SCIENTIFIC AMERICAN

CORAL

$1.50

August 1979

Corals and Coral Reefs

Tiny coral polyps, living in symbiosis with photosynthetic algae, build huge limestone reefs that harbor more plant and animal species than any other ecosystem on the earth

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Man's ability to alter the surface of the earth is rivaled among biological organisms only by colonies of tiny coral polyps, which over aeons of geologic time accrete massive reefs of limestone. True reef corals are limited in geographical distribution to the clear, warm, sunlit waters of the tropical oceans; they are found in the great reef tracts of the Indo-Pacific and the western Atlantic. Reefs are important land builders in tropical areas, forming entire chains of islands and altering the shoreline of continents.

There are three major types of coral reef. Fringing reefs grow in shallow water and border a coast closely or are separated from it by a narrow stretch of water. Barrier reefs also parallel a coast but are farther away from it, are larger and are continuous for greater distances; the best-known is the Great Barrier Reef off the northeastern coast of Australia, which forms an underwater rampart more than 2,000 kilometers long, as much as 145 kilometers wide and as much as 120 meters high. Atolls are rings of coral islands enclosing a central lagoon, and hundreds of them dot the South Pacific. Consisting of reefs several thousand meters across, many of them are formed on ancient volcanic cones that have subsided, with the rate of growth of the coral matching the rate of subsidence. This explanation of atolls was proposed by Charles Darwin during the voyage of the *Beagle* and was confirmed in the 1950's by Harry S. Ladd and Joshua I. Tracey of the U.S. Geological Survey when their extensive drilling programs on Pacific atolls hit volcanic rock hundreds of meters down.

Although tropical ocean waters are impoverished in nutrients, having low concentrations of dissolved nitrates, ammonia and phosphates, coral-reef environments have among the highest rates of photosynthetic carbon fixation, nitrogen fixation and limestone deposition of any ecosystem. The reef ecosystem also probably supports a larger number of animal and plant species than any other. The key to this prodigious productivity is the unique biology of corals, which plays a vital role in the structure, ecology and nutrient cycling of the reef community.

The Biology of Corals

Because corals are sessile they were for a long time thought to be plants. In Ovid's *Metamorphoses* he refers to the coral as an organism that is soft under water but hardens on contact with air. (What he was actually seeing was the death of the living tissue, which exposed the hard skeleton.) In 1723 the naturalist Jean André Peyssonel proposed to the French Academy of Sciences that corals are animals. His view was derided, and he subsequently abandoned scientific work. Since then, of course, he has been proved right. Corals belong to the large and varied phylum of coelenterates, which are simple multicellular animals. The phylum's name is from the Greek *koilos*, hollow, and *enteron*, gut, because the main body cavity of its members is the digestive cavity.

The closest relatives of the true corals are the sea anemones, which corals resemble in basic body structure and overall appearance. The soft coral polyp consists of three layers of cells and is basically a contractile sac crowned with a ring of six tentacles (or a multiple of six) surrounding a mouthlike opening. The tentacles have the specialized stinging cells called nematocysts, which discharge an arrowlike barb and a toxin that stuns animal prey such as microscopic crustaceans. From the mouth of the polyp the short muscular gullet descends into the stomach cavity and is connected to the body wall by six partitions (or a multiple of six), increasing the area of the digestive surface. The free edges of the partitions are extended into mesenterial filaments: convoluted tubes that can be extruded through the mouth or the body wall.

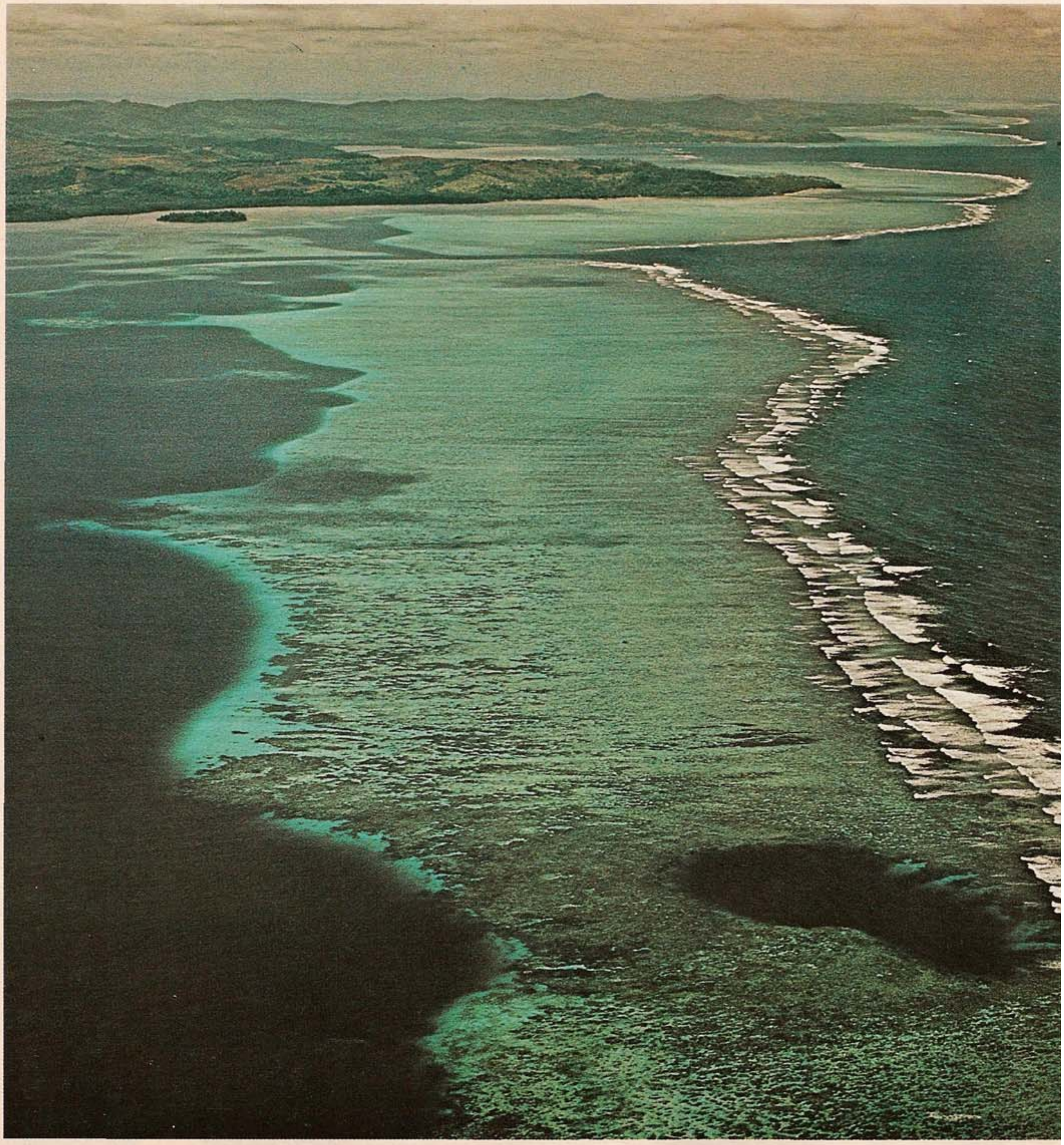
The size of the polyps is highly variable, from about one millimeter in diameter in some species to more than 20 centimeters in others. Each polyp can give rise to a large colony by asexual division, or budding. Corals also reproduce sexually, producing free-swimming larvae that settle and establish new colonies. The most striking feature of coral colonies is their ability to form a massive calcareous skeleton. Individual coral colonies weighing several hundred tons and large enough to fill a living room are common in many reefs. In most species the polyps are in individual skeletal cups, some extending their tentacles to feed by night and some partially withdrawing into the cups by day. In the contracted condition the polyps can resist drying or mechanical injury at low tide, when some of the colonies may be exposed. The skeletal cups consist of fan-shaped clusters of calcium carbonate crystals, which are arranged in patterns that are characteristic of each coral species.

A remarkable feature of all reef-building corals is their symbiosis with the unicellular algae known as zooxanthellae. The coral polyps contain large numbers of these algae within cells in the lining of their gut. The zooxanthellae are yellow-brown marine algae of the family *Dinophyceae*, to which many of the free-living dinoflagellate algae also belong. The algae live, conduct photosynthesis and divide within the cells of their coral host, and on this symbiosis rests the entire biological productivity of the coral-reef ecosystem.

