef hit by one of these plagues will be stripped of its live coral tissue after a few weeks. The corals are left as intact white skeletons when the plague of starfish moves on.

It was generally thought that there was only one Crown of Thorns species that affects reefs, *Acanthaster planci*, but recent genetic work has shown a marked difference between the Indian and Pacific Ocean forms, and indeed there may be four different species in the Indian Ocean. All behave similarly, and there are no clear visible differences between most of them.



Why these starfish develop into plagues is unclear. Initially it was thought that overcollection of predators, especially of the large Giant Triton mollusk, was responsible, and it may indeed be a small contributing factor. More plausible is the observation from Pacific islands that plagues develop a few years after major rain events on volcanic islands, when nutrients are washed off hills into the sea, where they fertilize the plankton that are food for Crown of Thorns larvae, enabling vastly greater numbers to grow into adults. This would not explain plague outbreaks in all places though. A contrary opinion is that they are part of a normal cycle, supported by evidence from spines in cores that suggest plagues also occurred thousands of years ago.

Management has been and continues to be to remove them, initially by collection and then by divers injecting them with poisons on reefs deemed to be of special importance. This is expensive and, while effective on very small scales, it does not significantly prevent their spread.



ABOVE | A Crown of Thorns starfish feeding on a *Porites* coral, working its way from left to right. The bare *Porites* skeleton is visible above the starfish.

ABOVE RIGHT | Plague numbers of Crown of Thorns starfish on branching coral, leaving the consumed, now white, corals still standing. The white is simply the bare limestone skeleton. The starfish wrap around each branch closely to contain their digestive juices.

SHORELINE DISTURBANCE AND DEVELOPMENT

Landfill and dredging are both inevitable consequences of shoreline development, but are two of the most harmful coastal activities affecting coral reefs. Sometimes this is because of direct burial of the shallow reefs, and this occurs because fringing reefs especially provide good building land for development. After all, broad, flat expanses on the coast are prime areas for building property. It is now the case that a coral reef is worth more in monetary terms to a developer when it is no longer a reef at all, but is simply a foundation upon which expensive property is then built. The scale of this activity can be huge: more than half of the shorelines of some Middle Eastern states are now artificial, meaning that the coral reefs in the Arabian Gulf are now mostly dead.

Fill material is needed for such development and often this comes from dredging the immediate offshore sandy substrates. Every hectare of fill used to raise the elevation of the new land above sea level may require dredging of approximately the same area of offshore substrate. This directly removes that sandy habitat, which commonly would have been rich in seagrasses and a nursery ground for marine life. Clearly this also destroys the marine life of the area being excavated, and around the world there are many examples of islands being built on top of formerly rich coral reef, for example in the Paracel and Spratly Islands (see page 169).

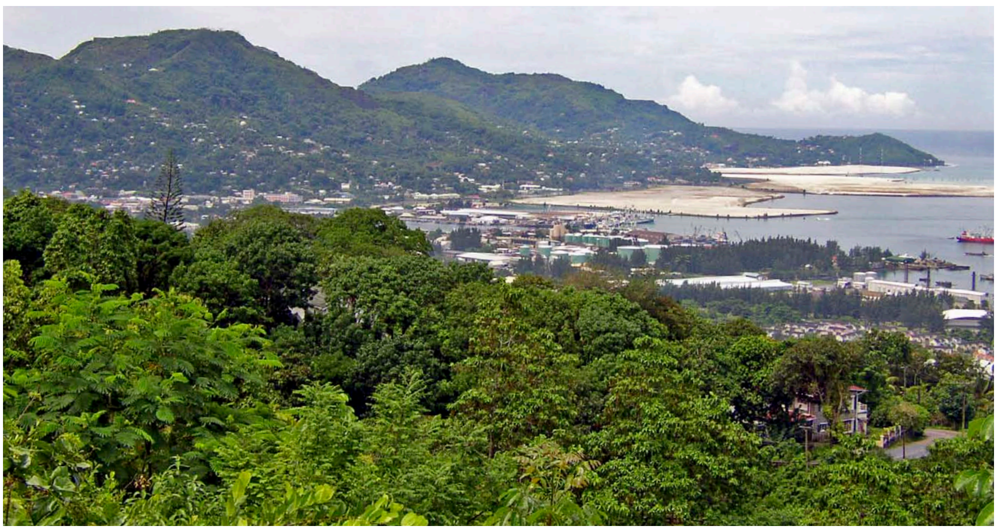
Along the shoreline, land and sea are usually in equilibrium, but dredging disturbs this, so the sea then starts to reclaim the newly built land, showing the irony of using the word "reclaiming" for the initial landfill activity.

In many areas, most notably atoll lagoons, there are countless coral pinnacles, often called bommies or knolls, and these are commonly removed by dredging or explosives to make conditions safer for shipping.

The damage to coral reefs from these activities has been huge, but may be masked by the sanitizing terminology used by developers. "Reclamation" instead of landfill has already been mentioned. Others include "borrow pit" for the area excavated, and even the term "soil improvement" may be used for landfilling over the adjacent coral reef during the process of turning coral reef into solid building foundations. These terms do not alter the fact that the reefs affected are permanently destroyed, along with adjacent rich habitats.

ABOVE AND TOP RIGHT | The artificial Palm Islands and a hotel in Dubai, both part of the coastal development of Dubai and the Arabian/Persian Gulf. The water is very shallow in this region, so water exchange is reduced.

RIGHT | Off the coast of Malé in the Seychelles. Much landfill for construction has taken place over the shallow coastal strip, burying all marine life, in this case, seagrass beds as well as coral reefs.



LEFT | The corniche at Jeddah, on the Red Sea, has been partly built over the flat of the fringing reef. According to two Saudi professors, Jeddah's corniche now contains the world's most polluted waters—ten times that of the global average. This is due to a mixture of sewage discharge and massive sediment during construction.

ABOVE | Some of the most substantial developments on reefs are military in nature, like those of the Paracel and Spratly Islands, in Southeast Asia. The ability of reefs to form expanses of flat land at near sea level makes them attractive sites for planners. Although each military development may destroy huge areas of reef, the amount of destruction globally is far smaller than that caused by countless small- and medium-size commercial developments around the world.

SEDIMENTATION

Seawater over coral reefs is generally very clear, an attraction for divers and swimmers. Visibility in nearshore reefs is commonly over 30 ft (10 m), and may reach 100 ft (30 m) or more in reefs surrounded by deep water. This water clarity is due to the lack of particles in the water, which allows light to penetrate deeply and permit the photosynthesis that allows corals and soft corals to flourish. One factor that can greatly reduce water clarity and the penetration of light is sediment, especially very fine clay particles, which can remain suspended in the water column for a long time.

Shoreline development, especially dredging, is a major source of increased sediment in shallow coastal waters. More responsible methods of excavation do exist, such as deploying underwater screens and better methods of cutting and extracting sediment, but in many projects these are simply not used. The resulting plumes of sediment are commonly carried for many kilometers down-current. Larger particles settle first, but the finer particles may be carried many times further before they precipitate onto the seabed.

Sedimentation is particularly damaging to coral reef organisms. Firstly, simple smothering takes place. Where this is mild, corals can slough the particles off to a certain degree, although this is an energy drain on the organisms which impairs their ability to grow and to reproduce. The energy needed to remain alive and functioning in the first place comes from photosynthesis, but this is reduced when sediment in the water reduces light penetration. Dredging excavates and disturbs the substrate to a greater depth than even a large natural storm does, so a greater proportion of finer particles—the more harmful kinds—are suspended. Whenever fine sediments are released into the sea, they clump together with organic particles like dead plankton to form marine snow. This settles to the seabed, where it blankets the substrate with soft sediment and denies coral larvae a place to settle. In this way it discourages reef development.

All marine species that live on the seabed can survive brief exposures of sedimentation, and do so after any storm. Engineering works, however, usually last considerably longer than a natural storm and typically release a higher proportion of the more harmful, finer particles.

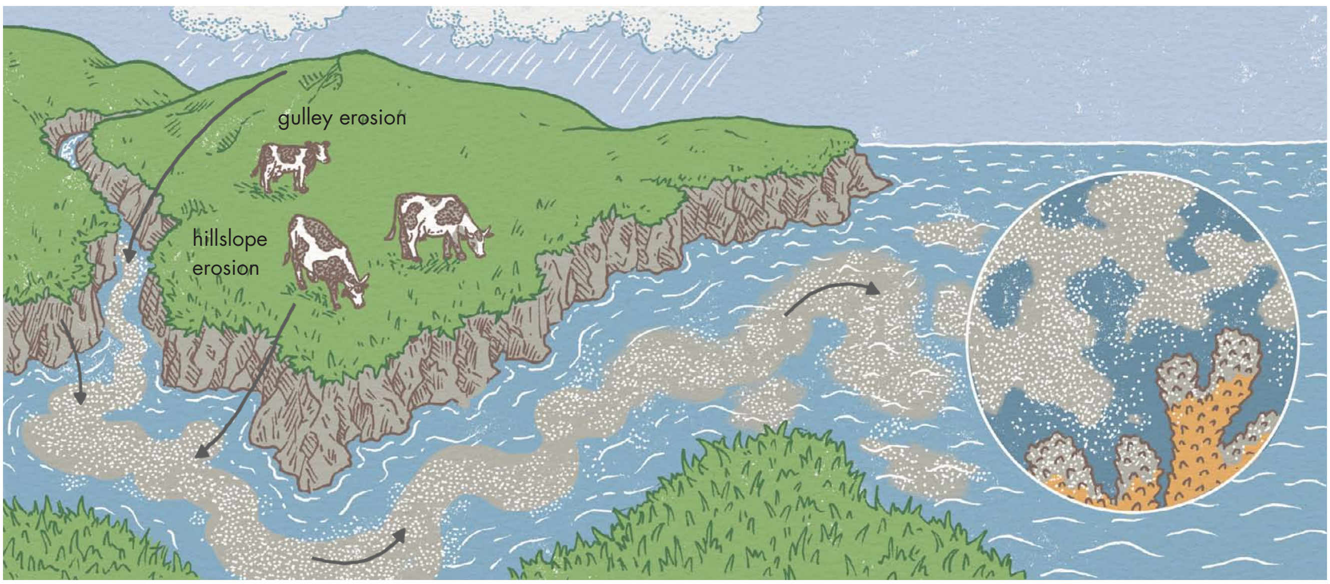
Another consequence of greatly increased suspended sediment is the release of phosphate and nitrate molecules that were attached to each sediment particle but which become released into the water. This can have damaging consequences to corals that are similar to those of sewage (see page 154).

ABOVE | Most corals on this sheltered reef flat have been killed by sediment; this sponge has survived because its branched shape has elevated it out of the layer of silt.

OPPOSITE TOP | Dredging is used to enlarge and deepen areas around ports. Ships excavate the seabed and discharge most heavier particles into their hold for later landfill. The rest are discharged, forming damaging plumes of silt that can spread for miles and blanket coral reefs and other marine habitats.

OPPOSITE | Deforestation and ploughing for agriculture can produce many tons of mud and silt from each acre of destabilized land. These can smother entire reefs. Excess nutrients from agriculture also flow into rivers and the sea with rain water running off the farmland.

RUN-OFF OF FRESH WATER AND SEDIMENT ONTO A REEF



FRESHWATER RUN-OFF

The natural salinity of seawater averages about 34 parts per thousand (ppt), though this varies according to evaporation and rainfall. On any one coral reef, dilution of the seawater on the reef flat to below 15 ppt after monsoonal rain, or concentrated to above 45 ppt after severe evaporation in the midday sun, may occur and may be tolerated by some species for short periods. The Arabian Gulf is a classic example of corals living in extreme salinity conditions.

Some coral species are more tolerant than others of fresh water. Fluctuating amounts of fresh water can be more harmful than a sustained high level. On a grand scale, the fresh water from the great Amazon River has had the major consequence of isolating the Brazilian assemblage of corals from the rest of the Caribbean, leading to numerous endemic species in Brazil as a result.

Rain itself usually directly contributes less than one percent of the nitrogen and phosphate to a reef, but rivers from inland watersheds are an important source of new nutrients to water surrounding coral reefs. Quantities vary seasonally and with flood events, so the effects on a coral reef fluctuate, but they are generally greater nearer river mouths, with the effects depending to a great extent on the nature of the agriculture on the catchment area and other uses of the land that the river has drained. Many reefs, especially oceanic atolls, have no rivers at all. In the case of many atolls, the undersea

mountain on which the reefs sit causes upwelling of ocean water from deeper, nutrient-rich areas instead.

While nitrogen and phosphorus are usually regarded as the main nutrients for reefs, fresh water may also carry others such as iron. As with most things, small amounts can be very beneficial, but excessive amounts can be very damaging.

Flooding events are increasing in those areas where rainfall is increasing due to climate change. Along with the freshwater input, which might be damaging in itself, significant quantities of toxic substances and sediment can be discharged. Where the adjacent land has been cleared of its forest cover, especially where it is steeply sloping, vast plumes of mud can be swept into the sea along with the toxic substances, and these smother considerable areas of reef. In some areas, freshwater effects are changing the composition of corals on the reefs.

OPPOSITE | Run-off from a small river in Indonesia, carrying pulses of dirty and sedimented freshwater from land into the sea.

BELOW | Land run-off after rain brings both sedimentation and huge volumes of freshwater onto the reefs fringing this island. Both are harmful to corals.

CHEMICAL, PLASTIC, AND OIL POLLUTION

Chemical pollution on coral reefs can be particularly insidious. Minute quantities of several chemicals are very poisonous, and many accumulate up food chains before being consumed by people. In all marine organisms, different metals or chemicals can affect different stages of the life cycle, while some are highly toxic to particular tissues, such as nerves or reproductive bodies. Where such chemicals are absorbed by a filter feeder, or by seaweeds consumed later by herbivores and then finally by people, the effects can be very damaging to human communities.

Organic pollutants are more numerous than metal pollutants and many damage natural biochemical processes of living tissues. Some become processed by the body into substances with even greater toxicity. Herbicides and antifouling paints used to keep boat hulls clear from animal and plant life are, after all, designed to be very toxic so are particularly damaging, affecting algal cells in corals and soft corals as well as larger plants. Chemicals such as "booster biocides" used in antifouling paint inhibit photosynthesis in concentrations as low as 50 parts per billion of water.

These pollutants come from industries, and some tropical countries have limited industrial regulation and pollution control. Disposal of toxic wastes may be unregulated and expensive, so many are simply dumped untreated into the sea. However, toxic chemicals may also come from inland agricultural practices. On the Great Barrier Reef, for example, numerous pesticides are discharged from farms into rivers, which then flow through catchments and move offshore with flood plumes, where they can be detected on coral reefs.

Plastics are both unsightly and damaging. Many animals become entangled and strangled in them, including in discarded fishing nets that continue to catch fish for years, called "ghost fishing." Further damage comes when plastics break down to plankton-sized particles—microplastics—which are consumed by filter feeders. There is no nutrition in them and they cannot be digested so the animals die of malnutrition. In addition, many pollutants bind specifically onto them so the animal is also poisoned.

Pollution from oil spills may come from the crude oil itself, as some substances in oil do dissolve in seawater. Some oils will float over a coral reef and cause little damage if their toxic components evaporate quickly in the hot sun, but the heavier residue can then sink and smother the coral. Oil from some regions contains toxic components with a higher solubility, poisoning corals to over 25 ft (8 m) deep. Clean-up procedures may use oil dispersants, but their use multiplies the effects of oils on corals and other reef life.

ABOVE | A turtle hatchling making its way to the beach, impeded by plastic debris. Birds easily pick these struggling hatchlings off for food.

OPPOSITE TOP | Plastic entangled in seafans. This will break down into smaller fragments in a few months, but possibly not before killing the seafan. In many parts of the world plastic pollution has become an inescapable blight.

OPPOSITE BOTTOM LEFT | Oil spilled on a shoreline can be cleaned up using various methods, some more useful or damaging than others. Here, oil-absorbing pads are being spread.

OPPOSITE BOTTOM RIGHT | Mangrove roots, which are located in the intertidal zone, are especially vulnerable to oiling. Mangrove trees oxygenate themselves through these parts of their roots and oil blocks these, killing the tree, which in turn allows more run-off to damage offshore reefs.

BOAT ANCHORING

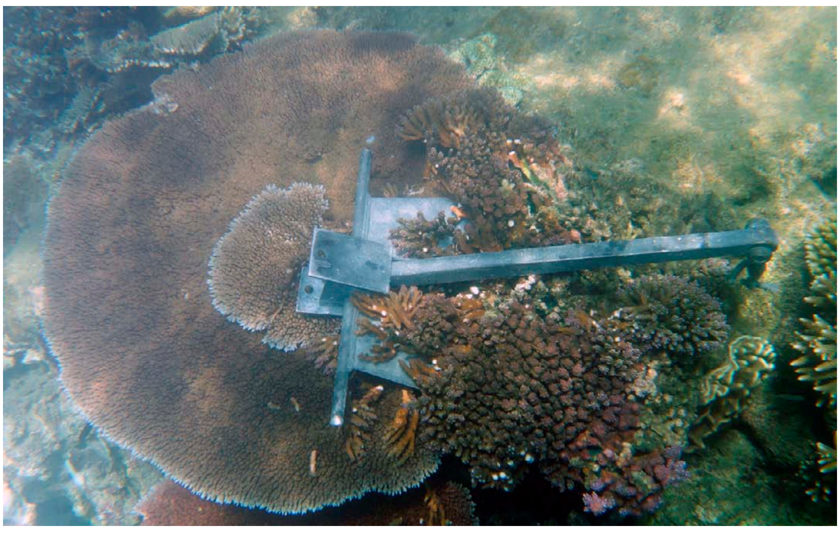
Boat anchoring on coral reefs is directly damaging. In areas where there is a lot of small boat activity, such as hubs for vacation sailing, rentals, or local fishing fleets, this can be very important. In other areas near the major tropical harbors of the world, large ships anchor while waiting their turn to enter port. Anchor damage is usually not evenly spread around the world but is localized and concentrated across selected parts of an archipelago or island, mostly in sheltered areas. However, in some of these localized areas, anchoring has destroyed entire coral reefs as well as extensive areas of seagrass.