Since the zooxanthellae of reef-building corals need light for photosynthesis, such corals grow only in ocean waters less than 100 meters deep. The corals also require warm waters (above 20 degrees Celsius) and do not tolerate low salinity or high turbidity. Where deeper colonies are shaded by a dense overgrowth of shallower ones, the deeper colonies maximize their light-gathering capacity by growing in ramifications like the branches of forest trees. In shallow water, where light is abundant but wave stress is high, the colonies deposit robust branching skeletons; in deeper water, where light is scarce, the colonies form horizontal platelike structures in which each polyp may harbor an increased number of zooxanthellae. Under highly adverse conditions such as prolonged darkness or freshwater flooding it is no longer advantageous for the coral polyps to maintain their zooxanthellae and they expel them from their tissues. Since the skeletal-growth rate of corals is dependent on their algal partners, true reef-building corals are almost never found outside the range of stable symbiosis.

Some coral species harbor no zooxanthellae; some of these species are found in crevices under the large structures erected by reef-building corals. Many of them are solitary cup corals such as *Astrangia,* which encrusts shells and rocks as far north as Cape Cod. Such corals can tolerate lower salinities, lower temperatures and greater depths: up to 6,000 meters in the deep sea. Even the deep, cold waters of the Norwegian fjords harbor great banks of *Lophohelia,* a colonial branching coral. Although these nonsymbiotic corals are distributed worldwide, their rate of growth is much lower than that of their symbiotic relatives, and they do not form massive reefs. In isolated instances colonies of these corals do contain symbiotic algae, but the algae do not appear to contribute significantly to the nutrition of their host.

The zooxanthellae are stored within individual membrane-bound cavities inside each of the cells in the stomach wall of the coral polyp. The feedback mechanism whereby the host regulates the number of its algal cells has not been determined, but there is little evidence that the corals "farm" and digest their



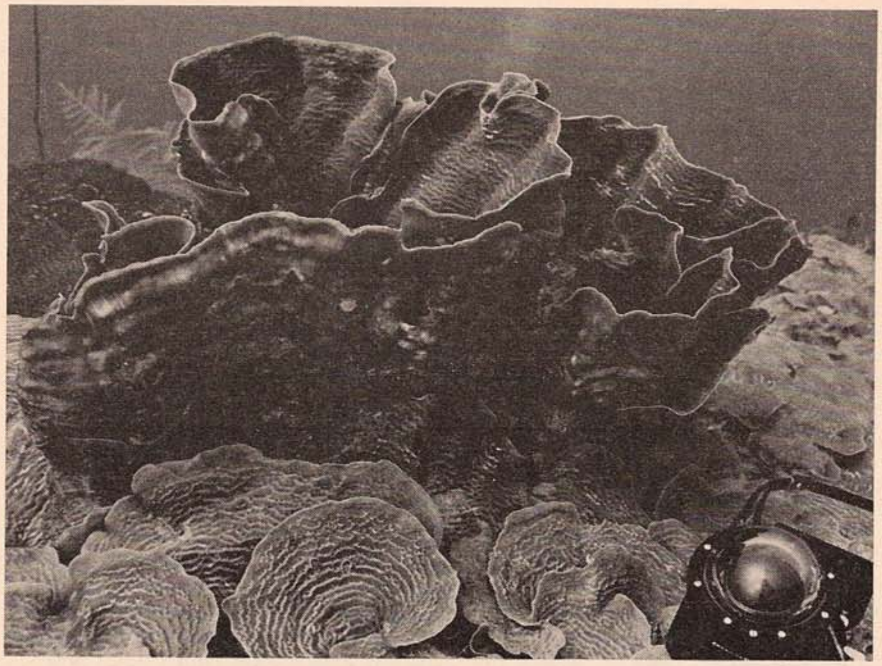
DIMES REEF off the Palau Islands in the western Pacific is shown in this aerial view. The shallow crest of the barrier reef is marked by the waves breaking over it. The Palau Islands, which are part of the Western Caroline group, are situated 1,060 miles southeast of Manila.

STAGHORN CORAL is a species commonly found in the shallow, sunlit waters of tropical coral reefs. Along the reef crest, where the corals must withstand the mechanical forces of waves, the staghorn colonies are robust and have short branches. In the sheltered waters behind the reef crest the colonies grow taller and have longer, slenderer branches, as is seen here. Corals always grow toward the light.

LIVING CORAL POLYPS were photographed at sunset, when they emerge to feed. By day they retract into their skeletal cups and so are able to withstand drying if the colony is exposed at low tide. The polyps, which reproduce sexually and by asexual division, coat the entire surface of the coral skeleton. They feed on small plankton animals, which they stun with stinging cells (nematocysts) on their tentacles.

algae. Instead the coral polyps seem to control the population of zooxanthellae by extruding the older and less metabolically active algae.

Robert K. Trench and his colleagues at the University of California at Santa Barbara have shown that specific strains of zooxanthellae are adapted to specific coral species. Some strains can live successfully in several different corals, and some corals are not discriminating about the lineage of their symbiotic algae. The fascinating problems presented by the symbiotic selectivity of corals are only beginning to be explored, and corals provide a valuable experimental system for the study of cellular interactions in general.



TWO SPECIES of the coral *Agaricia* growing side by side differ strikingly in shape and size. One type has whorled fronds, whereas the other has shinglelike plates. Such complex morphological differences are produced by subtle environmental gradients, such as the decline of ambient-light intensity with depth. The corals are at a depth of 43 meters off Jamaican coast.

The Physiology of Coral Symbiosis

The modern study of the physiology of coral symbiosis began with a series of elegant experiments done by C. M. Yonge on the Great Barrier Reef Expedition of 1929. Yonge showed that symbiotic corals take up phosphates and ammonia from the surrounding seawater by day and release them at night. In order to study this phenomenon in greater detail two of us (Thomas F. Goreau and Nora I. Goreau) supplied carbon in the form of the radioactive isotope carbon 14 to reef corals. During the daylight hours the zooxanthellae assimilated the radioactively labeled carbon and photosynthetically fixed it into organic matter at a rate that was dependent on the intensity of the light. Some of this organic matter was then "leaked" from the algae to the coral host. Subsequent work by Trench and Leonard Muscatine of the University of California at Los Angeles and by David Smith of the University of Oxford showed that the leaked compounds include simple nutrients such as glycerol, glucose and amino acids. These compounds are utilized by the coral polyps in energy-yielding metabolic pathways or as building blocks in the manufacture of proteins, fats and carbohydrates.

It has long been known that the rates of metabolic reactions are strictly limited by the rates at which waste products are removed from the immediate environment. In higher animals the task is accomplished by specialized circulatory and excretory systems. These systems are absent in the anatomically simple coelenterates, which rely largely on the slow process of diffusion to remove soluble inorganic waste products such as carbon dioxide, phosphates, nitrates, sulfates and ammonia. The zooxanthellae, however, need for photosynthesis the very substances the coral polyp must get rid of, and they are believed to actively take them up from their host.

The photosynthetic demands of the zooxanthellae therefore result in the cycling of the coral's waste products into new organic matter. During the daylight hours the symbiotic algae produce more oxygen than the coral polyp can utilize for its respiration, and some of the carbon dioxide produced by the respiratory process is refixed by the algae into new organic matter. In order to estimate the efficiency of the internal carbon cycling in corals one of us (Thomas J. Goreau) determined the abundance in the coral tissue and skeleton of carbon 13, a rare but nonradioactive natural isotope, with respect to the abundance of the common natural isotope carbon 12.

For reasons it is not necessary to explain here, photosynthesis takes up carbon 12 slightly faster than it does carbon 13. Hence the organic matter synthesized by the zooxanthellae will have a relative preponderance of carbon 12, and a pool of carbon compounds enriched in carbon 13 will be left behind. It is from the compounds in this pool that the calcium carbonate coral skeleton is built. By determining the relative amounts of the two isotopes with a mass spectrometer it was estimated that about two-thirds of the carbon taken up in photosynthesis and calcification is recycled from the respiratory carbon dioxide of the coral polyp, with the rest being taken up from the seawater.

Organic matter leaked by zooxanthellae is only one of the three major sources of coral nutrition. Corals are efficient carnivores, immobilizing animal plankton with the stinging cells of their tentacles or trapping them on filaments of mucus that are then reingested. A polyp can detect a potential food item chemically, and it responds by extending its tentacles, by opening its mouth or by extruding its mesenterial filaments. James Porter of the University of Georgia has analyzed the content of the coral stomach and found that the polyps feed mostly on tiny crustaceans and wormlike plankton that hide in the interstices of the reef by day and emerge at sunrise and sunset.