The damage comes both from the anchor and from the chain that is dragged around by the boat on every tidal cycle, scraping areas bare and killing life in a circle whose radius is equal to the length of anchor chain on the seabed. Preferred anchoring areas are where water is calm, in bays or protected reefs, places that are also favored habitats for delicate forms of corals, particularly branching and leafy forms. A relatively small pleasure yacht can create a "halo" of pulverized reef over 30 ft (10 m) in diameter with each drop, and each may anchor more than a couple of dozen times during a typical two-week vacation. Larger ships with chains whose links are each more than 100 lb (50 kg) will pulverize more than 32,000 sq ft (3,000 sq m) of coral reef with a single anchor drop, and links that size can splinter the largest brain corals of 300 years old in one day. Recovery has been quoted as taking more than 50 years, though when corals several centuries old are turned into rubble this can clearly be much longer.

The same effect occurs on seagrass beds, where anchor halos of white sand take the place of seagrass until these halos fuse to turn a seagrass bed into a bare sandy area.

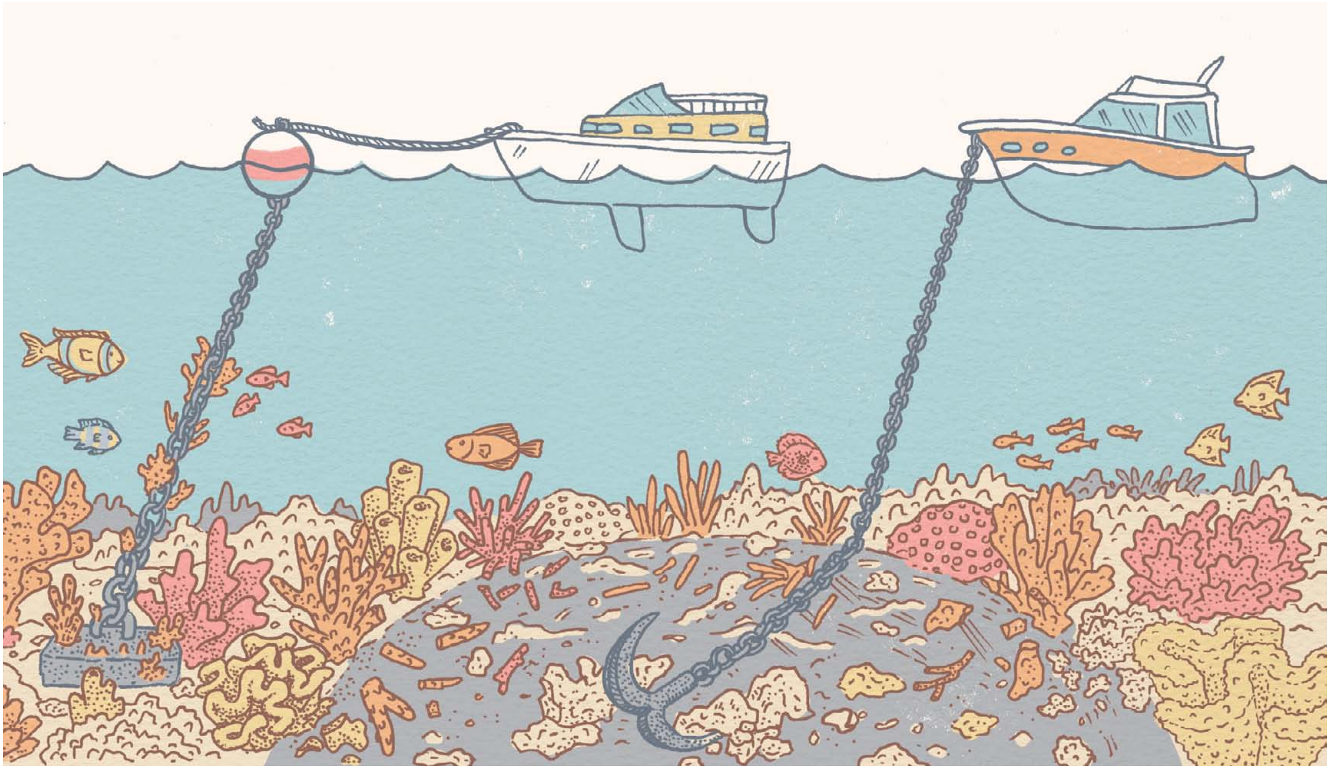
In several vacation destinations, entire reefs around islands have been destroyed. Continued anchoring then grinds the rubble to ever-smaller particles, creating clouds of silt which drift down-current, causing damage further afield.

The solution in many places is simple: provide moorings—fixed stationary points attached to the seabed to which a floating buoy is attached for boats to tie onto. Even though simple, for some Caribbean islands where boating tourism is popular, this has come into wide effect too late for many reefs.



LEFT | Anchor damage can be caused by both anchor and chains. Table corals and branching corals, like these in the Great Barrier Reef, are particularly vulnerable to anchors.

MOORING VS ANCHORING ON REEFS



ABOVE | Fixed-point moorings (left boat) have a riser from a fixed point onto which a boat can hook. No damage is done to life on the sea bed and moorings can remain in place for years. Anchoring, in contrast (right boat), may take place daily for each boat. The anchor crushes corals, as do the lengths of anchor chain lying on the bottom that pivot around the anchor as the boat swings on the tide.

RIGHT | Seagrasses around reefs are also damaged by anchoring. This shows tracks where anchors have dragged repeatedly across a shallow tropical seagrass bed.

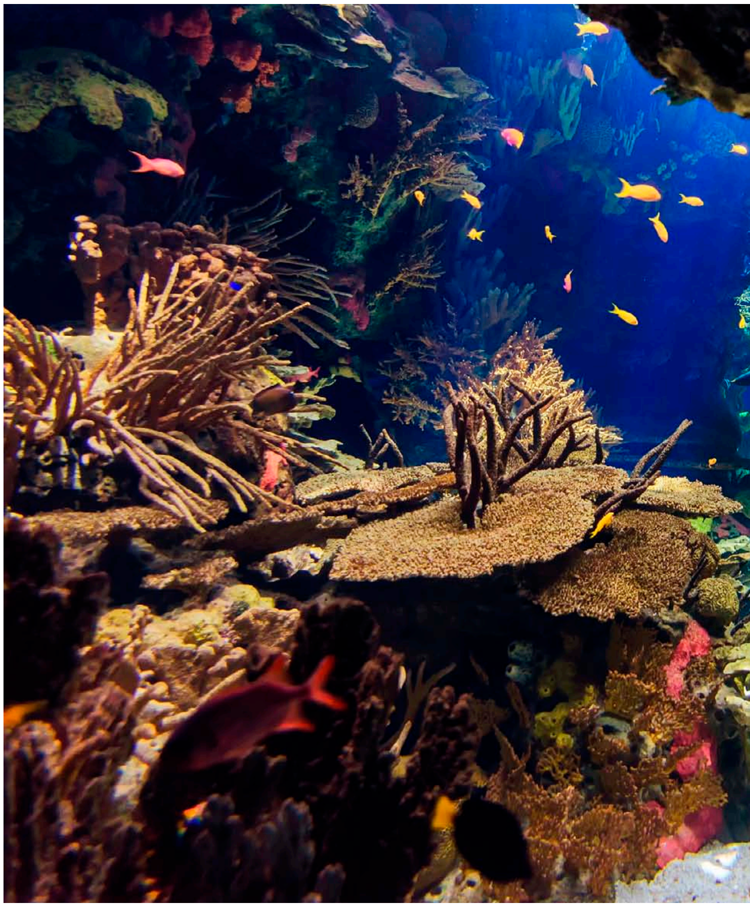
LIVE CORAL AND REEF FISH TRADE

Collection of live coral is principally for display in domestic and public aquaria. The same applies to reef fish, too, but with the major addition that larger, high-value species are collected for live export and consumption in restaurants.

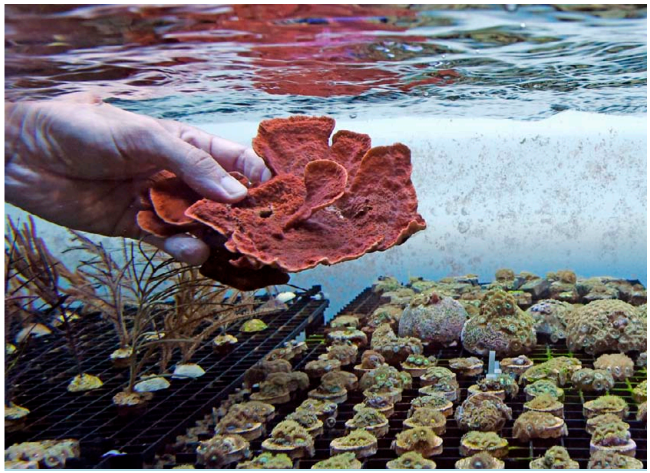
Live export of fish for consumption now exceeds around 65 million pounds (30,000 tonnes) per year, mostly of Indo-Pacific species that trade through Hong Kong before being shipped to China. Most of the remainder come from Caribbean reefs for consumption in the Caribbean tourist spots and the USA. This trade provides many jobs and is important to the economy of some small Asian countries, and the overall value may reach $1 billion per year, so demand is high. The rarer a species becomes, the higher its price rises and the more sought-after it becomes. Grouper of several species are favored, and some are now vulnerable to even low levels of fishing pressure. The incentive to capture them means they become depleted over increasing areas. Some capture methods use destructive chemicals, including cyanide, to temporarily immobilize fish, which causes considerable collateral damage and mortality to the habitat and other fish as well.

In the aquarium trade for reef fish, small and colorful species are favored. Supplying marine aquaria worldwide is a lucrative business: over 25 million specimens of fish are traded annually. There is substantial mortality during transport, and once in aquaria mortality may be high too. Captive cultivation of such fish is developing, but does not yet significantly reduce collection from wild populations.

Collection of corals for aquaria is also destructive. Methods to propagate corals in large tanks are sometimes now used, but the simplest methods in the wild, including the use of crowbars to prize a coral from a reef, remain widespread. Mortality also remains high. “Live coral rock,” meaning rock covered in algae and invertebrates, is needed to keep an aquarium healthy, and this too is commonly prized from reefs for sale. Some corals are easier to maintain alive than others in aquaria, but all require exceedingly low levels of nutrients in the water. Some species are perceived to be much more attractive than others, so are targeted in some areas almost to extinction.



It is argued widely that the educational value of aquaria is beneficial and, while undoubtedly true, much more regulation and control over the industry is needed to outweigh the destruction that occurs.



LEFT | Some fish are captured for public and home aquaria. Less damaging than some forms of fishing, these methods do target and deplete many small, colorful species. It is hoped the educational value surpasses the ecological damage.

ABOVE | Home and public aquaria are increasingly supplied by farmed corals rather than corals taken from reefs.

BELOW | Several kinds of reef fish are now grown on in tanks for the live seafood trade, though other facilities are trying to grow on colorful reef fish species for the aquaria trade too.

CHAPTER 5

CLIMATE CHANGE AND REEFS

CLIMATE CHANGE AND THE CO_2 STORY

Climate change is happening, caused primarily by human use of coal, oil, and other fossil fuels. Their burning converts a concentrated source of energy, which has been of immense value to humans over the last several centuries, into carbon dioxide (CO_2)—a "greenhouse gas"—and water vapor. There are still some people who deny that climate change is happening, but it is foolish to ignore the physics of what humans are doing.

Climate change happens because we both burn fuel and convert land from forest to other uses that do not store carbon, frequently burning these forests and releasing that stored CO_2 as well. We know how much oil has been extracted since its discovery, and we know how CO_2 absorbs infrared from sunlight to raise temperatures; we also have a good and ever-improving idea about how different industries and farming emit or sequester the gas. Regardless of the exact causes, global CO_2 has risen from about 270 parts per million (ppm) in pre-industrial times to over 400 ppm today. Global temperatures have, as a result, risen by about 1.8 °F (1 °C). The rise is neither smooth nor evenly distributed around the world. Many effects depend on the locality: it might make some dry places drier, and some wet places wetter, with massive consequences to agriculture and people.

One degree or so may not seem a lot, but in two places in particular it has marked effects. The first is the edges of polar regions, where the difference in, say, being 31 °F (–0.5 °C) and 33 °F (+0.5 °C) is the difference between being ice or water. The other is in tropical regions, including coral reef areas, where life forms have been thriving for millennia near the temperature limits at which their metabolism can

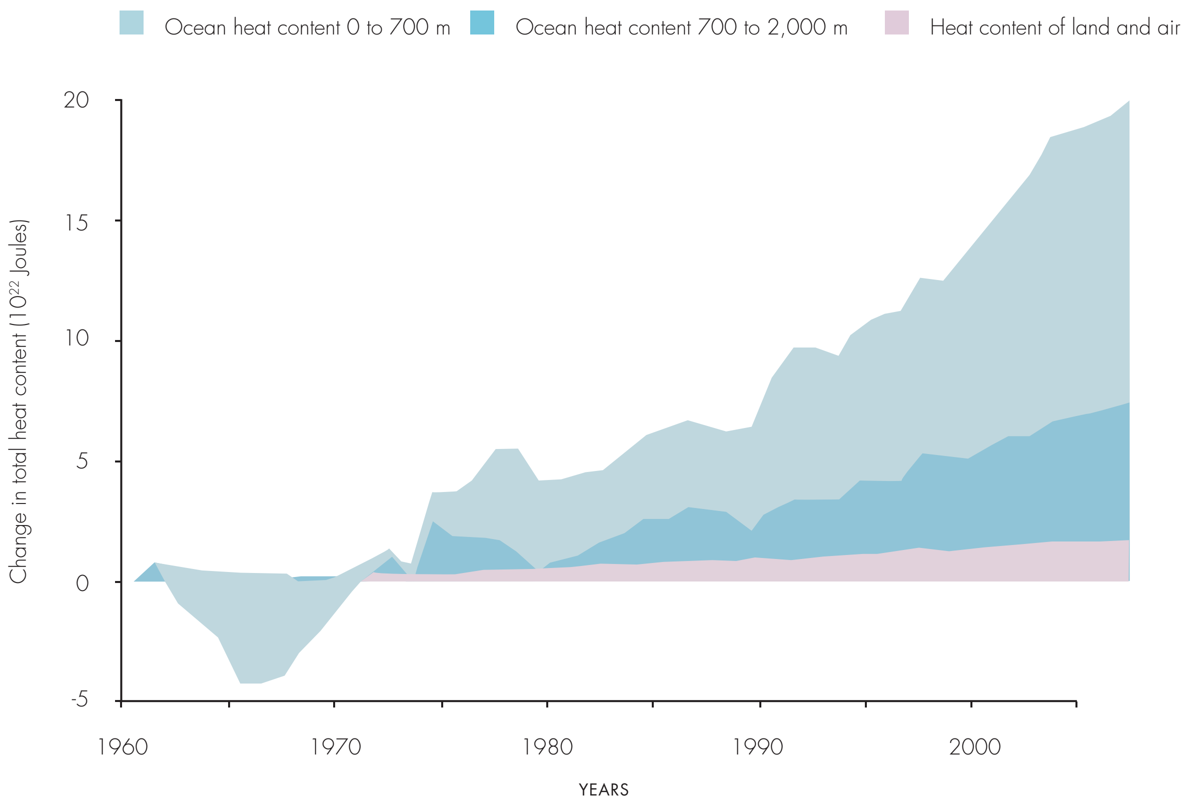
best function. Coral reef species have adapted to these warm temperatures and have never had to deviate from them, and for life forms in these regions a degree or so more means the difference between performing optimally to being overheated and struggling to survive.

Another effect of CO_2 is acidification, and the two factors work together. When CO_2 dissolves in water, it bonds with it to form carbonic acid, with a debilitating effect on many forms of marine life, especially calcifiers like corals (see page 189).

For corals, the gradual and seemingly modest temperature rise forms an ever-increasing background to the irregular temperature spikes, called marine heatwaves, that are now occurring.

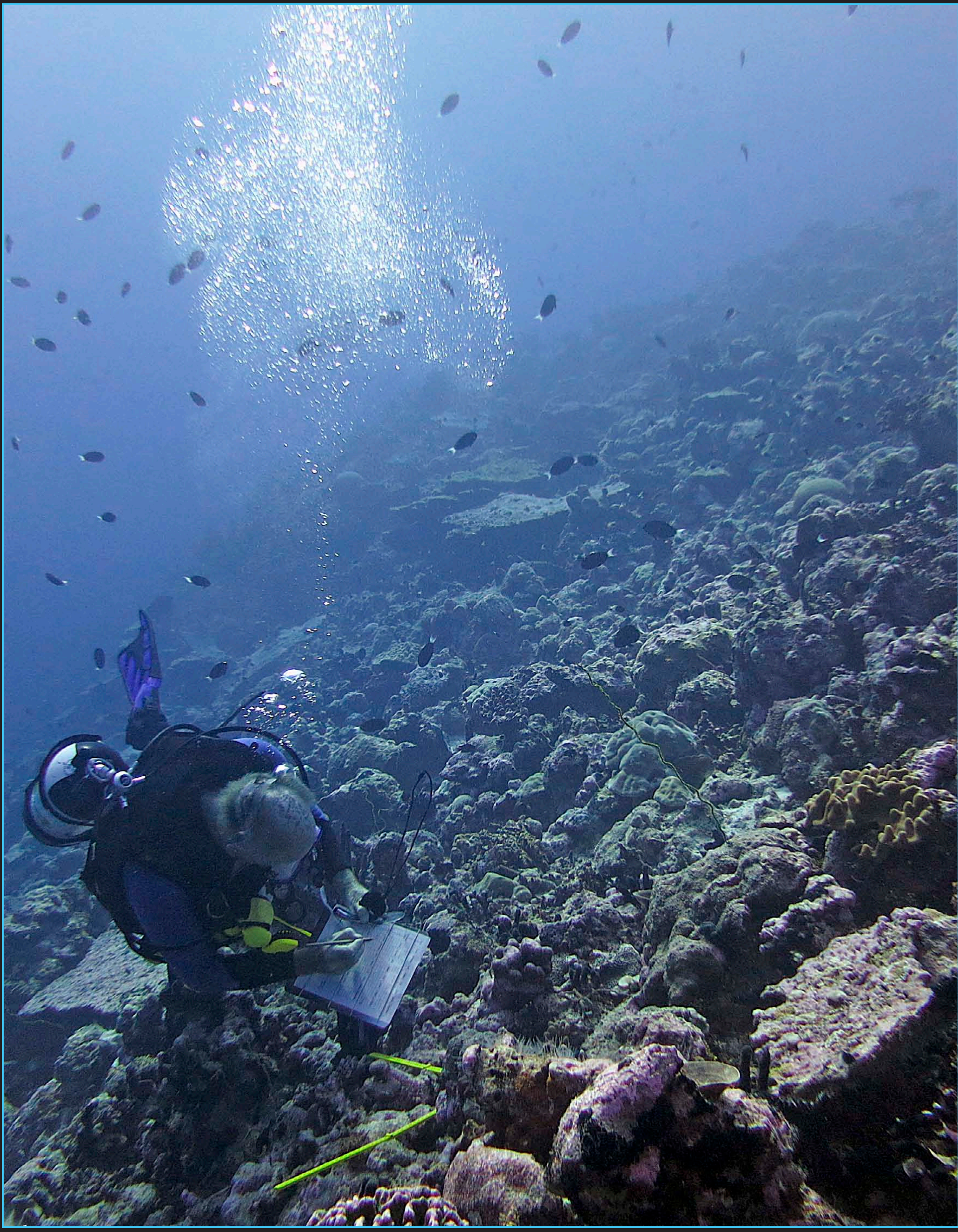
OPPOSITE | All the white corals have been bleached: their symbiotic algal cells have been expelled because of stress. They may recover or, if the warming was too great and lasted too long, they will die.

BELOW | Heat absorption over the last 60 years by different compartments of the planet: shallow ocean, deeper ocean, and land and air. By far the most has been absorbed by the shallowest part of the ocean, followed by the deeper part. The entire surface of the planet, meaning land (including the ice caps) and air, have absorbed a much smaller amount.



ABOVE | Healthy corals are dominated by greenish-brown colors because of the vast number of photosynthetic algae cells contained within their tissues.

RIGHT | A reef slope after corals have died in vast numbers during an episodic ocean heatwave. Small seaweeds and other organisms have grown on and eroded the skeletons.



EFFECT OF WARMING ON CORALS

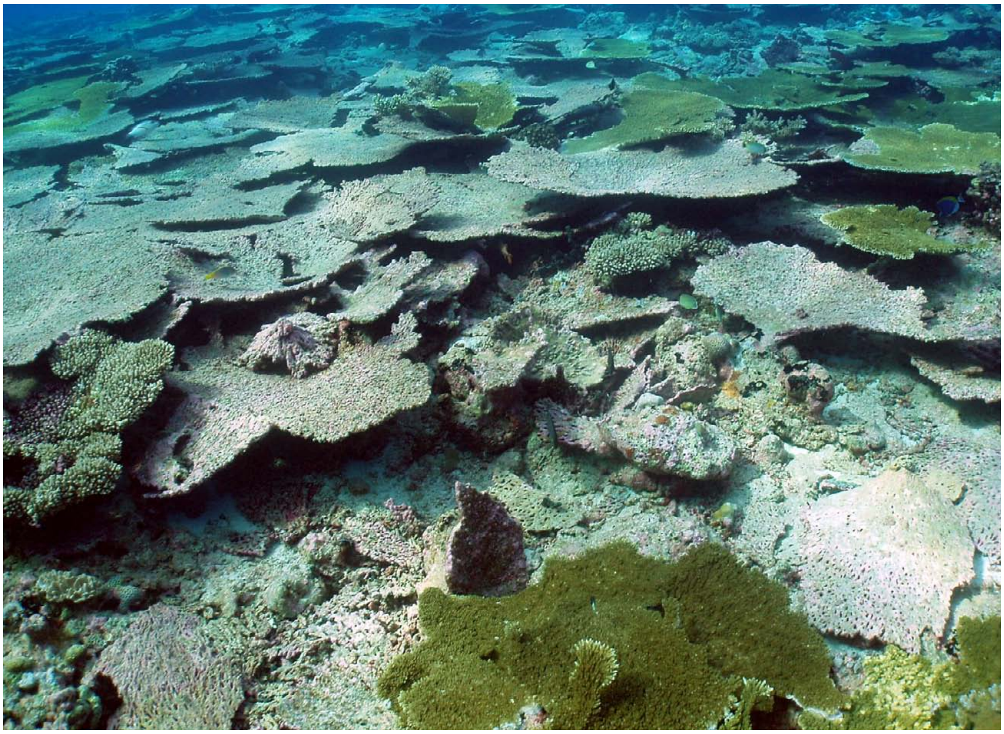
The now well-known phenomenon of coral bleaching that is increasingly being seen across the coral seas is the result of warmer seawater. Bleaching is caused when a coral is stressed, in this case by heat, because the coral expels its symbiotic algal cells and their strong color is lost, allowing the white coral skeleton to show through. The algae supply much, even most, of the food for the coral, so two things can then happen: if the warming is not too severe, the algae may later recolonize and restore the coral, but in more severe cases the coral dies. All over the world, both events have become widespread. Probably half of all the world's corals have been killed, though on some reefs recovery has since taken place.

This whitening does not happen immediately when water warms, but occurs after a lag of a few weeks, depending on the severity of the heatwave. It is not only the temperature that is important, but also the duration over which it is raised. A simple index has been developed to monitor and predict this, called "degree heating weeks" (DHW): the temperature in degrees Celsius above what is normal, multiplied by the number of weeks it is raised. At about four DHW many corals begin to bleach, and eight causes widespread bleaching on a reef. The latter can be made up of one degree for eight weeks, or two degrees for half that duration, or a mix of the two.

Why does the coral expel its essential algae in the first place? It is not heat alone that causes the problem. Stronger light can penetrate because the additional warmth may stall trade winds, which reduces the waves and makes the sea surface calmer. A less turbulent surface lets more light penetrate, so the light reaching the coral may be more intense than usual. The combination of more light and higher temperature causes the algae to photosynthesize much more, producing an excess of oxygen in its single atom state (not bound to others as molecules). These "free radicals" of oxygen are highly toxic. The coral animal expels the source of the damaging chemical—hence bleaching.

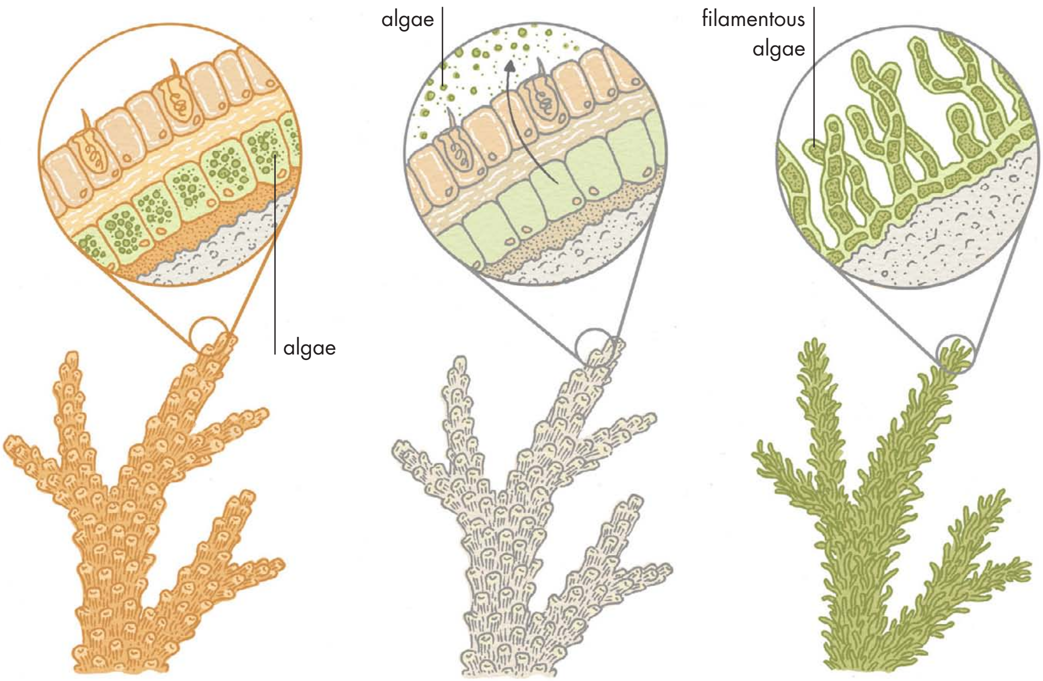
Many examples exist on reefs of massive-shaped corals where the tops were killed after a warming event but the sides were still covered in apparently healthy coral polyps. The water around the colony was the same temperature; only the amount of light differed, being highest on the tops, but much lower on the sides and shaded parts, so the sides survived.

BELOW (BOTH) | Both photos show that coral bleaching and death are caused by a combination of heat and bright light. In these, only the top (the part most exposed to sunlight) has been killed. The less illuminated parts around the sides have survived. Frequently, corals weakened by bleaching then succumb to disease.



LEFT | On this Indian Ocean reef, a carpet of table corals (*Acropora cytherea*) was affected by warming that was just at the specie's lethal threshold. Some died (the dusty gray tables) and some managed to survive and recover (the green tables).

STAGES OF CORAL BLEACHING AND MORTALITY



The healthy coral with numerous symbiotic algae.

The algae are expelled when the coral suffers stress such as that from heating. For a couple of weeks the coral appears white because the white limestone skeleton is visible.

When the coral dies, the tissue disappears and is quickly covered by brownish-green filamentous algae, darkening the color again.

ACIDIFICATION AND TIME LAGS

Carbon dioxide dissolved in seawater bonds with the water to form carbonic acid. There is a triplet of similar chemicals in balance with each other in water—carbonic acid, bicarbonate, and carbonate—the molecules continuously rearranging themselves in chemical equilibrium. It is the same system humans have in their blood for maintaining an acid level suitable for life. Remember that corals lay down calcium carbonate—at one end of the equilibrium chain—to make their skeleton.

Carbonic acid makes the water more acidic. Acidity is measured on a pH scale, the H standing for hydrogen. A pH of 1 is very strongly acidic, 14 is strongly alkaline, and pH 7 is exactly neutral. The oceans are slightly alkaline, with a pH of around 8.2 to 8.5, depending on temperature, the presence of upwelling deep water, and other factors. A pH of around 8.4 is good for corals' metabolic processes that use carbonate to make a skeleton. If more CO_2 dissolves, the pH falls and the acidity increases. In most tropical areas it has already fallen by about 0.1 unit, and this represents an increase in acidity of 30 percent. This diminishes the ability of corals to deposit calcium carbonate and grow their

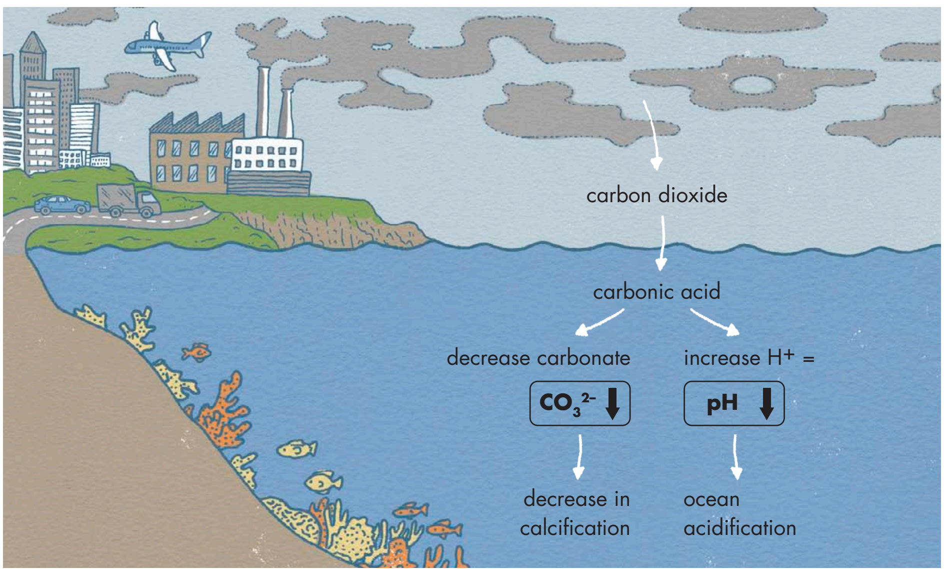
TOP RIGHT | Scientists on a reef flat measure the effects of acidification by bubbling carbon dioxide into the water. They add a purple dye to track the water flow.

RIGHT | Researchers in Florida relocating colonies of corals into tanks at a research lab, where pH and temperature conditions can be carefully controlled and manipulated to measure the effects of acidification and temperature on the corals' growth and survival.

skeletons. The crystal form of limestone used by corals, aragonite, is more susceptible than forms like calcite that some other marine life use.

The global problem is worsened because there is a time lag between the rise of CO_2 in the atmosphere and it dissolving in the sea. Because the ocean's major currents move around the world, sometimes being shallow and then overturning and becoming deep water, it takes about 30 years for the gasses in the air to reach equilibrium with the sea. This time lag means that even if we stop greenhouse gas emission today, the ocean will continue acidifying for the next 30 years. It is estimated that the maximum amount of CO_2 in the air which, after reaching equilibrium, is compatible with coral growth is about 350 ppm. Today it is already over 400 ppm!

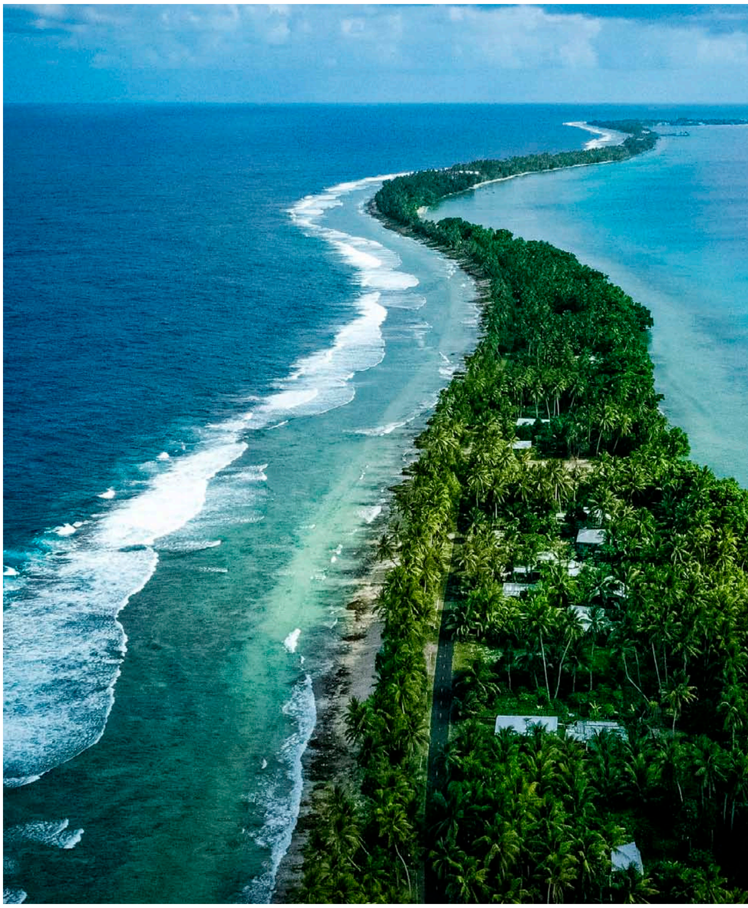
The Earth, a blue planet because of its 70 percent covering of water, has been absorbing the gas CO_2 as well as heat since the industrial revolution. Therefore, as ocean water with this heat circulates and returns, this has already committed our children to severe effects which will last long into the future.



CONSEQUENCES OF CARBON DIOXIDE DISSOLVING IN SEAWATER

LEFT | As CO_2 dissolves in seawater, there is a decrease in carbonate, which leads to a decrease in corals' ability to calcify. There is an increase in acidity (a decline in pH value), which leads to a further impairment. There are steps involving bicarbonate that are omitted for clarity.