Studies with radioactively labeled compounds have also shown that corals are able to take up dissolved organic matter across their body wall. Since corals actively feed on plankton, take up nutrients from seawater and absorb chemicals released by their zooxanthellae, they fill several ecological roles simultaneously: primary producer, primary consumer, detritus feeder and carnivore. This complex food web reduces their dependence on any single food source, which might be subject to random variation as environmental conditions change.

Calcification in Corals

Growth in corals is achieved by an increase in the mass of the calcareous skeleton and the overlying living tissue. The skeleton of corals is composed entirely of aragonite, a fibrous crystalline form of calcium carbonate ($CaCO_3$); calcite, the commoner crystalline form of calcium carbonate, is absent. In the reef many algae also deposit aragonite or a more soluble form of calcite with a high magnesium content. Working in Bermuda, Heinz A. Lowenstam of the California Institute of Technology showed that some calcareous organisms tend to deposit the less soluble calcite in the cold seasons and the more soluble aragonite in the warm seasons, but the mechanisms by which organisms regulate the mineralogy of their skeleton are still unknown.

Coral polyps absorb calcium ions from seawater and transfer them by diffusion and by an active pumping mechanism to the site of calcification. Calcium ions are a major biochemical regulator of cell metabolism and must be kept at extremely low levels if the cells of a tissue are to function. Although coral tissues have a total calcium concentration similar to that of seawater, the concentration of free ions in them is much lower because most of the calcium is bound to membranes or to organic molecules. Lothar Böhm, working in our laboratory at the University of the West Indies in Jamaica, has shown that the calcium bound in these organic complexes turns over rapidly.

One of us (Nora I. Goreau), working in collaboration with Raymond Hayes of the Morehouse College School of Medicine in Atlanta, recently made detailed electron-microscope studies of coral polyps. In the course of these studies minute calcium carbonate crystals enclosed within membrane-bound vesicles were observed in the outer cell layer of the polyp. The crystals are extruded through the membrane to the coral skeleton, where they act as nuclei for continued crystal growth. This work may serve to clarify basic mechanisms of calcification in the cells of a variety of organisms, particularly because corals lack the hormonal controls over calcification that complicate these mechanisms in more advanced organisms.

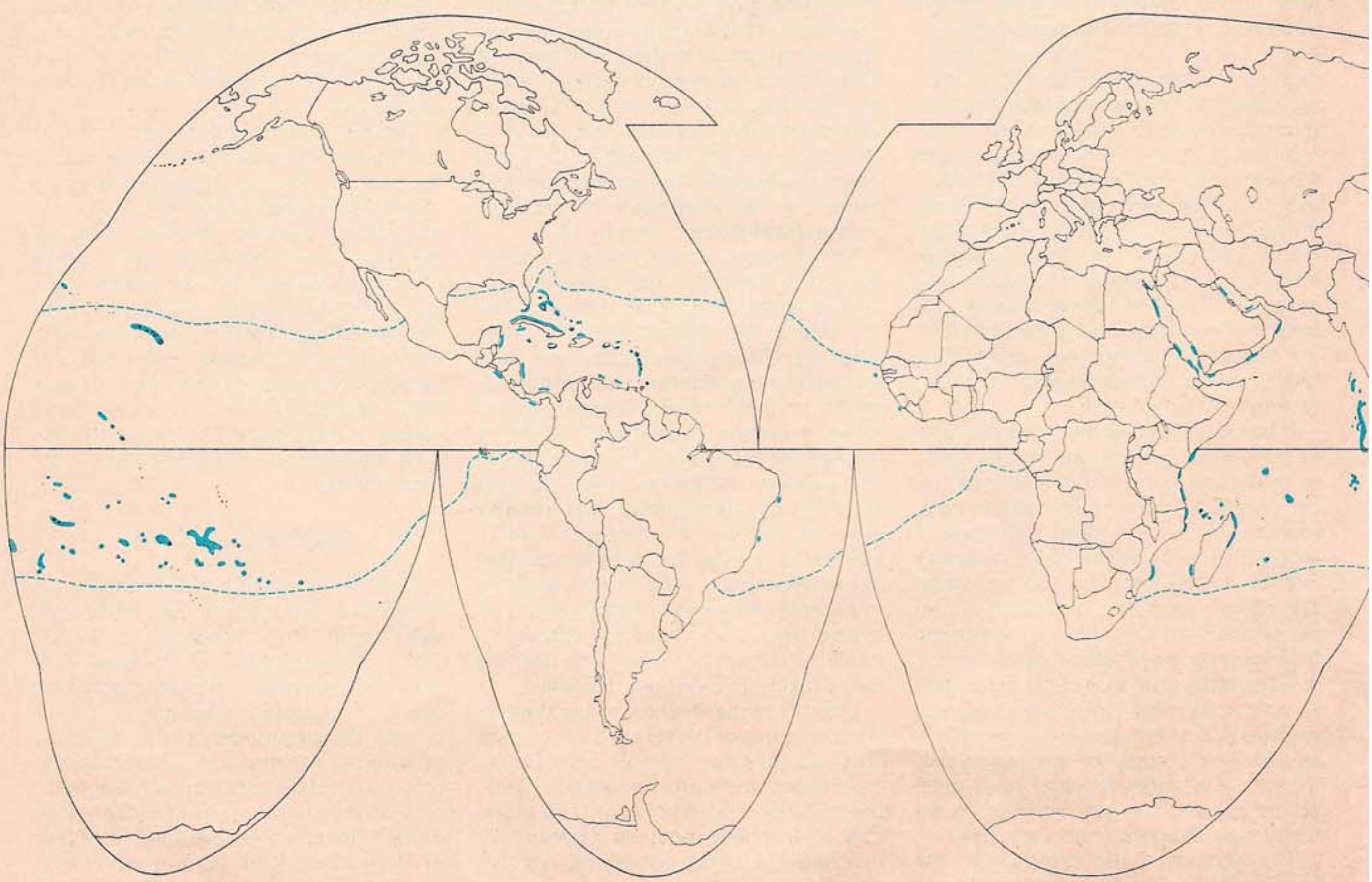
The major obstacle to the study of the physiology of calcification in corals has been the difficulty of keeping corals alive and healthy in laboratory aquariums long enough to make accurate measurements of the calcium uptake. One of us (Thomas F. Goreau) circumvented the problem by measuring calcification in situ in the living coral reef. This was done by providing the coral with calcium in the form of the radioactive isotope calcium 45 and measuring the uptake of the radioactive calcium into the coral skeleton. The method is so sensitive that growth can be detected in corals that have been exposed to the radioactive calcium for only a few hours, which is what makes field studies practicable.

Such studies have shown that although reef-building corals grow under fairly uniform conditions of temperature, illumination and water circulation, there are very large differences in the growth rates of different species. The highest rates are invariably found in the branching corals, such as the West Indian elkhorn and staghorn corals. *Millepora* ("fire coral") is a close second, with the *Poritidae* ("finger corals") third. The massive corals grow more slowly. In the branching corals most of the growth takes place at the tips of the branches, and new branches develop almost anywhere on the older parts of the colony.

Factors Influencing Calcification

A crucial factor influencing the rate of calcification is the conversion of respiratory carbon dioxide (CO_2) into carbonic acid (H_2CO_3), which is in turn converted into bicarbonate (HCO_3^-) and carbonate (CO_3^{--}) ions. The enzyme responsible for the addition of water to carbon dioxide to form carbonic acid is carbonic anhydrase, which is present in high concentrations in corals. The subsequent formation of bicarbonate and carbonate ions is rapid and does not require catalysis by an enzyme. Drugs that inhibit carbonic anhydrase bring about a dramatic decline in the calcification rate.