SEA LEVEL RISE AND REEFS

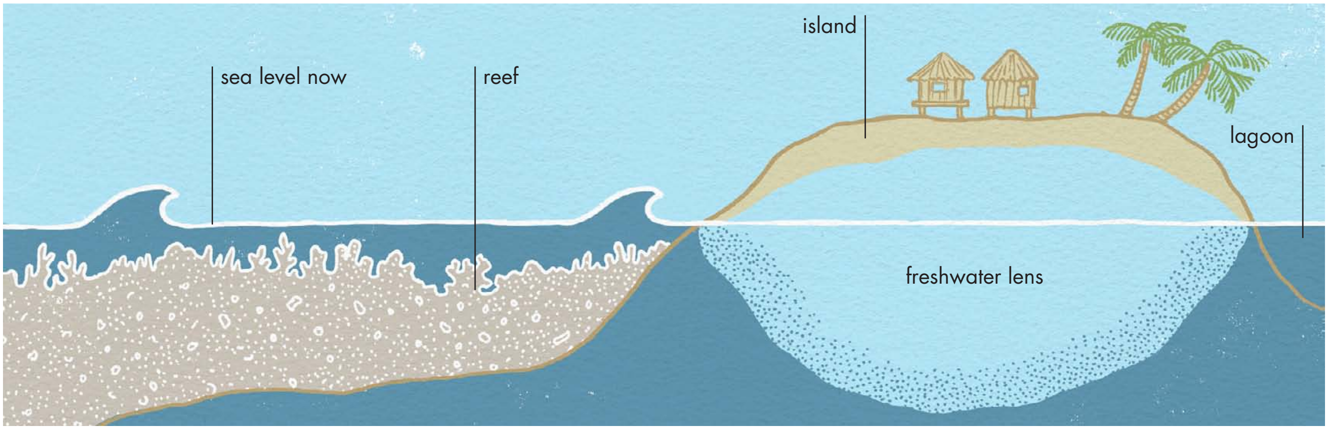


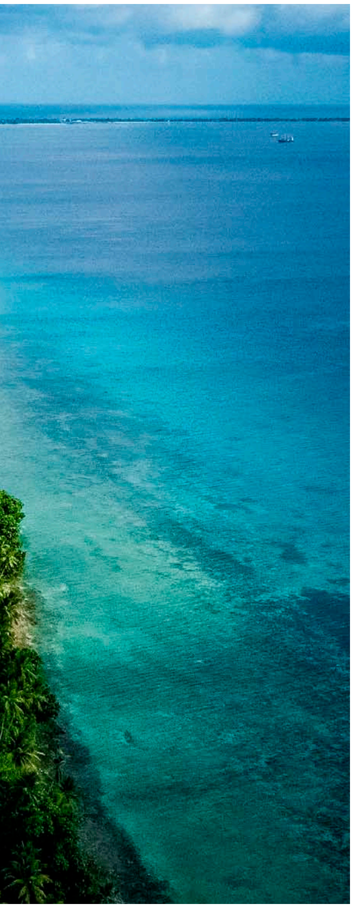
The sea is not particularly level around the world. The spin of the Earth, gravitational anomalies, ocean currents, weather, and obstructions caused by continents all ensure that sea level, and the rate of sea level rise around the world, varies. What is certain is that almost everywhere it is rising, and has been for some decades, slowly at first and now accelerating. The rate of rise now averages about 4 mm per year and is higher in some places.

Reefs will grow up to the contemporary low tide level. Healthy reefs can quite easily match the present rate of sea level rise, and oceanic atolls have demonstrably been doing so for millions of years, so that now their living caps are perched on top of mountains of older reef that grew as the land slowly subsided. Sometimes, perhaps for tectonic reasons, land subsidence was too fast so the living reef "drowned" when it was carried to depths where light was insufficient for the coral to grow. In several places, land has uplifted or tilted in repeated episodes, leaving reef terraces above water (see page 58).

Today, sea level is rising rapidly because the world is warming. This has two direct consequences. Firstly, water from the poles is melting and adding over 2 mm each year to sea level. Secondly, as with most solids and liquids, sea water

EFFECTS OF SEA LEVEL RISE



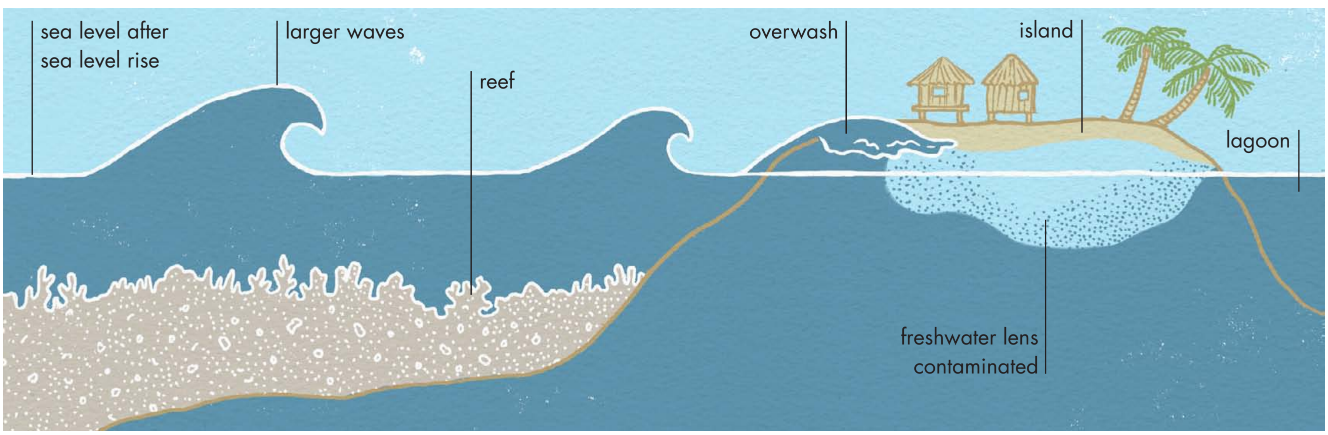


expands as it warms. This expansion adds another couple of millimeters to the sea level. For much of the tropics we can add a little more, too, from the little-known fact that as polar ice melts its own gravitational pull on the oceans diminishes, freeing huge volumes to flow toward the equator, adding a millimeter or two more in equatorial regions.

While the annual global rise in sea level may not drastically affect reef ecology straight away, there are immediate dire consequences for people whose homes are perched on top of oceanic atolls. Many islands have an altitude of only a couple of meters or less above high tide levels, which means that flooding of the land becomes more common, especially on high spring tides, called "king tides" in some places. Inundation ruins the freshwater lenses—the sometimes very thin layers of fresh water—that lie just below the surface in the interior of the islands, below ground level but floating above the deeper salty water. The ocean water also floods homes and infrastructure, kills the vegetation and agriculture, and eventually displaces the people living there.

LEFT | The rim of a typical atoll. Islands are very low lying, with elevations of only very few feet (1–2 m). Sea level rise has already inundated human settlements, killed crops, and led to evacuations. In addition to this result of rising CO_2 levels, the death of the reefs has reduced their ability to act as a breakwater, exacerbating the problem.

BELOW (BOTH) | Sea level rise on coral shores. *Left*: A healthy reef grows to low-tide level and breaks the force of the waves. *Right*: The sea level rises a little. Though a healthy reef could keep up with the rising level, warming has killed the corals and the reef structure has stopped growing (and may erode). The breakwater effect is reduced, shorelines erode, and freshwater tables are contaminated by salt water.



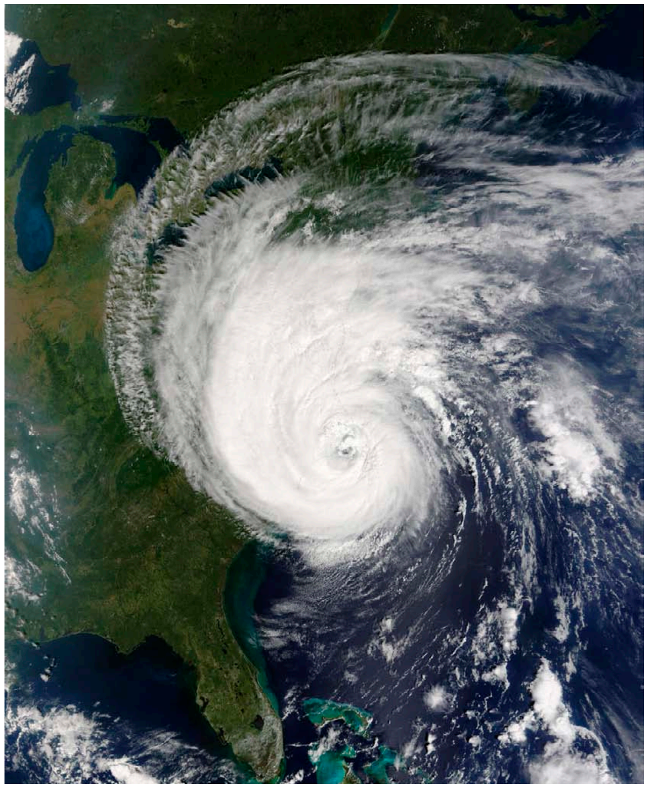
TROPICAL REVOLVING STORMS: HURRICANES, CYCLONES, AND TYPHOONS

Hurricanes, cyclones, and typhoons are different names for the same phenomenon in different parts of the world. These rotating storms are fueled by warm seawater of over 79 °F (26 °C), and their spin is triggered by the different velocities of the Earth's surface between their northern and southern extents. They can form only at latitudes farther from the equator than about 10 degrees because of the spin needed, but they cannot form too far north or south, because the ocean there is too cold for their development.

Reefs have always lived in ocean areas where hurricanes form, and for millennia they have been accustomed to being pounded by such storms. This can be seen in cores taken through a reef, which show that episodic severe storms have broken up both corals and the surface fabric of the reef at intervals, injecting foreign debris and mud onto it. Reefs usually recover after a few years.

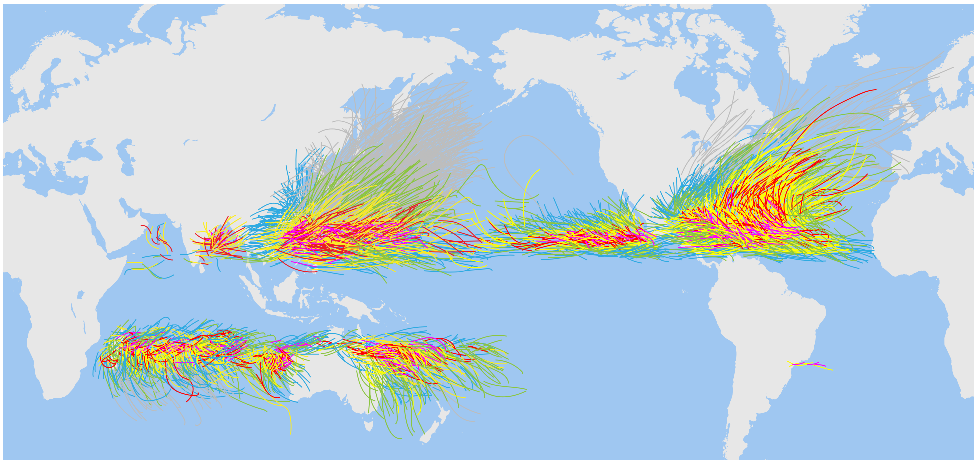
With warming oceans, more energy is being stored, and over the last decade the oceans have taken up 90 percent of all warming energy. This is why the land is not uninhabitably warm already, but it has its own consequences in that hurricanes are fueled more powerfully. The rate of heat now entering the oceans is equivalent to five Hiroshima-size bombs every second or, if bombs are too abstract, every person on Earth pointing 100 hairdryers at the ocean. And this is increasing.

The number of hurricanes does not increase as a result because as one passes, its violent winds stir up colder, deeper waters, which drops the surface water temperature to below that needed for hurricane formation. It takes another couple of weeks for the sun to warm the seawater again to the point where another can form. What happens instead is that each hurricane is likely to develop more powerfully. The number of severest category storms has doubled over the last 50 years. Each one lasts 60 percent longer, and many are larger. The total cyclone energy correlates with sea surface temperature. In the Pacific, two can develop near enough to each other to fuse, forming a "super storm." They may also stall for longer, with disastrous consequences. The area of ocean affected is increasing, too, with the first hurricane ever recorded in the reef zone of Brazil in the southern Atlantic in 2004.

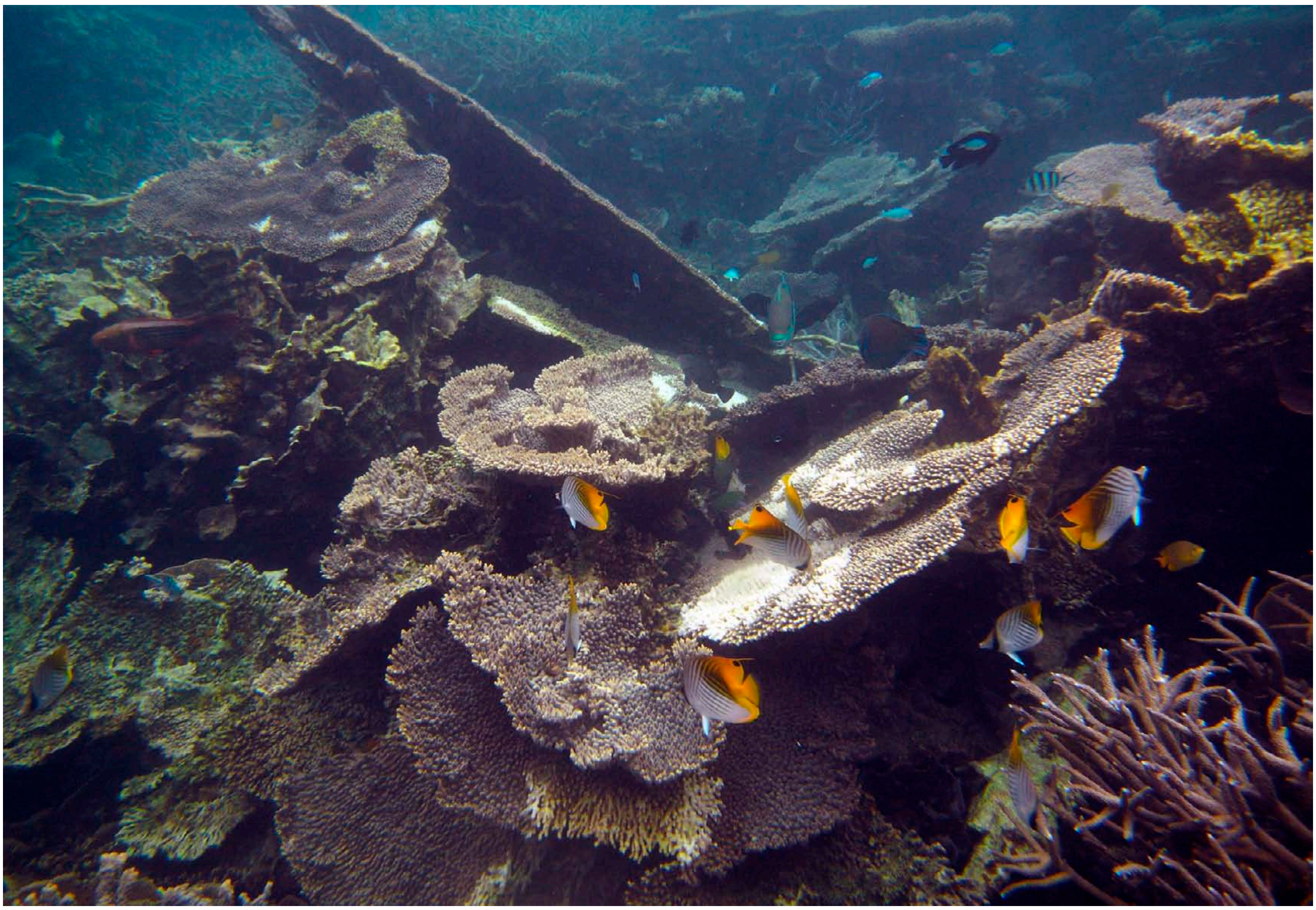


ABOVE | A category 5 hurricane approaching the coast of the USA. Due to the Earth's rotation, all northern hurricanes spin counterclockwise, and all southern ones (usually called typhoons or cyclones) spin clockwise. Such powerful storms cause great damage, from the wind and heavy rain but also because of the surge in ocean water that they drive.

BOTTOM RIGHT | A coral reef in Coral Bay, Ningaloo, Western Australia, showing cyclone damage. The table corals have been toppled and many will die as a result.



LEFT | A map showing hurricane, typhoon, and cyclone tracks between 1985 and 2005. The equatorial belt between approximately 10 degrees north and 10 degrees south does not experience these violent winds and, likewise, they do not occur in cool water. Note the first hurricane track ever recorded in the South Atlantic, which struck Brazil in 2004.



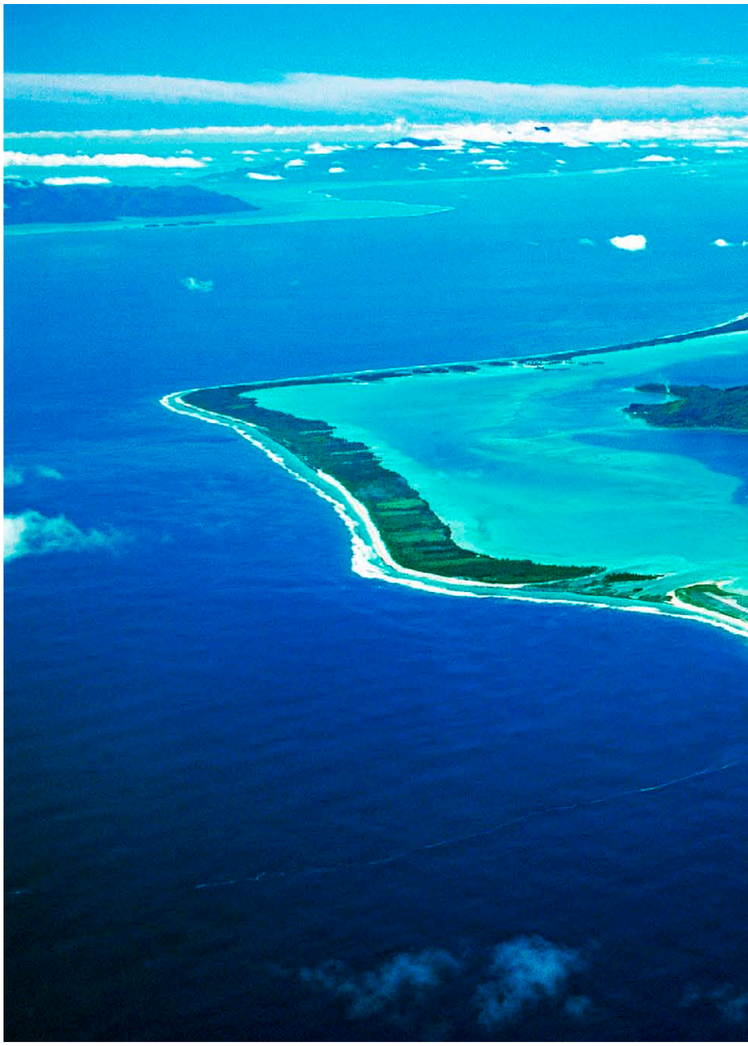
LOSS OF BREAKWATER EFFECTS

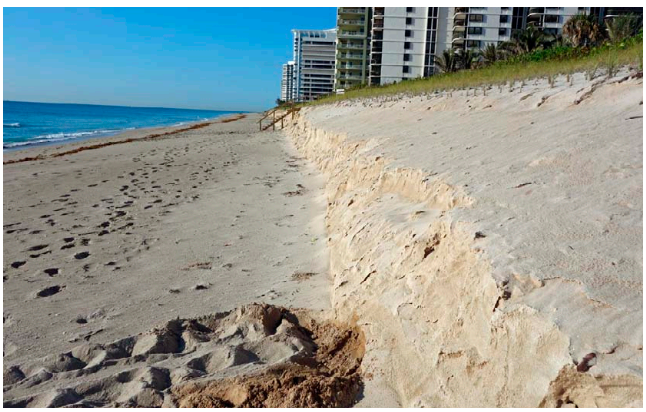
A crucial "service" that a coral reef provides is to act as a breakwater. Reaching to the low tide level, it reduces the force of waves reaching the shore. A sandy beach behind a reef is maintained by new sand coming from the reef, which balances the amount being washed away. Homes along the shore are protected, and industrial infrastructure is safe.

When the reef has been killed, perhaps by sewage discharge, other forms of pollution, or today by warming temperatures, the reef fabric decays. Then, wave energy reaching the shore intensifies, with severe and expensive consequences. Sometimes, sand on tourist beaches has been washed away, lobbies of hotels and their beachside bedrooms have been flooded, shoreline roads have been undermined so they collapse, and industrial infrastructure has been likewise endangered or destroyed.

In many small islands states, beach-based tourism is a major revenue stream. In less developed countries, the human cost is greater still: homes are flooded every high spring tide, freshwater tables are contaminated by salt, making them unusable, and crops are damaged. The end point when this happens is for the population to have to move. In many places there is a hillside to move to, but when the entire country is made up of atolls, there are no hills. Evacuation plans often exist, and some of those nations have purchased higher land in neighboring countries as part of these.

This flooding happens because of two combining factors: global warming is causing sea levels to rise anyway, sometimes by several millimeters each year, and the protecting reef decays when the warmer water kills the corals (see pages 186 and 190). When the corals die, the normal reef growth turns into reef degradation, causing a drop in height of the natural breakwater provided by the reef. Thus, wave energy striking the shore is greater, and more water floods the land.





The decision in many places has been to let the sea reclaim the land. It has been termed "managed retreat," but this rather benign phrase conceals the point that it was simply too costly to prevent the process of shoreline erosion. Where there is important and expensive infrastructure, however, sea walls and other barriers may be constructed to hold back the high tide.

BELOW LEFT | A rising sea level and concurrent stormier conditions are eroding shores fronting highly developed nations, as well as affecting settlements in poorer countries. Some shoreline protected by reef, as seen here in Florida, is extremely valuable real estate.

BELOW | The volcanic island of Bora Bora, in the South Pacific, is surrounded by a ring of reef. The encircling reef acts as a breakwater that is both growing because of corals and being eroded by tunneling reef life and waves. With its corals killed, growth stops, yet erosion continues, lowering the reef and diminishing its breakwater effect. Greater wave energy strikes the shore as a result.

CORAL RESISTANCE, RESILIENCE, AND REFUGES FROM CLIMATE CHANGE

Resistance, resilience, and refuges are seen as the three main ways that coral reefs could prolong their existence in the face of ocean warming and more frequent ocean heatwaves. Resistance is the ability of a species to withstand the stress from warming, and different kinds of corals show different amounts of resistance. Some, including branching forms, are sensitive and quickly eliminated, while others, such as giant boulders, can survive a heatwave. Resilience refers to the ability of corals to bounce back after a heatwave has ended, or the ability of the reef as a whole to recover its coral cover. Refuges are areas less affected by warming where most corals may survive. All three are crucial for the continued existence of a functioning reef in a warming ocean.

The symbiotic algae in corals that are expelled during warming events occur in several different species (see page 18). Some are more tolerant to warming or strong light than others. Thus the same species of coral in the Persian Gulf and central Indian Ocean may exhibit different tolerances to climate change. It is not only the coral animal that is important, but also the species of algae it contains.

BELOW LEFT AND BELOW RIGHT | Two massive-shaped corals that were mostly killed in the 2015 warming event but had some parts that survived. These "phoenix" corals seemingly arise from the dead. Their surviving polyps expand over the skeleton of their killed clones, eventually recolonizing the whole skeleton.

After a coral has bleached in a prolonged heatwave it will die, but in many recent years the warming was not quite lethal. The degree to which a coral can recover varies according to species. At the scale of the whole reef, resilience is often measured as the extent to which the total covering by corals and soft corals is regained. High cover may be achieved by a different species, especially one capable of producing vast numbers of larvae that settle and grow. Some branching and table-shaped *Acropora* corals do this in a spectacular manner, and can almost cover a reef in a decade. Those resilient corals may, however, be susceptible to the next heatwave.

Many areas provide refuges from warming water. They might benefit from a greater flow of cooler water currents or, for species with a wide depth range, refuges may simply be deeper areas below the layer of warm water. All these features affect the long-term survival of some corals and coral reefs during this time of warming climate.

LEFT | "Weedy" species of corals can rapidly settle onto reef substrate that was recently killed by warming. Especially quick to do this are several *Acropora* species, seen here growing on a dead table coral.

BELOW LEFT AND BELOW RIGHT | Two juvenile branching corals, both around one to two years old. Such juveniles can extend their branches by several inches each year once they have developed branches from the initial few polyps. They can generally breed after about five years, depending on the species.

REEF LOSS AND SOCIAL INSTABILITY

It is certain that loss of reefs will lead to substantial social disruptions. It already has in some places. What is also certain is that this is not being addressed anywhere near sufficiently by most world leaders, perhaps because they are not yet so obviously or critically affected. Leadership has instead been shown by some coral atoll nations, such as Kiribati and the Maldives. Some have raised awareness by holding "cabinet meetings" underwater, and more than one coral atoll nation has closed off large areas to foreign commercial fishing to aid reef stability, incurring financial loss. Opposition in such cases is common and comes from local fishing organizations who, understandably, fear a loss of income.

There is recognition in some countries that there will be a significant displacement of people as their coral island homes flood, a feature of life becoming more frequent in

ABOVE | Children playing in the flooding seawater illustrate how deeply the island of Funafuti is flooded on this particular king tide. The tide will recede after a couple of hours, but the salination of the freshwater lens will probably already have taken place.

islands where land is not more than a couple of meters above sea level. Rather than having large numbers of climate refugees, some governments have arranged for training of their citizens to have valued careers overseas, and provide economic incentives for emigration and establishing communities in other countries. These are pragmatic and welcome efforts, though issues of substantial societies being developed in culturally different host countries are aspects of integration that have not been adequately tackled yet.

Western militaries have shown considerable concern about climate change, identifying aspects that can lead to many problems. A 2014 report by the USA's CNA Military Advisory Board identified that national security risks from projected climate change are even more serious than traditional threats that have been faced during the last century, and that climate change is adding to social dangers in a world becoming more socially unstable. It also notes that climate change impacts are accelerating instability in vulnerable regions and are a catalyst for conflict. In addition, it claims that instability and conflict are inevitable results of extreme weather, including flooding and resulting food shortages, causing population dislocation and mass migration. This military perspective alone is sobering.

BELOW LEFT | With warming water leading to rising sea levels, and killed corals reducing breakwater effects, settlements in Kiribati, in the Pacific Ocean, are being inundated and people evacuated.

BELOW | Flooding of villages can occur even when the water has not risen to the height of an island. Here, in the Maldives, strong waves still force sea water over the rim and into the village.

CHAPTER 6

PEOPLE AND REEFS

TRADITIONAL USES OF REEFS

For as long as people have lived beside coral reefs, we have derived benefits from them. When populations were lower in the past, reefs were a plentiful source of food, and for hundreds of millions of people today they provide the main or almost only source of protein.

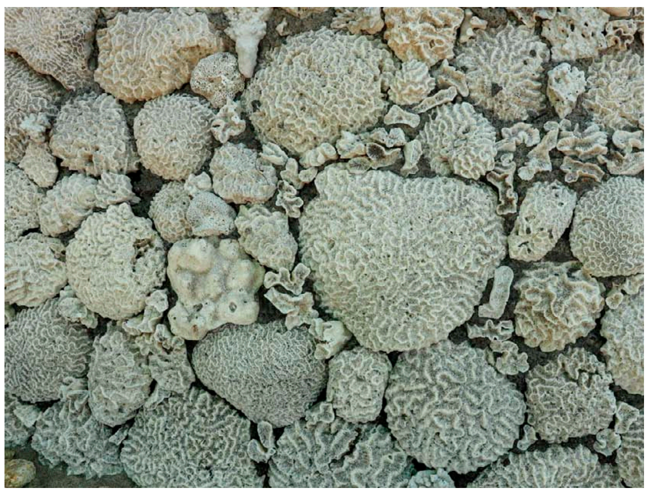
There are two major ways of obtaining protein from the sea: by fishing, mostly of vertebrates (fish), or by gleaning—the collection of invertebrates from shallow reef areas where people can walk. Fishers use a variety of nets, lines, and traps set on reef flats and other adjacent shallow parts to catch fish. Gleaners gather a wide range of species: mollusks, including octopuses; mollusks with shells, such as bivalves of all sizes, from oysters and mussels up to giant clams; gastropods such as the Queen Conch in the Caribbean; and sea cucumbers. The last of these have long been an Asian food and medicine source. Recently, many of the gathered species have risen greatly in value, reflecting their increasing scarcity, and because several are commonly regarded in Chinese society as having medicinal functions.

Reefs also supply building materials. The soft limestone is more easily worked than most rock and is easily prized up with bars. This includes living colonies as well as the reef rock between them. In countries made entirely of atolls it is usually the only rock available to build homes, but centuries of prizing coral rock from the reef flat surrounding the island has resulted not only in wide-scale mortality of the reef but also a drop in its height by 20 in (50 cm) or more. This reduces its breakwater effect (see page 194), leading to problems later on of greater erosion of the land.

Related to this is the practice of baking the collected coral rock in kilns to make lime, also for building. The fuel for the kilns often comes from felling trees inland which, in countries with high rainfall, has led to deforestation. When this happens, greater run-off occurs, bringing smothering mud onto the reef with its own harmful effects, including reduction of the reef's ability to produce protein.

BELOW LEFT | Homes are commonly built from large numbers of both fossil and living coral colonies, in atolls, where coral was the only available building stone, and continental coastal towns, such as this one on the Red Sea coast of Massawa, Eritrea.

BELOW | Corals are the most easily collected building material on many coral islands, and often practically the only material available. These have been built into the wall of a small dwelling.



LEFT | The calm waters behind the reef crest may be used for bathing or fishing. The calm conditions result from the sheltering effect of the crest, marked by the line of breakers on the far edge of the reef flat.

BELOW | Over centuries, middens of discarded conch shells have accumulated, having been harvested for their fleshy foot. Today, conch is a prized food for tourists as well as local people.

NEWER USES OF REEFS AND THEIR VALUES

The affluence that now exists in many societies around the world has led to a greatly increased tourism industry, including the recreational use of reefs. Nature tourism, including that centered on coral reefs, is important economically in many places. Money that comes from tourism benefits more than 100 countries and regions, and is often a high and much-needed proportion of foreign earnings. This comes not only from direct reef users such as divers and snorkelers, but also from the larger associated component that comes from simply centering a vacation on tropical beaches, with hotels, travel to them, and food being major components. The attractive beaches themselves are made from coral sand derived from the reef just offshore, and even the building and maintenance of the islands is a direct result of the existence of the coral reef.

There have been several efforts to quantify the monetary value of reefs, partly because this is one way to emphasize their importance; the world is run by governments and accountants, not scientists, after all. Values of $96,000 for each hectare of reef per year have been estimated, ranging from $36 billion to a couple of trillion dollars in total annually, which is several percent of the "services" provided by all nature—a value that is not unreasonable considering the diversity and productivity of coral reefs. For some small countries, revenues from reefs can be a quarter or more of their foreign revenue. Reefs are more valuable to local communities when healthy than they are when damaged.

However, there are also, unfortunately, negative impacts from reef-based tourism, for example from degradation and even elimination of marine life in quite wide areas through thoughtlessly planned coastal construction, including dredging and fill on top of reefs themselves. Sewage pollution can also be prevalent in such areas. Direct impacts from divers and snorkelers can be significant in shallow water, from direct breakage of coral colonies. Sometimes the sheer numbers of people enjoying reefs can cause significant damage which, of course, sooner or later negates the benefits originally obtained from them. On the other hand, many visitors to coral reefs already have a well-developed environmental awareness, and their visits, together with additional environmental levies or taxes, have been useful to encourage or fund local reef conservation.

ABOVE | Beach-based tourism has become an important part of the economies of many tropical countries.

ABOVE RIGHT | Seychelles atolls and fringing reefs are popular locations for divers, especially those from wealthier countries.

RIGHT | Diver training schools, such as this one in Ningaloo, Australia, are now commonplace in all countries that have waters containing coral reefs. The clarity and warmth of the water, and commonly benign sea conditions, make these safe and popular.

ABOVE | Recreational divers usually love to see large fish, and large groupers are fairly sedentary. They allow divers to pose for photos with them, especially when they have been fed by divers!

RIGHT | In subsistence economies, gleaning, or searching the reef flat and shallowest parts of the reef slopes for food, is commonly done at low tide by women, older people, and children.

MAJOR CONSTRUCTION ON CORAL REEFS

Given that it has been known for decades that substantial construction, pollution, and resource extraction from reefs eventually degrades them and causes them to lose their resource value, it is perhaps surprising that some of the most damaging uses still continue. Malé, the capital of the Maldives, is a case in point. Although the country has numerous other sparsely inhabited islands, in Malé fill has covered its reef flats almost out to where the now long-dead reef plummets to great depths. More recently, this island has joined to two adjacent islands with causeways, one supporting the airport and another that is an equally densely crowded residential island.

This dense development is mirrored in numerous other island-fringed shores in several parts of Southeast Asia and the Caribbean. In many such places, massive disturbance has essentially killed most reef life for several kilometers,

ABOVE | A small coral island has been almost entirely converted into an airstrip, likely to service a larger reef-based tourist development nearby.