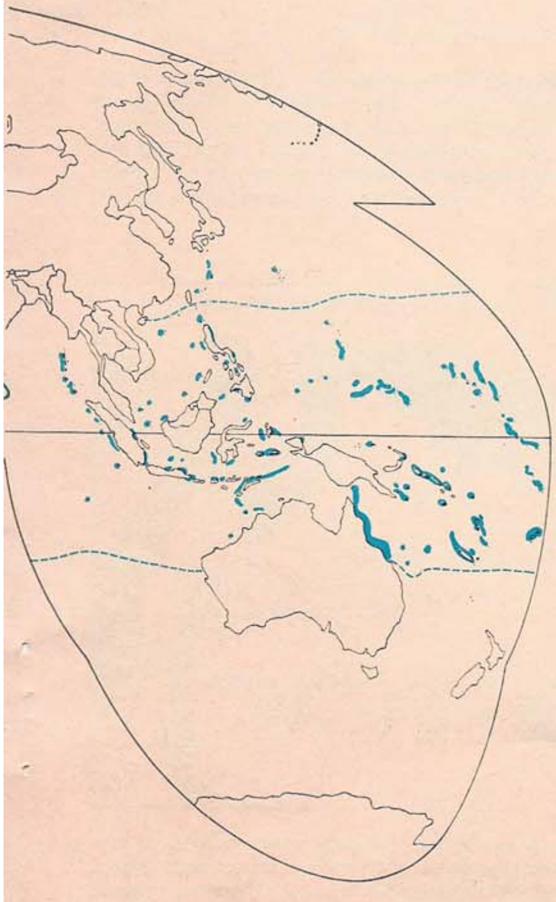
The growth of the coral skeleton is on the average 14 times faster in sunlight than it is in darkness, and it can be decreased by drugs that block photosynthesis. Even daily variations in light intensity have a measurable effect on the



WORLD'S CORAL REEFS (*color*) can be divided into three basic types: atolls, barrier reefs and fringing reefs. Reefs of the West Indies are primarily fringing ones. Reef-building corals are found only in sunlit tropical waters (*broken lines*) because their ability to rapidly

calcification rate: the uptake of calcium is fastest at noon on a clear, sunny day, is reduced by 50 percent on a cloudy day and by nearly 90 percent in total darkness. The intensity of the ambient light also decreases with depth: the flux of light at a depth of 60 meters is only 4 percent the flux at the surface. As a result the rate at which calcium is deposited into the coral skeleton probably decreases rapidly with increasing depth.

The striking dependence of the growth of coral on the intensity of the ambient light is observed only when the zooxanthellae are present. If the symbiotic algae are removed (by keeping the coral colony in darkness for several months), the rate of calcification is low and is no longer affected by changes in light intensity, as is normally the case with nonsymbiotic corals. How do the zooxanthellae enhance the calcification rate? The answer seems to be that the fixation of carbon dioxide by the algae gives rise to an increase in the concentration of carbonate ions in the cells of the coral polyp through a series of linked chemical reactions, raising the *p*H of the fluid in the cells so that it is more alkaline. By precipitating its excess carbonate ions in the form of insoluble calcium carbonate the polyp is able to restore its *p*H to the normal level and at the same time build up its limestone skeleton. The zooxanthellae may also stimulate calcification indirectly by increasing the amount of free energy available for the active transport of calcium ions to the site of calcification. The algae therefore work synergistically with carbonic anhydrase to enhance the formation of calcium carbonate. Calcification can proceed in the absence of algal photosynthesis but only at a greatly reduced rate.



accrete limestone skeletons depends on their symbiosis with algae known as zooxanthellae.

The fact that calcification in corals is biologically controlled is further indicated by seasonal variations in the growth rate. These variations are reflected in measurements made by one of us (Thomas J. Goreau) of the concentration of the trace metal magnesium and of the heavy and light isotopes of carbon and oxygen in seasonal growth bands. Once the environmental and physiological influences that affect the growth of coral are better understood the variations in the composition of coral skeletons will provide a detailed chemical record of past environments much as tree-ring records do.

The synergistic effect of zooxanthellae on the calcification rate was clearly a decisive factor in the evolution of coral reefs. The development of enormous coral communities in the face of battering by heavy seas became possible only when the processes of calcium carbonate deposition became efficient enough for the rate of deposition to exceed the rate of loss through physical and biological attrition.

Reef Architecture

Coral polyps may not dominate the biomass (the total mass of living matter), the biological productivity or even the calcification in all parts of a coral reef. Nevertheless, the existence of many of the animal and plant communities of the reef is based on the ability of coral to build a massive wave-resistant structure. The dynamic interactions of the geological and biological processes that control the growth of coral reefs are well illustrated in the 150-mile fringing reef along the northern coast of Jamaica, which we have studied for the past 28 years.

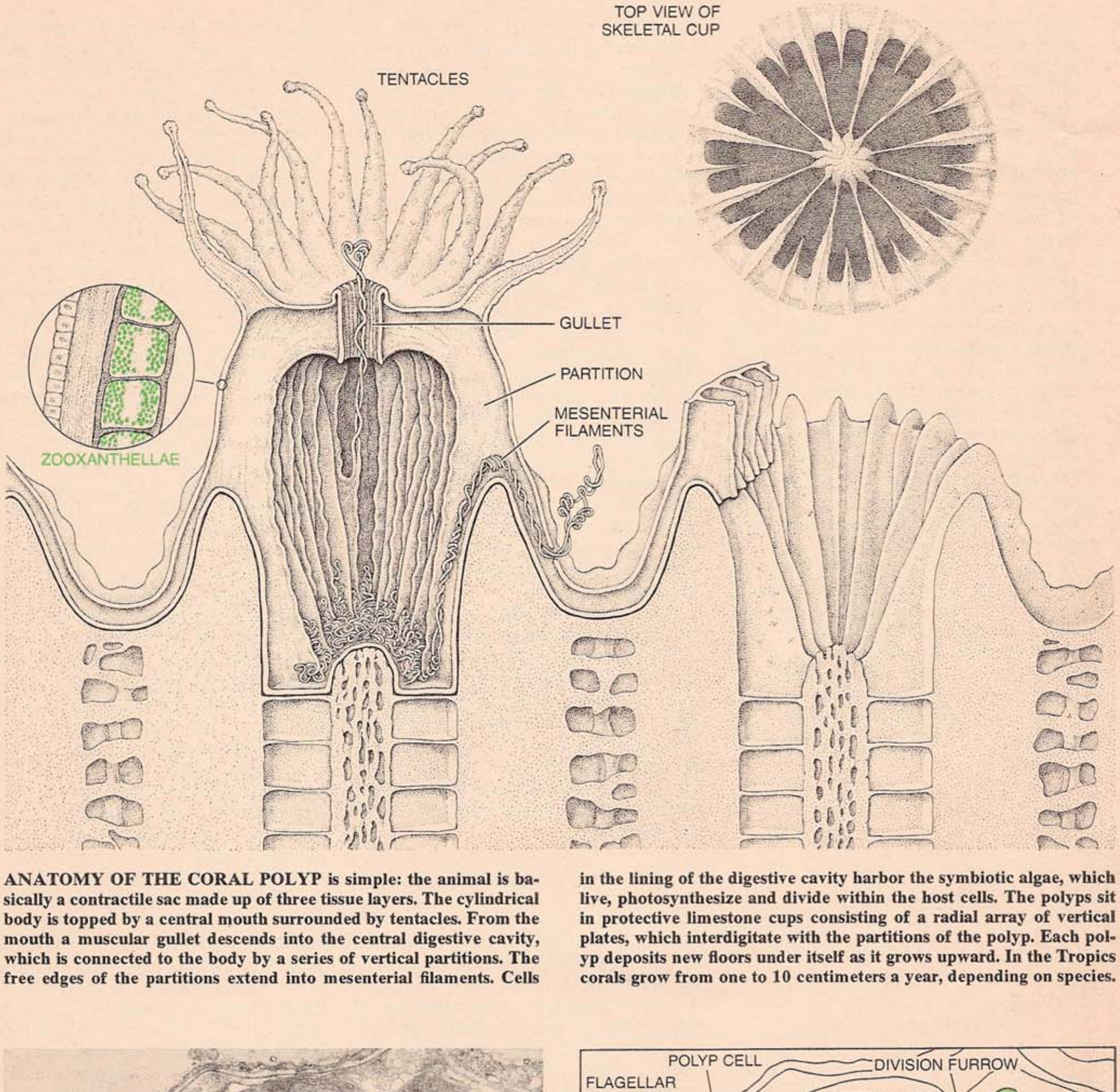
The major structural feature of the living reef is a coral rampart that reaches almost to the surface of the water. It is made up of massive rounded coral heads and robust branching corals, which build a rigid, cavernous palisade of intergrown coral skeletons. Living on this framework are smaller and more fragile corals and large quantities of green and red calcareous algae. The biomass of these algae is small compared with that of corals, but their productivity and turnover are so high that the sand consisting of their skeletal remains makes up the bulk of the calcium carbonate deposited in the reef.