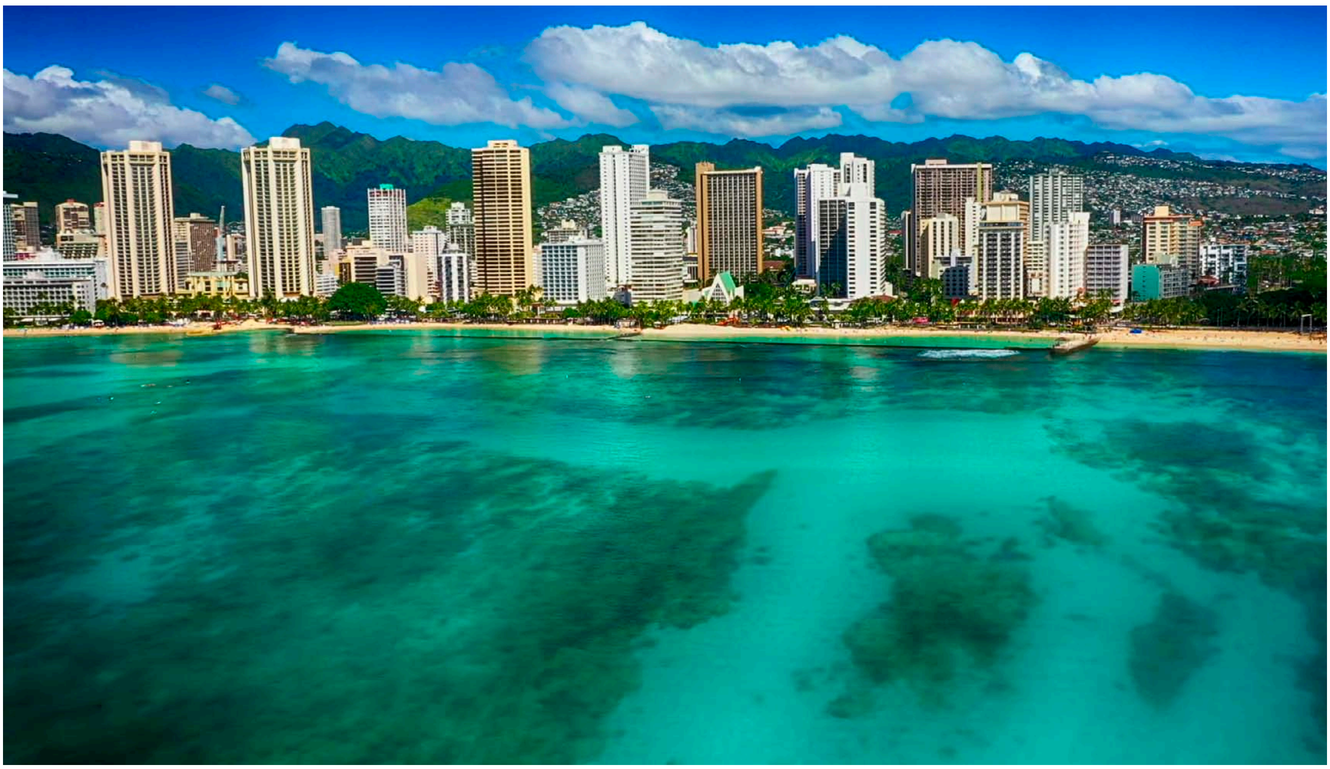
BELOW | Developments on coral atolls, such as in Malé, the Maldives, cause sedimentation on surrounding reefs and generate problems in their requirement for sufficient fresh water and disposal of waste.

replacing the rich reef with either algae-covered limestone or with loose, mobile beds of sediments.

Militaries have long used coral reefs. Swathes of the globe are dotted with little land except for reefs, which provide expanses of flat ground suitable for building airfields and other military structures. As a result, the tops of many reefs around the world have been used for building on, both on the coral islands perched on them and, when there are no islands, even on the reefs themselves. Pacific islands especially have been the home of many military facilities and airfields, some with particular resonance from the Second World War, such as Midway, Johnstone, and Wake. Then, in the later Cold War, atolls such as Bikini were used for nuclear testing, while farther west in the Indian Ocean, Addu Atoll in the southern Maldives and Diego Garcia Atoll in the Chagos Archipelago had huge airfields built upon them. Today in the Spratly and Paracel Islands, numerous Southeast Asian nations have territorial claims over several reefs and tiny specks of land that are little more than sand cays, some of which are now being covered with runways and harbors.

All these facilities are within 3–6 ft (1–2 m) of the high tide level, and often below the level of storm waves. It is already costing tens of millions of dollars per year to protect some of them against rising sea levels, but where this money is not available, increasing poverty and difficulty persist.

BELOW | High-rise and expensive infrastructure in Waikiki, Hawaii. Over a century ago, this was mostly wetland and marsh. Landfilled with imported sand, it is now one of the most famous tourist spots in Hawaii.

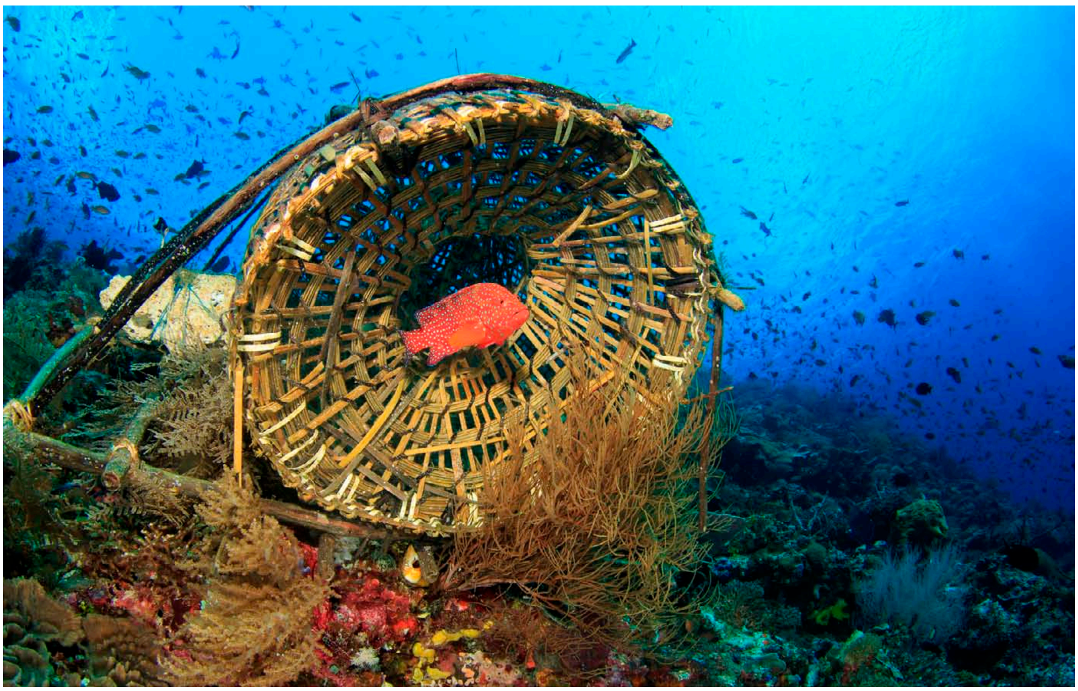


CORAL REEF FISHING

Remote or uninhabited coral reefs have large populations of reef fish, and much of the biomass lies in the largest species and in schools of medium-sized species. Many of these are predators at the top of the food chain. Fishing, even for subsistence, is well known to remove the largest fish first as they may be remarkably easy to catch, so it does not need a great deal of fishing to severely distort the trophic structure of a coral reef. Most fish populations near even small fishing communities are now very disturbed, and quite different from unfished populations.

Reports from a century ago describe coral reef fish numbers that are hard to imagine today. Now, totally unfished reef communities may support ten to 50 times more fish than even so-called protected reefs in marine parks. Many fish populations are close to collapse, with previously abundant species being very rare or even locally extinct. With schooling species especially, entire schools can be removed by one net, and fishing of spawning aggregations has severe longer-term consequences. "Fishing down the food web" then occurs, with smaller and smaller species, including herbivores, being targeted.

The problem is amplified by increasing numbers of people requiring protein. There has been a pervasive image of local people fishing in a small boat perfectly sustainably for their supper, but this is usually no longer the case. People need to eat, so attaching blame is unfair and pointless. The fishers may buy a motor to help them, and again nobody can hold this against them. To pay for the motor they must catch more fish to sell. Freezing fish with ice or perhaps in a freezer plant is then needed, so even more fish must then be caught to pay for that. It escalates, until so many fish are caught that not enough are left to produce sufficient young to replenish the reef. As a banking analogy: the reef's capital stock of fish are increasingly depleted, not just the surplus fish, or interest. A downward spiral takes over. This has often proved to be



damaging or even fatal to the ecology of the reef, and it needs remarkably few fishers to destroy the ecological balance.

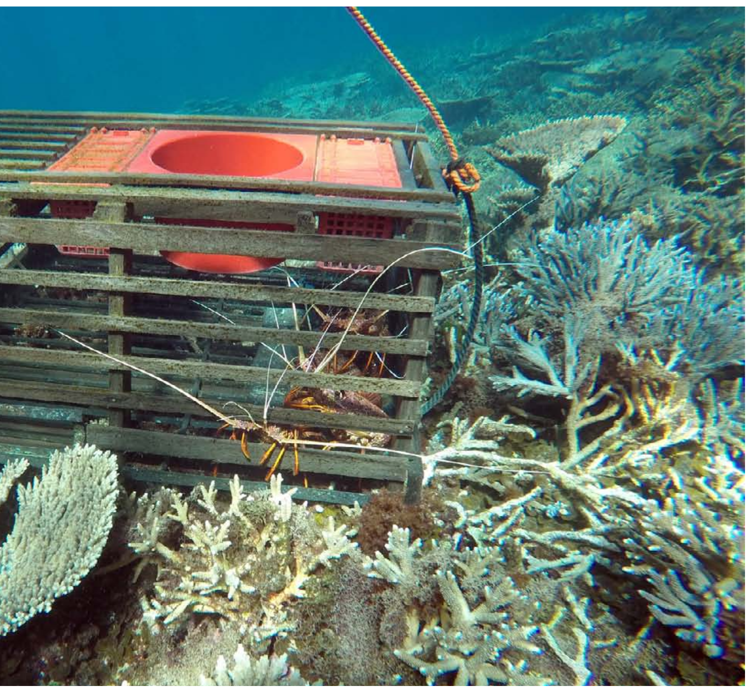
Alternative livelihoods must be found if this process is to be halted. Well-thought-out tourist industries are one such. Sharks caught for food or fins are sold for a relatively modest sum, whereas a single shark may be many thousands of times more valuable for diving tourism.

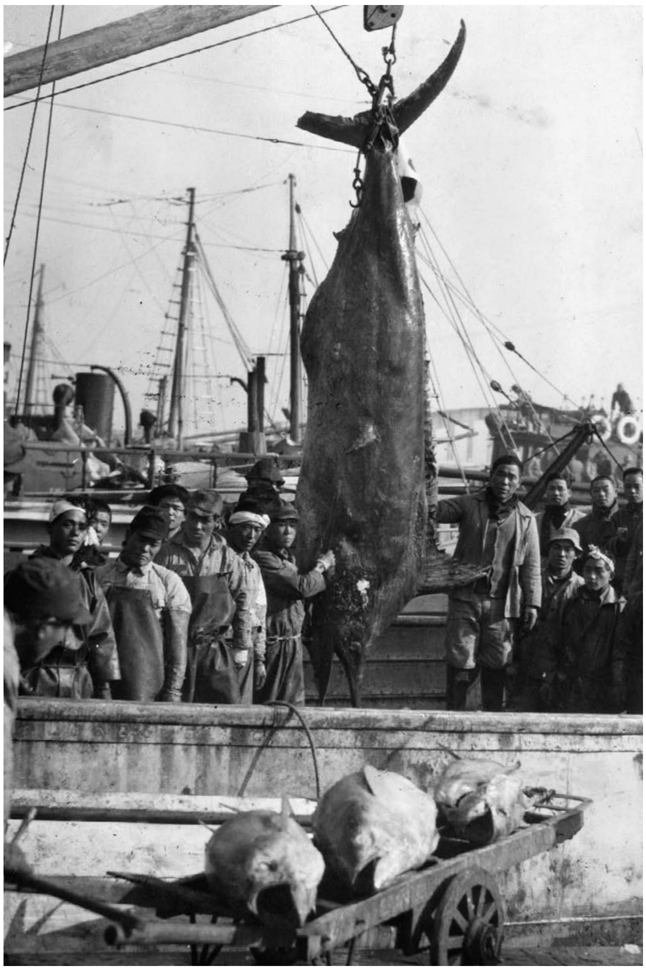
BELOW LEFT | A traditional fish trap in Alor, Indonesia, made from sticks and cord. The fish swim into the entrance, which is angled to prevent them leaving the trap.

BELOW | Lobsters in a trap in the Abrolhos Islands, Western Australia.

TOP RIGHT | Illegal shark fishing is a huge business in many countries. Some, as with this confiscated catch, is for meat for poor communities, but much is simply for fins to make soup in Asian kitchens.

RIGHT | In past decades sport and trophy fishing depleted populations of higher predators. Today, fish of this size are vanishingly rare.





MEASURING CHANGES ON REEFS

One key part of trying to mitigate human impacts on coral reefs lies in understanding not only what changes have taken place on the reef, but also what exactly the causes of that change are. The amount of coral cover, and the species that provide the cover, are two widely used key measurements, as might be the number of juveniles or recently settled corals that exist there. Juvenile corals are, after all, the next generation of reef builders. However, measuring the degree of change is sometimes far from straightforward; while gross changes from one year to the next following, for example, a marine heatwave or a major construction might be simple, many changes are small and incremental, developing slowly year on year. This makes it very difficult to provide advice on what should be done or on what is causing the deterioration.

The resulting ecological changes have been called the "shifting baseline syndrome." Often a site is compared with a baseline, but what may be believed to be the baseline

ABOVE | A temperature logger being attached to a stake hammered into the reef. Instruments are commonly located inside a piece of pipe to prevent them being destroyed by grazing fish.

ABOVE | A scientist using a quadrat to quantify particular species or processes on the reef. Small quadrats are used for small-scale measurements, such as juvenile corals.

ABOVE | Transects are another commonly used method to measure species or processes on reefs. Tape measures are here laid out at right angles from a stake that can remain in place for years.

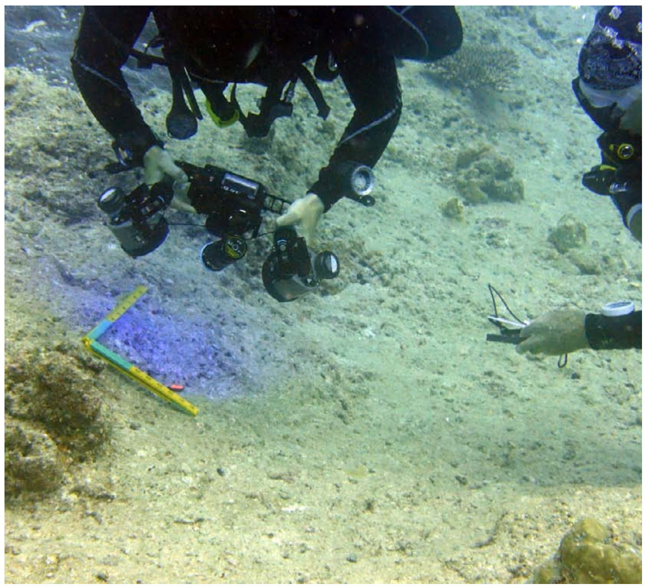
condition may itself have drifted far from what would have been its real condition a century earlier. Moderate sewage discharge and even very small-scale fishing are highly likely to have shifted the condition away from its pristine state.

Each successive generation shifts the baseline of their experience further from the origin, as many surveyors have, unfortunately, perceived the baseline to be the condition that they saw when they first started performing surveys. This is a considerable problem when foreign and short-term consultants are called in and where there may perhaps not be earlier surveys of the location they are studying to use for comparison.

It is also common in areas undergoing considerable development for a mandatory impact assessment to be performed, which compares the situation before construction, which they might call the baseline condition, with the condition after the construction. The change might be minor, but this development might only be the latest of half a dozen earlier projects, each one adding another minor change, the total amounting to a considerable alteration. Planning legislation may permit a change of, not uncommonly, ten percent, but the legislator will not have appreciated that the project's damage is just another ten percent over the several that have gone before.

Declines due to these causes remain very important in the overall decline of coral reefs. Only long-term monitoring might be able to detect the ecologically modest—but sustained—deterioration.

ABOVE | Reefs can change markedly from year to year, so stakes are commonly hammered into the reef to ensure that a survey site can be relocated in surveys measuring changes over several years.



ABOVE | Photography is a popular scientific method. Ultraviolet lighting, here casting a blue glow in the quadrat, makes coral tissues glow, so tiny, juvenile corals can be seen and counted.

LEFT | The banded sea krait is common on reefs of Southeast Asia. It feeds around reefs, mainly on fish and eels, which it flushes out of small crevices, but returns to land to digest its meals and to breed.

ABOVE | The migration routes of several whale populations, including this humpback calf in Tonga, in the South Pacific, pass along coral reefs in several parts of the world.

REEF LIFE ON ARTIFICIAL STRUCTURES

In many places around the world we have built structures from steel or concrete that have attracted huge densities of marine life. Near coral reefs this has led to some magical places. Where a pier juts out into an otherwise sandy bay, for example, an oasis of life can form that makes a remarkable contrast to the otherwise rather barren sandy expanses around it. The same is often the case on a shipwreck that has settled in a coral lagoon; whether the ship was scuttled, as is the case with several warships, or, more commonly, was wrecked in a storm, life on these structures can be exceptionally rich, more so in a visual sense than life on the natural reef just a few miles away.