Hundreds of species of encrusting organisms live on top of the coral framework, binding the coral branches together with their thin growths. Innumerable fishes and invertebrates also hide in the nooks and crannies of the reef, some of them emerging only at night. In addition sessile organisms cover virtually all the available space on the underside of coral plates and on dead coral skeletons.

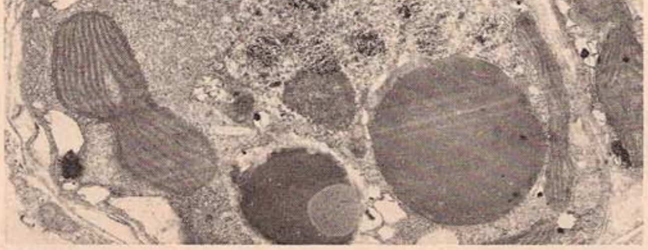
The crest of the reef runs parallel to the coast, in some places touching the shore and in others enclosing a sandy lagoon about five meters deep and up to a few hundred meters wide. This area is protected from the surf and is dotted with isolated coral heads. The lagoon is dominated by patches of calcareous algae and a community of bottom-living animals, notably sea urchins and sea cucumbers, which earn their keep by filtering organic matter out of the sediments or the overlying water. Many of these organisms graze on filamentous algae; if the grazers are removed from an area of the lagoon, a dense mat of algae forms after only a few days. The burrowing and churning activities of the grazers are important because they release nutrients created by the bacterial decomposition of organic matter buried in the sediments. Dense "lawns" of the sea grass *Thalassia* form special habitats harboring their own community of sea urchins, conchs and many other species.

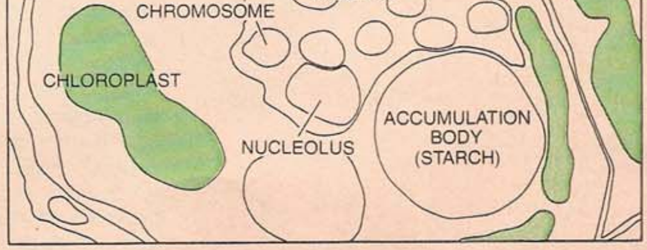
Seaward of the reef crest is the fore reef, where corals blanket nearly the entire sea floor. The corals form massive buttresses separated by narrow sandy channels, down which passes a steady flow of fine sediment originating with the disintegration of dead corals, calcareous algae and other organisms. The channels resemble narrow winding canyons with vertical walls of solid coral growth. They may be as much as 10 meters deep, and some are completely roofed over with coral. This dramatic interdigitation of buttresses and channels dissipates wave energy and at the same time allows the free flow of sediments that would otherwise choke the growth of the coral.

Down from the buttress zone is a coral terrace, a slope of sand with isolated coral pinnacles, then another terrace and finally an almost vertical wall dropping into the darkness of the greater depths. The distribution of coral species and other animal communities in the reef is zoned by depth, a feature that enables paleontologists studying a section of an ancient reef now on dry land to accurately estimate the original depth of that section from the fossil animals associated with it. In water deeper than 100 meters few algae or symbiotic corals grow well because of the low light levels, and the fauna is dominated by animals that catch or filter the organic detritus sifting down from the reef above. The detritus feeders include the true sponges, the antipatharians ("precious corals") and the gorgonians (sea



ANATOMY OF THE CORAL POLYP is simple: the animal is basically a contractile sac made up of three tissue layers. The cylindrical body is topped by a central mouth surrounded by tentacles. From the mouth a muscular gullet descends into the central digestive cavity, which is connected to the body by a series of vertical partitions. The free edges of the partitions extend into mesenterial filaments. Cells in the lining of the digestive cavity harbor the symbiotic algae, which live, photosynthesize and divide within the host cells. The polyps sit in protective limestone cups consisting of a radial array of vertical plates, which interdigitate with the partitions of the polyp. Each polyp deposits new floors under itself as it grows upward. In the Tropics corals grow from one to 10 centimeters a year, depending on species.





DIVIDING ALGAL CELL, or zooxanthella, is enlarged 13,250 diameters in the electron micrograph at the left. The striated sacs within the cells are sections through a single large chloroplast, where photosynthesis takes place; the other cell organelles are indicated on the map at the right. The zooxanthellae greatly increase the metabolic efficiency of the coral host by absorbing the waste products of coral respiration and recycling some of them into new organic matter. They also "leak" essential nutrients to the coral polyps and enhance the rate of calcification. The electron micrograph was provided by Robert K. Trench of the University of California at Santa Barbara.

fans). Also common here are the sclerosponges, an ancient group that were major reef builders in the geological past but were long thought to have become extinct hundreds of millions of years ago. Our diving studies of the deep reefs of Jamaica showed them to be alive and well but displaced to deeper habitats by the faster-growing corals, which evolved later.

Reef Growth

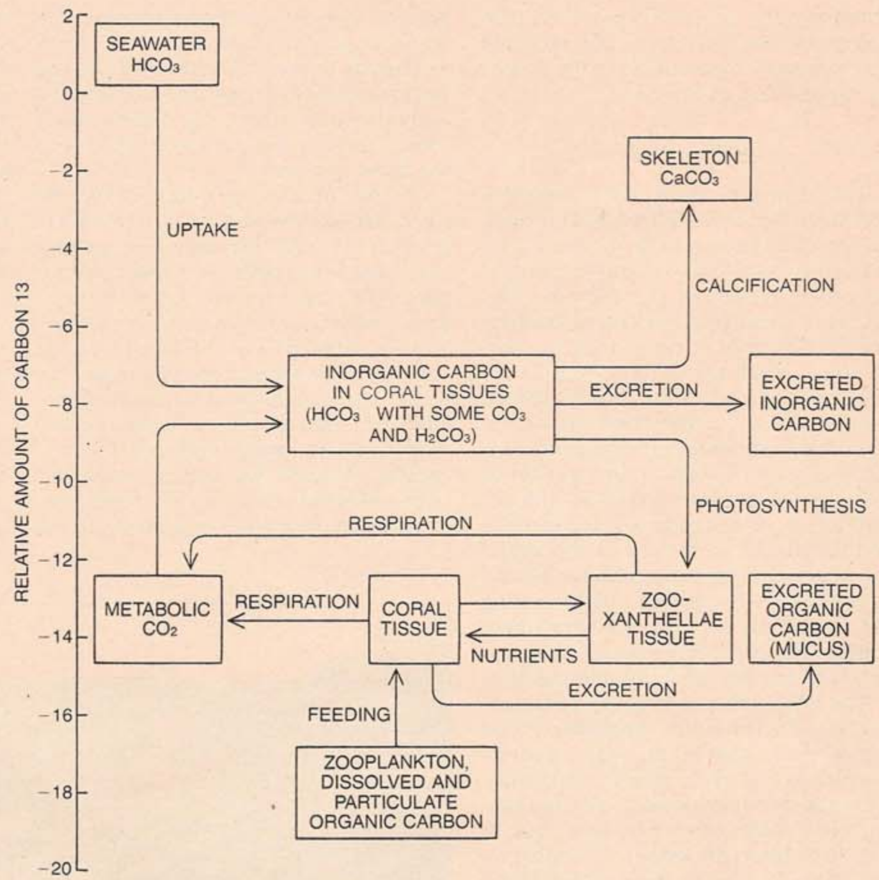
The growth of the reef is the result of a dynamic relation between the upward extension of the coral framework and the flushing away of a much larger volume of fine-grained detritus. The export of sediment from the reef is largely accomplished by gravitational flow and creep, either into the lagoon or down the channels of the buttress zone into deep water. Unstable piles of coral may also grow until they topple under their own weight and slide away. When the lower Jamaican reef was explored in the research submarine *Nekton Gamma II* at depths of more than 200 meters, enormous piles of sediment and huge blocks of solid reef were observed at the base of the drop-off; they may have been dislodged by earthquakes. Such dislocations create fresh substrates for encrusting organisms and help to establish coral communities on the steep lower slopes, particularly the platelike whorled colonies of *Agaricia*.

Two other major processes influence the growth of the reef: biological erosion and submarine lithification. Many species of filamentous algae, fungi, sponges, sea worms, crustaceans and mollusks bore into coral skeletons, excavating holes by mechanical rasping or chemical dissolution. The commonest is the boring sponge *Cliona*, which saws out tiny chips of calcium carbonate; the chips are a major component of the fine sediments. *Cliona* can riddle a coral skeleton with holes without damaging the living coral polyps. In the deeper waters many corals grow in flat, thin sheets to maximize their light-gathering area and hence are quite susceptible to erosion by borers, which can cause the corals to break off and fall downslope. In some places, however, the coral is so overgrown with encrusting organisms that it remains in place even though it is no longer directly attached to the reef.

Counteracting the effects of biological erosion is submarine lithification: the deposition of a fine-grained carbonate cement in the pores and cavities of the coral skeleton. Sediments trapped in the reef framework are rapidly bound together by encrusting organisms and the calcareous cement. The origin of the cement is not yet clear; it may be an inorganic precipitate manufactured by bacteria that live in the crevices of the reef. Studies at the Discovery Bay Marine Laboratory in Jamaica done in conjunction with Lynton S. Land of the University of Texas at Austin showed that once the cement has hardened it is in turn bored and refilled; the filled holes are apparent when thin sections of the aggregate are examined under the microscope. Submarine lithification results in the outward accretion of the fore reef and stabilizes the steep profile of the drop-off wall. The growth of reefs is therefore the product of a dynamic balance among framework growth, sediment transport, bioerosion by borers, mechanical destruction and submarine lithification, with the relative importance of these factors varying from reef to reef.

The living reef is basically a veneer growing a few millimeters a year on top of a complex topography of superposed ancestral reefs. In Jamaica as much as nine meters of reef has built up since the present sea level stabilized some 5,000 years ago. The ancient reefs remain, providing a record of changes in sea level and of the uplift of land by the movements of tectonic plates.

The rise and fall of the sea level over the past few million years has been caused by changes in the volume of water tied up in land glaciers and ice sheets during the Pleistocene ice ages. When ice sheets grew in the Northern Hemisphere, the sea level dropped and coral reefs were stranded above the waterline. Today fossil ridges and wave-cut notches mark the ancient sea level. A succession of stranded reefs are found in Jamaica, Barbados, New Guinea and on other coral coasts; these reefs were formed 80,000, 105,000, 125,000 and 200,000 years ago, when the climate was warmer and the sea level higher than it is today. Conversely, in Jamaica a series of drowned and overgrown ridges can be seen at 25, 40 and 60 meters below the present sea level. These drowned reefs were formed during periods of intensive glaciation 8,000, 11,000 and 14,000 years ago, when the sea level was considerably lower than it is today. The ancient reef is therefore a dimly visible palimpsest under the living reef, like a medieval manuscript that has been repeatedly erased and written over but shows faint traces of its history. Such



CYCLING OF CARBON among the zooxanthellae, the coral host and the environment is outlined. The various carbon pools are plotted on a vertical axis according to the ratio of the two stable isotopes of carbon: carbon 12 and carbon 13. The position of each pool is therefore an indication of the relative importance of the processes by which each pool gains and loses carbon and the extent to which these processes utilize one of the two isotopes preferentially. For example, because photosynthesis takes up carbon 12 faster than carbon 13 it leaves behind a pool enriched in carbon 13, from which the calcium carbonate of the coral skeleton is formed. About two-thirds of the carbon utilized in photosynthesis and calcification is recycled from respiratory carbon dioxide. Level of carbon 13 in coral tissue reflects the composition of its food sources.

features help in establishing the chronology of the Pleistocene ice ages and the volume of water added to the oceans by the melting of the ice.

Reef Ecology

The history of the modern Jamaican reef since the sea stabilized at its present level 5,000 years ago has not been long enough to establish a climax community: an ecosystem in equilibrium. This fact is evident from the almost haphazard development of reefs along any coral coast: some areas have well-developed reefs and others have only isolated patches of coral. Often there are no obvious environmental influences or catastrophic factors (such as earthquakes or tidal waves) that would explain such differences in development. It seems rather that chance variations in the settlement of free-swimming coral larvae and growth play a major role in determining the formation of reefs, and that there simply has not been enough time for corals to occupy all favorable habitats.

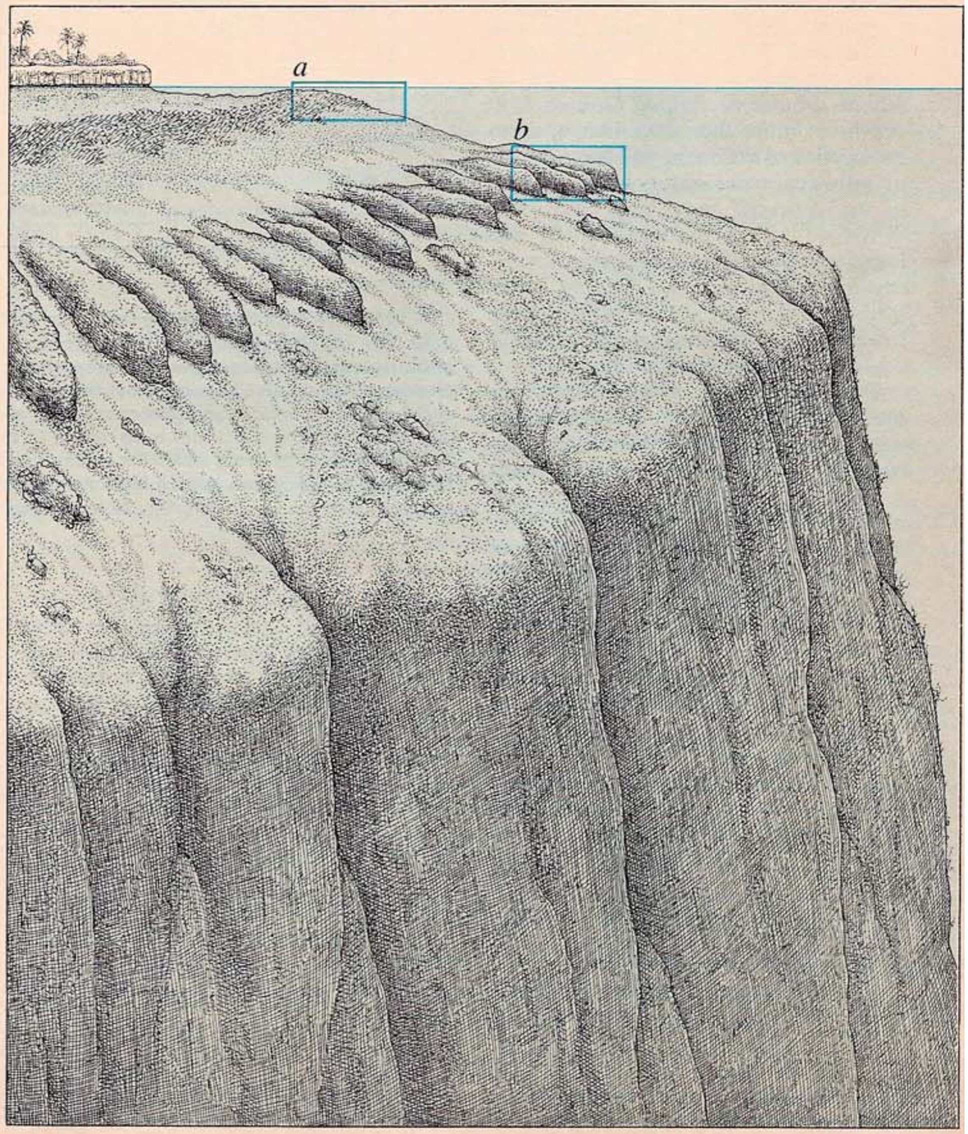
The role of chance in coral settlement is also reflected in the variability of the major species that fill the same structural roles in any reef. In some Jamaican reefs the dominant coral is the branching coral *Montastrea annularis,* but in similar habitats the same role is filled by the different species *Agaricia tenuifolia,* which forms colonies of identical shape, size and orientation. Hence in the creation of diversity in a coral reef historical variation is in many reefs just as significant as the approach to an ecological equilibrium where many specialized organisms coexist.

The many localized habitats and species in the reef give the reef community a wealth of interactions within and among species whose complexity can only be dimly grasped. An intuitive understanding of the major interactions can be gained only after years of field experience. Even then one may focus on so few components of the community that it is easy to miss the significant roles played by many obscure, unexamined or unknown organisms.

The intense competition for food and space in the reef habitat has given rise to a wide variety of survival strategies. For example, Jeremy Jackson and his students at Johns Hopkins University have shown that many encrusting organisms possess specific toxins for defensive or offensive purposes. Corals growing close together compete for space, and some species are able to extrude mesenterial filaments from the gut to kill the polyps of adjacent colonies. Judith Lang, working at Discovery Bay, has shown that among coral species there is a hierarchy of aggression such that slow-growing but aggressive corals can avoid being overgrown by faster-growing but less aggressive ones. This process may lead to an increased diversity of species. In some instances, however, the result is precisely the opposite: James Porter has found that in the reefs on the Pacific coast of Panama the overwhelmingly dominant coral, *Pocillopora damicornis,* is both the fastest-growing and the most aggressive.