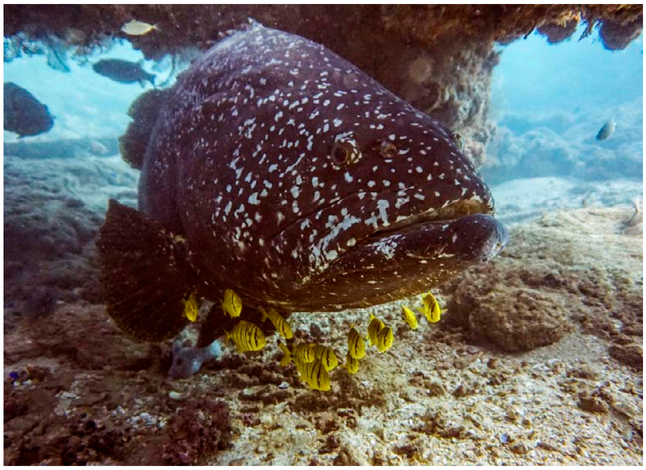
The first life to settle on such a structure will be nondescript bacterial films, algae, and filamentous organisms. These are followed swiftly by corals, soft corals, sea whips, and all the forms that can be found on a natural reef. Fish rapidly accumulate from the start, drawn by the food but also by the shelter itself. Many fish like to have structures to hide in, and to have some structure over their heads. "Fish aggregating devices" are deployed by artisanal and industrial fishers to exploit this preference; these are structures floated across the ocean, not necessarily very large, but some with radio trackers on them, that attract and accumulate fish underneath them; the fish are then easily collected by a fishing boat.

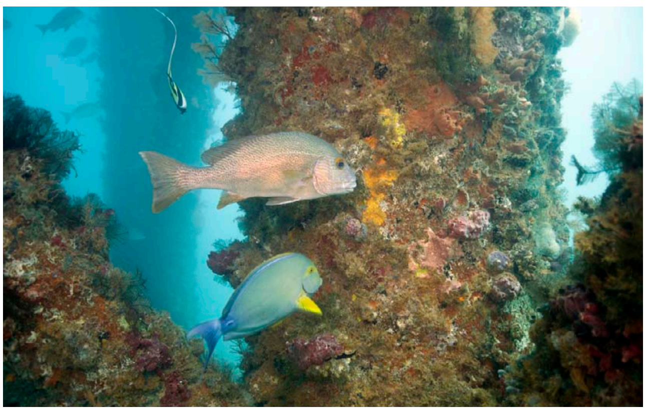
The density of fish under structures which have protection from fishing can be astonishing. Individuals can reach huge size, and their numbers can become concentrated in these oases—more so even than on a protected coral reef nearby. This will only happen if the life accumulating there is not fished, of course—such structures are relatively small and it does not take much fishing to eliminate the life that will have accumulated there over several years.

To maintain their density, protection must be very effective. If this is done, however, they can be awesome places. The structures, such as piers, are mostly built for industrial and commercial purposes or, in the case of shipwrecks, result from accidents, but today more and more are built specifically for attracting marine life.

ABOVE | The undersides of piers attract exceptionally large populations of schooling fish, provided fishing is prohibited. Several, such as the Navy Pier in Exmouth, Western Australia, are strictly protected areas.

RIGHT | Pilings of any underwater structure attract marine life. When pilings exist on huge sand expanses they can be the only solid substrate for miles, and so act as vibrant oases of life in otherwise relatively barren areas.





TOP| A large grouper, which is an ambush predator, rests under an overhang under a steel ledge. This one is accompanied by a school of golden trevally pilotfish, which are safe from being eaten.

ABOVE | An abandoned lobster trap on a reef attracts good growth of marine life. While steel is not as attractive a place to settle as limestone reef, it is raised above the surface rubble and sediment, so life that does settle on the steel can survive and grow.

PURPOSE-BUILT ARTIFICIAL STRUCTURES FOR CORALS

Artificial structures have had a long but rather mixed history. Some have succeeded to a degree, though many have failed to achieve their intended effect of replacing, augmenting, or restoring damaged natural reefs. A range of materials have been used, from old car tires, or old cars themselves—which probably never had much hope of succeeding but were really garbage disposal projects with hoped-for green credentials—to much more successful structures made of concrete, usually impregnated with limestone chips.

Sometimes the structures have been built in places where pollution that killed the original reef was not cleaned up; astonishingly, it is often overlooked that coral transplanted onto the artificial structure will not survive unless the conditions are improved first. The structure must be located in a suitable site, with no toxic sediments and no pollution input. It should provide substrate elevated above the seabed because the mobile sand left where a reef was previously killed acts like liquid sandpaper, which will prevent larval settlement. Some emplaced structures have been disastrous, becoming unsecured during storms and rolling around, causing further damage. Several have had to be removed.

However, in other places artificial reefs have had some success. Some have brought high-value benefit, for example around windows of underwater restaurants. But they will always be a poor second best to adequately protecting the original reef, and in fact, initial protection often would have been cheaper. Others are criticized because they are built to attract fish for fishers, leading to a net depletion of fish from the surrounding area. Sediment stabilization may be all that is needed, but all structures must be properly anchored or later storms will undo years of progress. Alongside these, coral nurseries are usually required to supply thousands of coral fragments, which are later cemented into place.

When the cement contains limestone chips they are more successful, because coral larvae selectively prefer limestone to concrete. The best structures are hollow so provide three-dimensional space, and have a rough texture. Their correct spacing will minimize cost and materials, and will optimize species movement between them while maximizing the area covered. These methods are becoming more important. Proper management and protection is essential for them to succeed in their objective, though artificial reefs never have the biodiversity of a rich, natural reef and must not be considered an equal replacement.

LEFT | Planting coral fragments at an artificial coral garden, in North Male Atoll, the Maldives. Many attempts are made to plant attractive "gardens" in areas visited by tourists that have been previously damaged by climate change or other forms of disturbance.

RIGHT | These hollow cement reef balls are placed with optimal spacing, and soon attract a lot of attached growth and fish that otherwise would not exist in such areas.

BELOW | Box-shaped concrete structures have also been used to create three-dimensional habitats for fish. These do not yet show growth on the boxes but schooling fish have quickly discovered them.

CORAL CULTIVATION AND GENETIC "SUPER CORALS"

Restoration of coral reefs relies on collecting fragments of living corals which are then grown and transplanted to artificial structures or areas where reef growth needs to be encouraged. Initially corals were simply fragmented, and those fragments cemented onto the damaged reef, but more recently, fragments are being "farmed" in nurseries first, then subdivided and grown further, before being planted out. Farms may be tanks on land, but may also be structures that are floating near the area where the corals are eventually going to be cemented onto the reef. The farms grow the fragments to a larger size, since larger transplants are more likely to be successful. About 100 species of coral so far have been farmed to various extents and with varied success.

Further developments are being sought. One is to "improve" the capabilities of the corals being farmed, in particular their ability to tolerate higher temperatures—to develop so-called "super corals." The aim is to assist and speed up the process by which corals can adapt to warmer temperatures. Whether it will work or not, however, does not reduce the need to slow, and reverse, the warming!

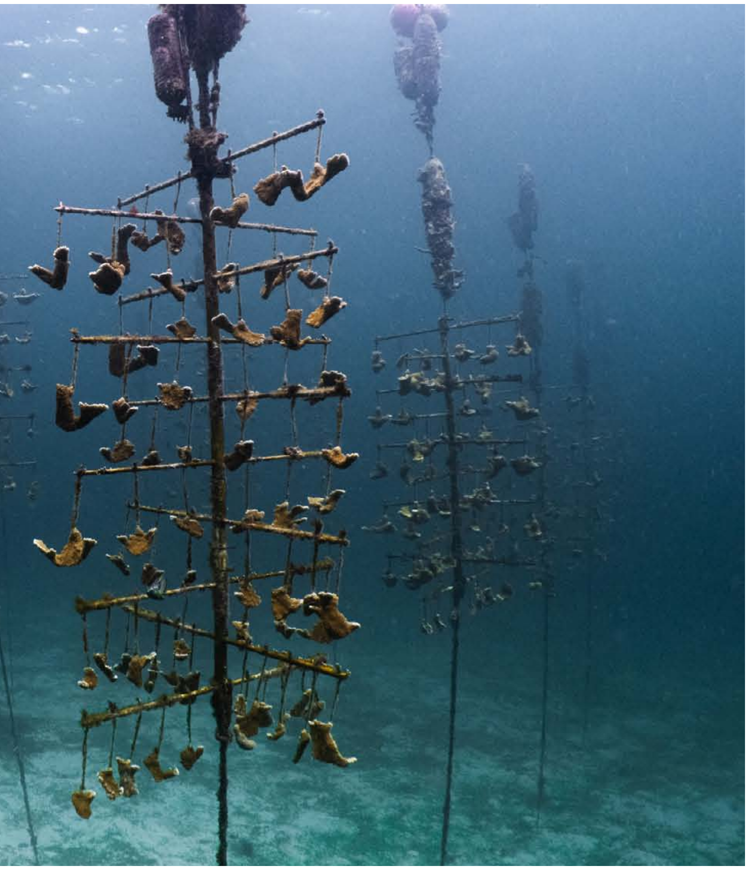
One approach used is selective breeding. Three aspects potentially exist. Genetic changes are changes in the central

ABOVE | These 25 fragments will completely cover a larger, dead coral in two to three years. This is *Orbicella faveolata*.

ABOVE | These 20 1-in (2.5-cm) coral fragments grown from one fragment will fuse and grow into a medium-size head.

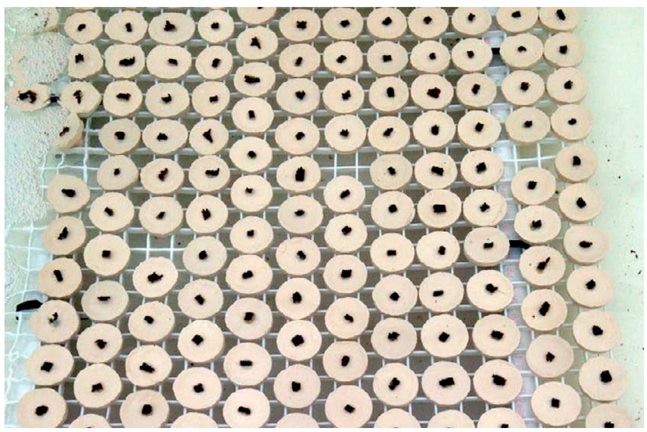
set of instructions that organisms have that can be passed on to the next generation. Acclimatization is a non-genetic change, but instead is a change in an individual that improves its ability to cope with a warming environment; however, this is not passed down through generations—or at least, that used to be the understanding. It is becoming clear that a third method exists: some non-genetic changes can be passed on as well; these are "epigenetic" changes, which are not changes in genes but in factors that cause genes to work better or to be turned on or off. Human-assisted changes to the genes and to epigenetic factors have been used for commercial species for many years and these are now being researched for increasing the tolerance of corals to raised temperatures.

Genetic modification has been controversial in the food industry, and is likely to also be controversial with coral restoration. The fact that it is being tried is indicative of the urgent need to help repair damaged coral reefs.



LEFT | In the Caribbean, coral fragments are grown suspended on frames. They are later transplanted to grow into a rudimentary reef.

ABOVE | A dead coral skeleton covered with hundreds of aquarium-grown fragments, which will cover the old coral with new tissue.



ABOVE | Hundreds of tiny fragments can be made in one day in tanks. They are ready to be transferred in six to nine months.

FARMING ON CORAL REEFS

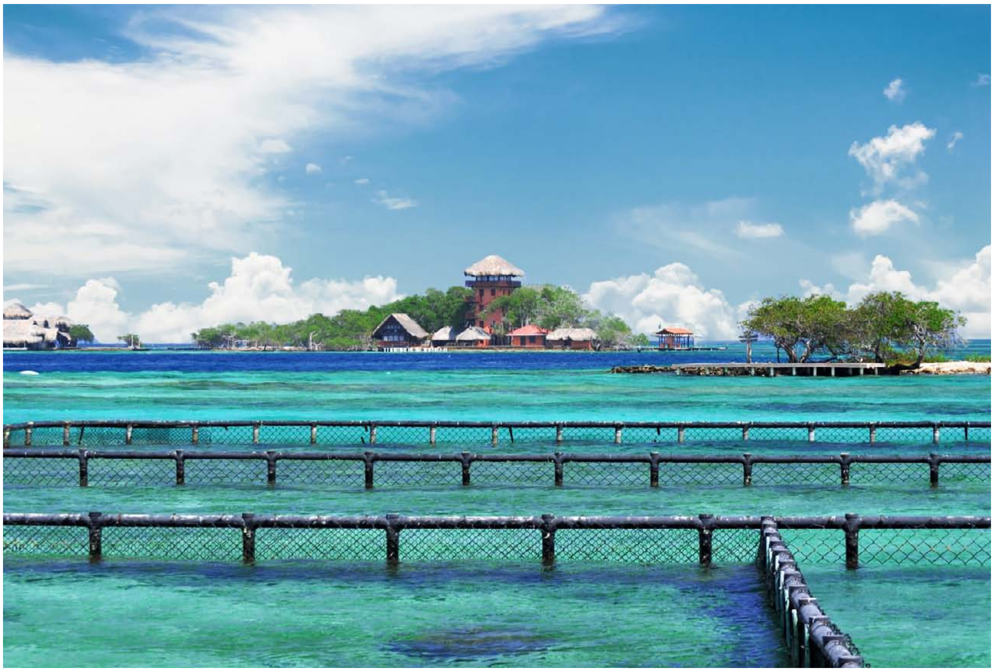
Fish farming on reefs covers two rather different areas: the raising of small and colorful species for aquaria, and raising reef species for consumption.

The reef fish aquarium trade previously relied on catching fish from the wild, but this usually involved damage to the original reef. The trade also faced other problems: wild-harvested fish tend to die sooner, they might introduce diseases into the aquarium, and the fish were commonly more aggressive after being confined in a tank. So many sources have begun to breed fish in facilities on land in which the above problems are mitigated or controlled to some degree. Many organizations that breed fish for the aquarium trade also culture the corals—an additional benefit.

Mariculture is the cultivation of marine life. It is mostly of fish and various invertebrates for food, but can also include organisms that are not eaten but which have value of other kinds. In coral reef areas it is mostly for consumption and involves several invertebrate species as well as fish. Reef mariculture is a rapidly expanding alternative to wild capture. It tends to focus on high-value species, and for some species the industry has existed at low levels for centuries. In some Pacific islands, pearl oysters and giant clams are examples of high-value species farmed in reef areas. Few reef fish species are currently grown from larvae in hatcheries to adult stage, though Milkfish are a successful exception. However, many of these hatcheries are now being converted to rearing high-value fish for the live export trade to Southeast Asian restaurants, and often these still require juveniles that are caught from the reef first, although some grouper are now successfully bred in hatcheries as well. Unfortunately, the rearing of one large grouper still requires large amounts of wild-caught fish to feed it, up to ten times the biomass of the final grouper, so ecologically the process is still damaging.

ABOVE | Giant clams, large bivalve mollusks, are grown in shallow water in several Pacific islands. These produce high-value flesh and their shells are sold to tourists.

Vast areas of shoreline in reef-fringed countries have been converted into mariculture ponds, including rice fields and mangrove forests. Even larger areas of netted enclosures just offshore can now be seen off many tropical cities. These cause problems of disease, of chemicals including antibiotics, and ecosystem disturbance caused by the vast quantities of waste. Such culture does not usually benefit local communities anyway; the now huge tropical shrimp farming industry, for example, has been termed the "dollar crop" because the shrimp are exported for a company's profit rather than being consumed by the local and generally poor populations.



LEFT | Shallow water in a Caribbean reef area is fenced off for a fish farm breeding several species of fish.

BELOW | Tropical shrimp farms are commonly located between land and reef, as here in Java.

MARINE PROTECTED AREAS AND SPATIAL PLANNING

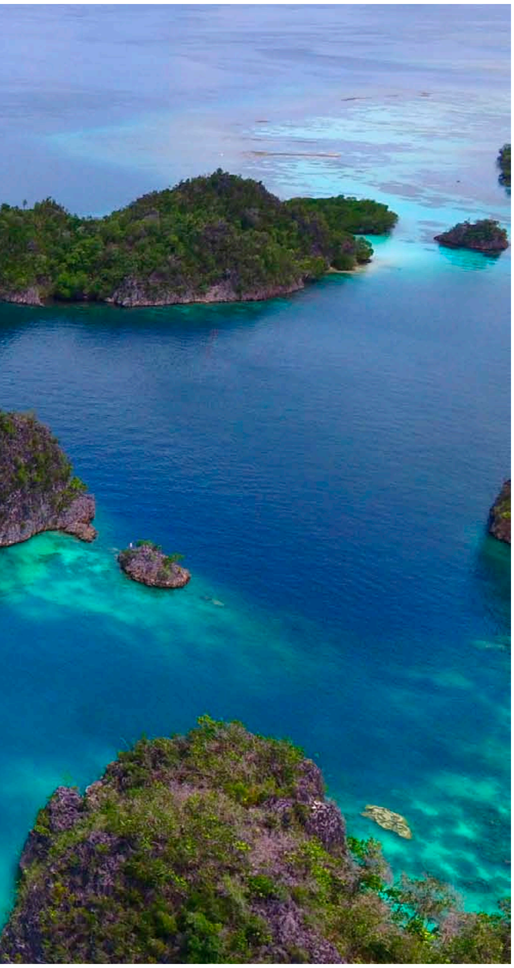
It has taken centuries of progress to realize it, but one reason why we need to protect the ocean is because we depend on it. We need it to sustain our growing population, and we now know the ocean regulates our climate, produces half our oxygen, feeds many millions of us, and absorbs most of the heat and carbon dioxide we produce. We also know that we cannot really "manage" the oceans to any sensible degree—we can rarely manage, rather than farm, a single species in it—and that the once- trendy phrase "managing the ocean" is simply hubris! The best way to allow ecosystems to recover is to simply let them be: to not touch them, so they will recover themselves when they can. This applies to coral reefs especially.