Grazing on algal and coral tissues by fishes, sea urchins and other animals has two important effects. Selective grazing may keep a few dominant species of algae from crowding out the more marginal species, so that a diversity of species are able to exist. Experiments in which grazers are excluded from an area of the reef usually result in choking densities of a few dominant algal species, which is rare under ordinary circumstances. Grazers that scrape tissues off hard substrates also create fresh surfaces where new algae can grow and the larvae of sessile organisms can settle. Leslie S. Kaufman of Johns Hopkins has found that some fish species systematically kill patches of coral tissue so that "farms" of algae can grow on the bare coral skeleton. The fishes, which graze on the algae, chase any intruders on their territory, including much larger fishes and even human divers. How much damage to the reef is done by such biological space clearing compared with that done by slumping and storms is not known.

Much also remains to be learned about the nutrient and energy cycles of reefs. The richness of reef biological processes in the face of the poverty of dissolved nutrients in tropical surface waters is evidence that there is an efficient internal cycling of nutrients within the reef ecosystem, but the matter



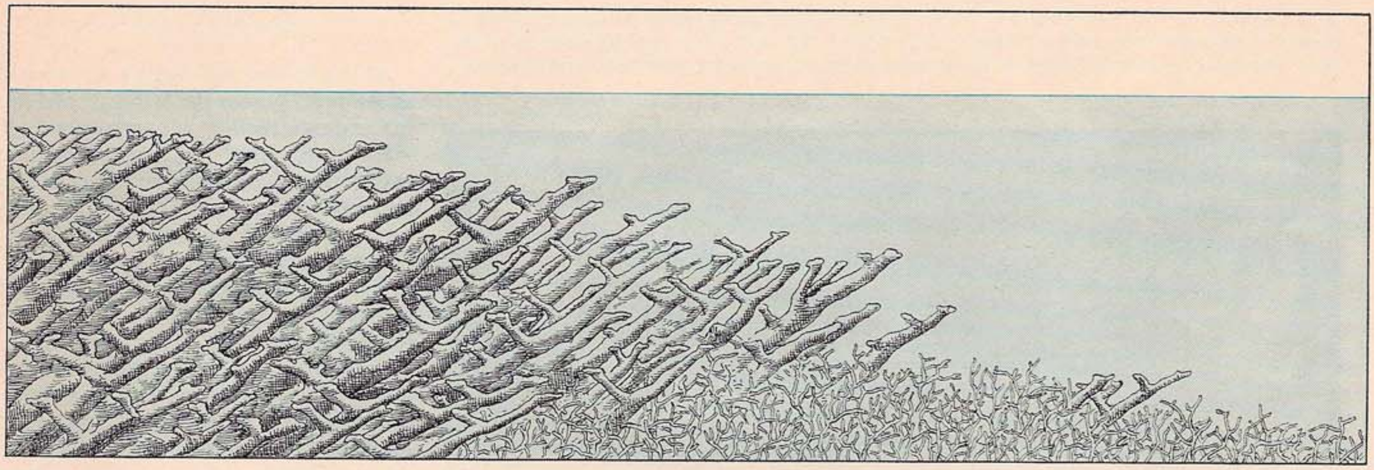
ARCHITECTURE OF THE FRINGING REEF along the northern coast of Jamaica is depicted in these three-dimensional views. Several zones can be distinguished on the basis of reef structure, depth and the associated animal and plant communities. The reef crest extends to a depth of about 15 meters and comprises the shallow coral rampart and the surf zone (*a*). The fore reef extends from 15 meters to 30. This region is a medium-energy environment, with an ambient-light intensity about 25 percent that at the surface. The buttress zone (*b*), where coral

has yet to be investigated in enough detail. The major limiting nutrient in the oceans is generally thought to be nitrogen, and in coral reefs large amounts of the atmospheric nitrogen dissolved in the seawater are fixed in utilizable forms by filamentous blue-green algae. Another source of nitrates is the oxidation of ammonia by bacteria in the course of the decomposition of organic matter in the sediments of the reef lagoon. Recent work indicates that the oxidation of ammonia to nitrate is particularly intense in the fine-grained organic sediments trapped by the roots of sea-grass beds.

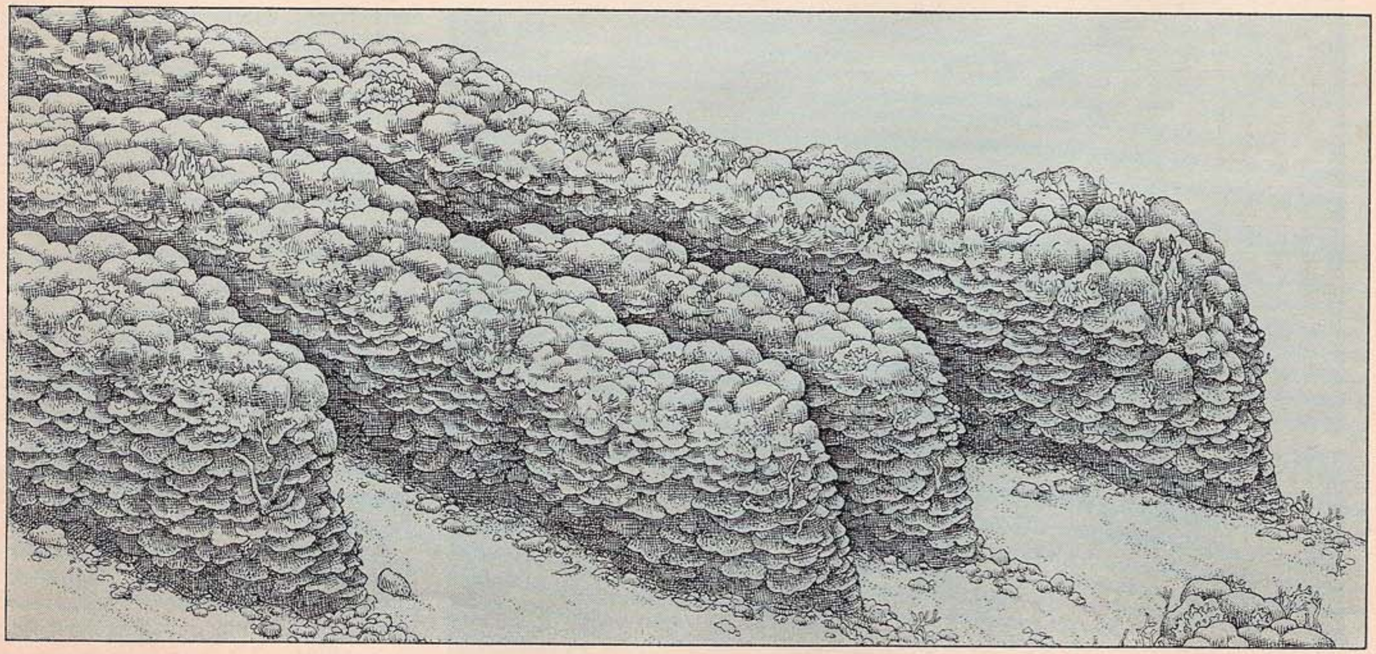
The coral reefs of the Atlantic, the Caribbean and the Indo-Pacific do not differ fundamentally in their structural forms, their habitats and the interactions of their species, even though the organisms occupying specific ecological roles vary greatly between oceans and even between individual reefs. Between the Pacific and the Caribbean, however, there is one significant difference: in the Pacific the active growth of coral goes down only to 60 meters, and in the Caribbean it goes down to 100 meters. The reduced range in depth of the Pacific corals may be due in part to periodic infestations by the crown-of-thorns starfish (*Acanthaster planci*), which feeds on coral by turning its stomach inside out, spreading it over the coral and digesting the coral tissues. Before the recent well-publicized outbreak of *Acanthaster* the organism was limited to deeper water and was rarely seen. Then an unexplained population explosion gave rise to a food shortage that forced the starfishes to move up to shallower water, where their destructive effects were readily apparent. The lower limit of reef growth in the Pacific may therefore be affected by periodic starfish grazing. Much remains to be done to prove the hypothesis, however, not least because many Pacific reefs also show signs of being more intensively eroded mechanically than Caribbean reefs.

These points illustrate some of the handicaps ecologists face in attempting to predict the stability of reef populations in response to environmental changes or the sensitivity of reef food networks to alterations in the abundance of particular species. Since coral reefs are localized centers of high biological productivity and their colorful fishes are a major source of food in tropical areas, many marine biologists view with alarm the spread of tourist resorts along coral coasts in many parts

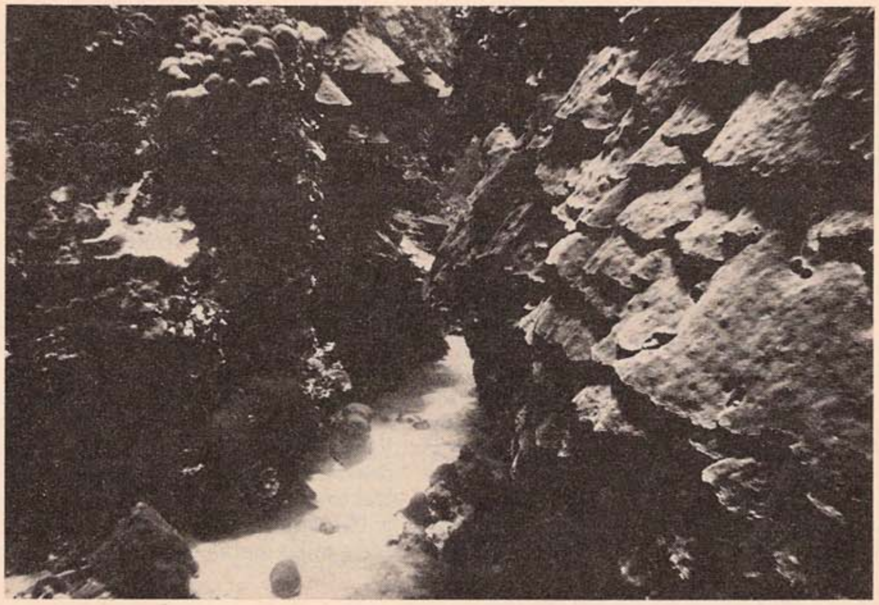
a



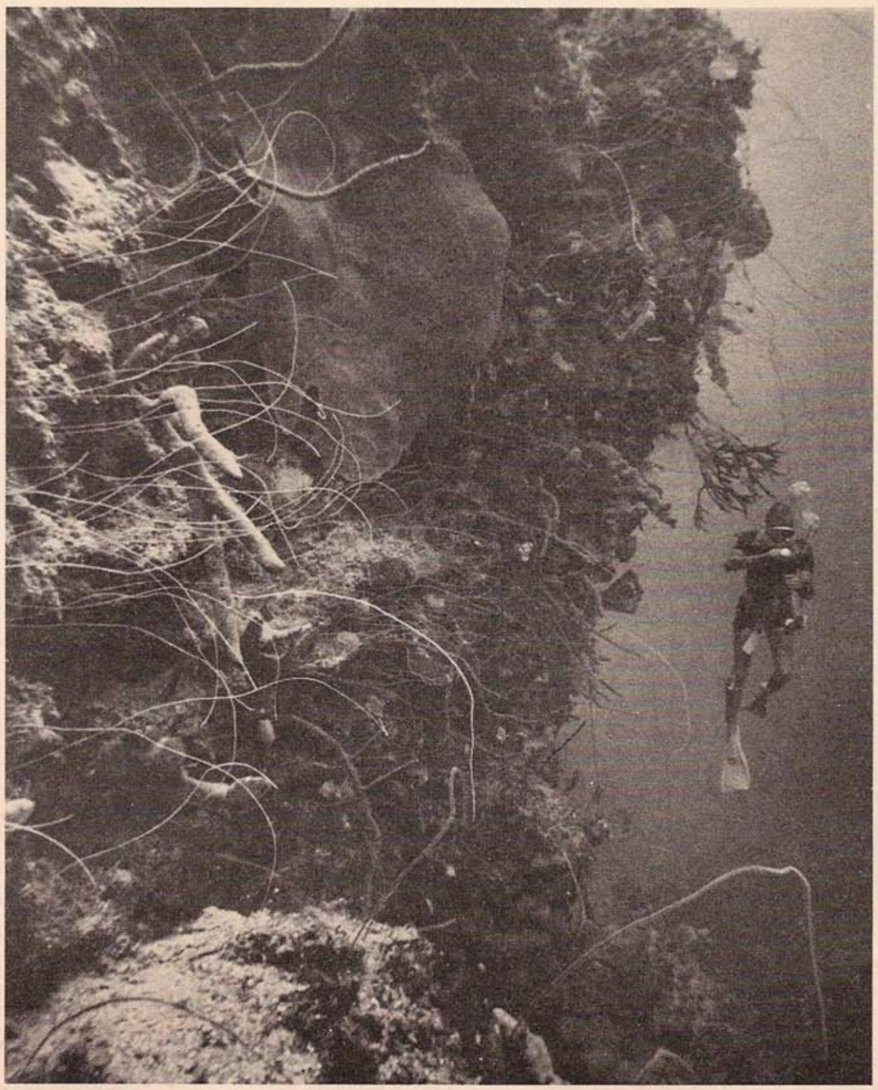
b



buttresses alternate with sandy canyons, serves to dissipate the mechanical energy of the waves and allows the flow down the reef of fine sediments, which would otherwise choke coral growth. The coral colonies are still varied but smaller in size, and much of the available space is occupied by sand-producing calcareous algae, sponges and large gorgonians (sea fans). The deep fore reef extends from 30 meters to 70. This zone has a steep topography and is poorly illuminated, with a light flux about 5 percent that at the surface. At depths below 30 meters coral growth becomes patchy, with a progressive reduction in number of species and size and density of colonies. There is also extensive transport of sediment from the shallow zones above. Beyond the deep fore reef the vertical wall drops off into darkness.



BUTTRESS CANYON between two walls of coral was photographed at a depth of about 12 meters off the northern coast of Jamaica. The wall at the right is covered by colonies of the coral *Monastrea annularia*. Shape of the colonies serves to maximize their light-gathering area.



DROP-OFF WALL of the Jamaican fringing reef is shown at a depth of about 40 meters. The steep fore-reef slope is covered by a dense growth of sponges, gorgonians and whip corals.

of the world. Such developments are almost always accompanied by increased dumping of sewage, by overfishing, by physical damage to the reef resulting from construction, dredging, dumping and landfills, and by destruction of the reef on a large scale to provide tourists with souvenirs and coffee-table curios. In many areas (such as Bermuda, the U.S. Virgin Islands and Hawaii) development and sewage outfalls have led to extensive eutrophication: the overgrowth and killing of the reef by thick mats of filamentous algae, which in turn support the growth of oxygen-consuming bacteria. The results, which are being intensively studied by Stephen V. Smith and his colleagues at the University of Hawaii, include an increased sensitivity of corals to bacterial diseases, the death of living coral and the resulting erosion of the reef, and the generation of foul-smelling hydrogen sulfide.

Breaching a Barrier

The proposal for digging a new canal at sea level across the Isthmus of Panama arouses further concerns about the viability of coral reefs and their intricately interwoven physical and biological resources. The large range of the tides on the Pacific side of the isthmus and the smaller range of the tides on the Caribbean side, together with the higher mean sea level on the Pacific side, would result in the effective movement through the canal of Pacific marine species into the Caribbean and the Atlantic. Since the reefs of the Caribbean and the Pacific have been evolutionarily isolated for millions of years, such a large-scale incursion of species into new habitats could enable certain species to multiply and spread unchecked, with ecological consequences similar to the explosive multiplication of the English rabbits introduced into Australia. For example, the crown-of-thorns starfish is common on the Pacific side of the isthmus but is not present on the Caribbean side, and its spread through the sea-level canal could decimate the corals of the Caribbean and the Atlantic. In addition, poisonous sea snakes, unknown in the Atlantic, are common on the Pacific side of the isthmus. Peter Glynn and Ira Rubinoff of the Smithsonian Tropical Research Institute in Panama have warned that the sea-level canal could cause a greater perturbation in the natural environment than any previous engineering work.

The proposed sea-level canal illustrates not only the concerns of coral-reef biologists but also their ignorance, since it remains difficult to predict the deleterious effects of human activities in an environment as complex as the reef ecosystem. All the same it does not seem unduly alarmist to caution against taking the stability and productivity of the reef community for granted.