Hence marine protected areas (MPAs) came into being. Some areas have been protected for a thousand years or more for hunting purposes, but protecting areas purely for conservation or preservation is a relatively new concept. This is particularly important for the very diverse coral reef ecosystem, and some of the largest MPAs surround coral reefs.

MPAs provide many benefits. They conserve and protect natural species and systems, and provide social and economic

benefits. They can only work, however, if human activities in them are properly regulated; far too many are "paper parks" which fit government targets but are otherwise ignored and achieve nothing. Numerous categories of MPA exist that permit varying levels of human interaction and extraction. Activities in them are usually intended to be "sustainable," but often in coral reef MPAs fishing continues to be allowed, thus negating many of their benefits.

Marine spatial planning (MSP) builds on this. It is a process of allocating areas to different purposes and a practical way to organize people's use of these areas. Rather than allow, for example, piecemeal and unorganized development or fishing, MSP allocates areas for a particular task in a way intended to be less random. When done best it is based on science. Instead of focusing on MPAs only, MSP focuses equally on areas planned for human use. It is a process that is becoming mandatory in many countries. It is not foolproof when conservation takes a backseat to development, but it can avoid accidental problems arising.



LEFT | Large marine protected areas (MPAs) can encompass island groups, along with substantial areas of rich reef as well as the open ocean surrounding them. In Raja Ampat, Indonesia, there are several MPAs that are ecologically connected.

ABOVE | Tubbataha in the Philippines is a World Heritage Site and a protected area in the rich and diverse Sulu Sea. It is popular with divers but also benefits from a high level of protection, being located far from centers of population and having no fresh water of its own. Terrestrial parts are a bird sanctuary.

REEF DECLINE: INERTIA AND POLITICS

The present rates of coral reef loss and of climate change have been measured intensively. We also know there is a many-year time lag for the atmosphere and ocean to reach equilibrium for heat and CO_2, which means there is no real prospect in the near or medium future of reversing coral reef decline. It has been said that if the two major damaging forces, overfishing and CO_2 emissions, were each to act alone they would cause the collapse of coral reefs by 2050, but together they have the chance of doing it by 2025. Yet, on the other hand, never has there been such interest, concern, and activity concerning this issue.

One major problem is that CO_2 emissions are still rising, and there is now an additional 1.2 °F (0.7 °C) rise in sea temperature ready to happen because of CO_2 already in the air. We know that 350 ppm of CO_2 in the air is the maximum that will allow coral reefs to function once the CO_2 is in equilibrium with the ocean, but today we are approaching 410 ppm. However, our existing fossil fuel infrastructure has a 20- to 50-year lifetime left, and we can be sure it will be used! In addition, complex, fair, and workable international agreements to get on top of any problem are rarely made in less than a couple of decades. Solutions to overfishing and pollution control suffer from similar human inertia.

We now know a tremendous amount about coral reefs, and it is probably fair to say that we do not really need to know much more, in principle, to understand what must be done to halt their decline. The science used has been what is often called reductionist science, in which people discover "more and more about less and less." It is perhaps realistically the only possible way to do science, but what is missing is an

understanding of how the whole coral reef system integrates with completely different branches such as economics, social structures, poverty, and governance. For example, reef management methods under democracies differ widely from those used by some tropical dictatorships where many reefs are located. But a more holistic approach is crucial if we are to save this very vulnerable ecosystem. This is difficult, but will be central to progress.

ABOVE | Plastic in the oceans has become a major form of pollution. Entanglement of marine animals is now common. As plastics disintegrate to plankton-size particles, they are then consumed by filter feeders and cause more damage.

BELOW | Burgeoning human populations have led to severe overcrowding in many places. Several Asian islands with similar crowding support fishing communities, though on this island, Santa Cruz del Islote in Colombia, people mostly work on the adjacent mainland.

REEFS AT THE CROSSROADS

Coral reefs have the dubious distinction of leading the way on responding to rising CO_2—they are the "canaries in the coal mine." In the past 50 years they have been changed more profoundly than in the preceding 5,000. We have entered a new geological epoch many call the Anthropocene, replacing the Holocene that has existed since the last ice age ended, a name reflecting the overarching influence of people.

We understand a great deal about reefs in one sense, but in another we have perhaps missed some of the crucial questions that would enable us to live more harmoniously with them. It is said that to understand what we are doing, we need to understand what nature would be doing if left alone. However, we do not have a baseline extending far enough back to know what unaltered reefs might have been like, and we have limited means of finding out now. Multiple stressors are changing them: first, removing many of the vertebrates and invertebrates, then corals yielding space to seaweeds and then to very primitive communities of blue-green algae and bacteria—a greenish-brown slime. It has been called a "slippery slope to slime," and the decline is in one sense a sort of reversal of the evolutionary process back to a condition not seen for millions of years. In the process, reefs, which should be noisy ecosystems that snap and crackle continuously with the bustle of fish, snapping shrimps, and many interacting species, are becoming much quieter. Most have lost their bustle. Weakened by pollution, overfishing, and warming, they are quite simply dying and their ecosystems fading in grandeur.

This is the trend for reefs at present. Graphs have been produced for all tropical regions showing their alarmingly high decline, and marine heatwaves since 2015 have killed a further fifth of remaining corals. Nobody can doubt that the

ecosystem is in profound trouble. Massive reduction of CO_2 that drives the warming is needed. It will be expensive, though much less expensive in the long term than doing too little now. Importantly, reef decline is as great in the world's most affluent countries as in the poorest. Although most human society has, until now, had its head in the sand over the issue, recovery is possible—if we want it enough.

BELOW LEFT | Reefs destroyed by careless misuse, overuse, or destructive dynamite blasts during fishing operations, for example, take at least a decade or more to regain their former diversity and abundance of life.

BELOW | Undamaged and unexploited reefs are notable for the biodiversity of their abundant corals, soft corals, and fish life.

THE FUTURE OF REEFS

We should end on a positive note! This book shows just a small part of the natural glories of coral reefs and the huge benefits that they can provide. True, we have now destroyed nearly half of them, but at least we now realize that this destruction is to our own disadvantage in terms of lost diversity, protein production, and revenue, and increased erosion. We are in a position to arrest the decline. We humans are, after all, extraordinarily resourceful and determined! Our gain from the beauty of nature is surely incalculable, too, but this aspect is commonly omitted from most assessments.

It has been said that poverty is the worst form of pollution, and few would disagree that many communities living along coasts fringed by coral reefs have many fewer options in life than those in affluent countries who may visit tropical places. It is wrong and pointless for the latter to blame poor subsistence people for reef destruction caused because they seek resources that they need.

But how should we do what needs to be done? We now have the technical ability and understanding of the system to work out effective ways forward. There are two alternative arguments surrounding the best approach to encourage progress. One, "ocean optimism," is the view that being positive about conservation, showing its benefits, and showing ways to go about it is the sensible way forward,

because being negative is not only depressing but also counterproductive. The opposite argument develops when an ecosystem such as a coral reef continues to decline despite optimistic approaches. This view holds that increasingly strident warnings and information need to be given to achieve the necessary conservation measures—to shame decision-makers where necessary and to publicly allocate blame; that a "kick in the pants" approach is needed to force the necessary action.

Both approaches are needed. Education and building ocean literacy is an essential part of the solution, as is no longer allowing people and businesses to treat the ocean as a place that can be exploited without responsibility for the costs. Technically we can achieve the necessary progress. Progress must be achieved as it would also benefit people in the communities that rely on healthy reef ecosystems. And that is all of us!

OPPOSITE | Caves and overhangs on steep reefs commonly have different complements of species. They appear brightly colored when artificial light is added by a photographer.

BELOW | Southeast Asia has the highest diversity of reef life, but also some of the highest pressures from people.

GLOSSARY

Anthropocene The present geological epoch in which humans have been the dominant factor changing the Earth, its ecosystems, and species extinctions. Most define its start from the beginning of the industrial age, or from the advent of nuclear testing.

Aragonite A form of calcium carbonate that corals deposit. It is a relatively soft rock.

Asexual reproduction Reproduction that does not need two parents. Budding of polyps and fragmentation of branches are both asexual methods in corals.

Atoll A ring-shaped reef structure formed on top of subsiding substrate, mostly volcanoes. It may have islands on the rim or may be entirely submerged.

Benthic Living on the seabed or the reef floor.

Bioerosion Erosion caused by animals and plants. In a reef context, erosion of the reef fabric by boring, tunneling, and burrowing animals and plants.

Biomass The amount, or mass, of biological or living material.

Bleaching The whitening of a coral under stress (often heat). Caused when the stressed coral expels its brown-green algal cells, making the coral tissue transparent, so the white skeleton beneath becomes visible.

Budding The division of a polyp by splitting into two.

Calcite A form of calcium carbonate. Harder than aragonite, which turns into calcite over many years.

Calice The dish-shaped depression or cup on a coral in which the polyp lives.

Cay Name for islands made mostly or entirely of sand and sitting on coral reefs. Usually used for Caribbean reefs.

Center In a brain coral, where each mouth or individual in the chain of polyps is located, or the skeletal structure beneath it.

Cnidaria The phylum of animals defined by having tentacles with stinging cells. Contains stony corals, soft corals, jellyfish, and others.

Commensalism A close relationship between two different species in which one benefits and the other derives no benefit or harm. See parasitism and symbiosis.

Corallite A unit of a coral skeleton including the walls, septal plates, and other structures associated with a polyp.

Costa (costae) The radial skeletal plates in each corallite.

Cryptic Hidden, or living in holes and crevices.

Demersal Feeding or living near to or on the ocean bottom.

Dinoflagellates Unicellular (single-celled) algae; they are the symbiotic algae in corals and soft corals, but their free-living form is mobile, moving with two flagella (beating whip-like structures that allow locomotion).

Ectodermis The outer layer of tissue of a coral polyp or the top layer of tissue connecting polyps. It contains the stinging cells.

Endemic When applied to species, native to a particular place or region and limited to that place.

Epigenetic Changes in an organism caused by alterations in the activity of a gene, but not alterations of the gene itself.

Extra-tentacular budding Where polyp budding takes place on the polyp outside its ring of tentacles.

Fluorescence Emission of visible light by complex proteins which have absorbed ultraviolet light.

Fragmentation The breaking off of parts of a coral colony, usually branches, which then reattach to the substrate to form a new, genetically identical colony.

Gastrodermis The inner layer of tissue of a coral polyp or the lower layer of tissue connecting polyps.

Genus In taxonomy, the level of classification one level above species. All species in a genus are closely related. The coral genus *Acropora* has over 150 species worldwide, while some coral genera have just one.

Hexacoral Coral polyps whose radial symmetry is basically of six sections. Stony corals are hexacorals.

Holocene The geological epoch that started after the last ice age and lasted about 16,000 years until the Anthropocene.

Hydrozoans A group in the phylum Cnidaria. Mostly marine, mostly colonial animals that trap plankton.

Intra-tentacular budding Where polyp budding takes place inside the ring of tentacles. The resulting daughter polyps may completely separate, or a chain of polyp bodies may develop within one elongated ring of tentacles.

Meandroid Where the coral surface has long meandering chains of connected polyps.

Medusae One of two body types in the phylum Cnidaria. Medusae are free-swimming and may dominate in animals such as jellyfish, or may be a much shorter stage in the reproductive cycle, as with the medusa stage of a fire coral.

Mesenteries Folds of tissues inside a coral polyp, including its digestive structures.

Mesoglea The gelatinous material between the two layers of the polyp body wall.

Nematocysts The stinging structures found in the tentacles of all Cnidaria.

Ocean acidification A decrease in pH (increase in acidity) of seawater due to dissolved carbon dioxide, making conditions less favorable for organisms to deposit limestone.

Octocoral Where the radial symmetry of the polyp is in eight segments. The soft corals are octocorals.

Parasitism An association between two species where one benefits and the other is harmed.

Pelagic Living in the water column.

Phaceloid Corallites whose walls are separated from each other except at the base.

Phytoplankton Plant plankton, mostly single-celled, and smaller than zooplankton.

Planula (planulae) The free-swimming, juvenile, or larval stage of a coral.

Polyp The coral or soft coral animal, consisting of the central body and its ring of tentacles.

Scleractinia The taxonomic name for the stony or reef-building corals. An order (a major division in taxonomy) that includes several families.

Septum (septa) A plate-like structure in a corallite; these are arranged in a radial form.

Spicule A minute and very angular or lumpy piece of limestone. In soft corals large numbers of these are present in the otherwise gelatinous matrix, and most species develop them in unique shapes, which can be used in species identification.

Substrate The surface of the ocean bottom; on a coral reef, the substrate is rocky or sandy.

Symbiosis A close association between two or more unrelated species. This may be microbial, as with algae living in the tissues of a coral polyp, but also includes mutually beneficial relationships between two larger animals or plants. Both or all partners receive benefits. See commensalism and parasitism.

Tentacle Structures of soft corals and corals surrounding the mouth. Most are retracted during the day. They contain the nematocysts (stinging cells) used to catch zooplankton, and also contain the photosynthetic algal cells.

Trophic level The “feeding level” of an organism: photosynthetic plants are the base at level 1, herbivores which eat plants are level 2, primary carnivores that eat herbivores are level 3, secondary carnivores which eat primary carnivores are level 4, etc. Usually not clear-cut, as when a secondary carnivore feeds on herbivores as well as primary carnivores.

Zooplankton Animal plankton. Many zooplankton spend their entire life floating freely as part of the plankton, but it includes larvae of almost any species too.

Zooxanthellae Single-celled algae that live in coral and soft coral tissues.

FURTHER READING

Anderson, R.C.
1990.
Living Reefs of the Maldives.
NOVELTY PRINTERS AND PUBLISHERS, MALDIVES.

Bemert, G. and Ormond, R.
1981.
Red Sea Coral Reefs.
KEGAN PAUL INTERNATIONAL, LONDON AND BOSTON.

Birkeland, C.
1997.
Life and Death of Coral Reefs.
CHAPMAN & HALL, NEW YORK.

Birkeland, C. (editor)
2015.
Coral Reefs in the Anthropocene.
SPRINGER, DORDRECHT.

CNA Military Advisory Board
2014.
National Security and the Accelerating Risks of Climate Change.
CNA, ALEXANDRIA, VIRGINIA.
A report by 16 retired admirals and generals, mostly USA with one UK.

Côté, I.M. and Reynolds, J.D. (editors)
2006.
Coral Reef Conservation.
CAMBRIDGE UNIVERSITY PRESS, CAMBRIDGE.

Cousteau, J-Y.
1971.
Life and Death in a Coral Sea.
CASSELL AND CO., LONDON.

Gray, W.
1993.
Coral Reefs and Islands: The natural history of a threatened paradise.
DAVID AND CHARLES, NEWTON ABBOT, UK.

Hopley, D. (editor)
2011.
Encyclopedia of Modern Coral Reefs: Structure, form and process.
Encyclopedia of Earth Sciences Series.
SPRINGER, DORDRECHT.

Jones, S.
2007.
Coral: A pessimist in paradise.
LITTLE, BROWN, LONDON.

Riegl, B.M. and Dodge, R.E. (series editors)
Various dates from 2008.
Coral Reefs of the World.
SPRINGER, DORDRECHT.
This is an ongoing series of research-level books by multiple authors. Most are based on a single region, and some are based on themes.
1 Coral reefs of the USA.
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6 Coral reefs at the crossroads.
7 The Red Sea (Fisheries).
8. Eastern Tropical Pacific.
9 Mediterranean corals.
11 Red Sea.
12 Mesophotic reefs.
13 Japan.

Roberts, C.M.
2019.
Reef Life: An underwater memoir.
PROFILE BOOKS, LONDON.

Rower, F.
2010.
Coral Reefs in the Microbial Seas.
PLAID PRESS, USA.

Sheppard, A.L.S.
2015.
Coral Reefs: Secret cities of the seas.
NATURAL HISTORY MUSEUM, LONDON.

Sheppard, C.R.C.
2014.
Coral Reefs: A very short introduction.
OXFORD UNIVERSITY PRESS, OXFORD.

Sheppard, C.R.C., Davy, S., Pilling, G. and Graham, N.A.J.
First edition 2009, revised edition 2017.
Biology of Coral Reefs.
OXFORD UNIVERSITY PRESS, OXFORD.

Sheppard, C.R.C., Price, A.R.G. and Roberts, C.
1992.
Marine Ecology of the Arabian Region:
Patterns and processes in extreme tropical environments.
ACADEMIC PRESS, LONDON.

Shick, J.M.
2018.
Where corals lie: A natural and cultural history.
REAKTON BOOKS, LONDON.

Stone, G.S. and Obura, D.
2013.
Underwater Eden: Saving the last coral wilderness on Earth.
UNIVERSITY OF CHICAGO PRESS, CHICAGO AND LONDON.
(About the Republic of Kiribati.)

Veron, J.E.N.
1995.
Corals in Space and Time.
CORNELL UNIVERSITY PRESS, NEW YORK.

Veron, J.E.N.
2008.
A Reef in Time: The Great Barrier Reef from beginning to end.
HARVARD UNIVERSITY PRESS/
BELKNAP PRESS, CAMBRIDGE.

Wells, S. and Hanna, N.
1992.
The Greenpeace Book of Coral Reefs.
BLANDFORD, LONDON.

Wright, J.
New edition, 2014.
The Coral Battleground.
SPINIFEX PRESS, VICTORIA, AUSTRALIA.

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