

Coral Bleaching

Environmental stresses can cause irreparable harm to coral reefs. Unusually high seawater temperatures may be a principal culprit

by Barbara E. Brown and John C. Ogden

Late summer of 1987 seemed typical for that time of year in the Virgin Islands. Huge, flat-bottomed cumulus clouds moved westward on light trade winds. Calm seas were rarely disturbed by squalls sweeping into the northeastern Caribbean Sea from the Atlantic Ocean. The only suggestion that something might be amiss was the water, which, though not systematically measured, seemed unusually warm to people swimming near the shallow coral reefs.

Something atypical had indeed occurred. The normally golden-brown, green, pink and gray corals, sea whips and sponges had become pure white. In some cases, entire reefs were so dazzlingly white that they could be seen from a considerable distance. In other areas, pale corals punctuated the reef surface while unbleached corals of the same species grew as neighbors.

The phenomenon, which can be lethal to coral, was not confined to the Virgin Islands. Observers at numerous marine laboratories in the Caribbean

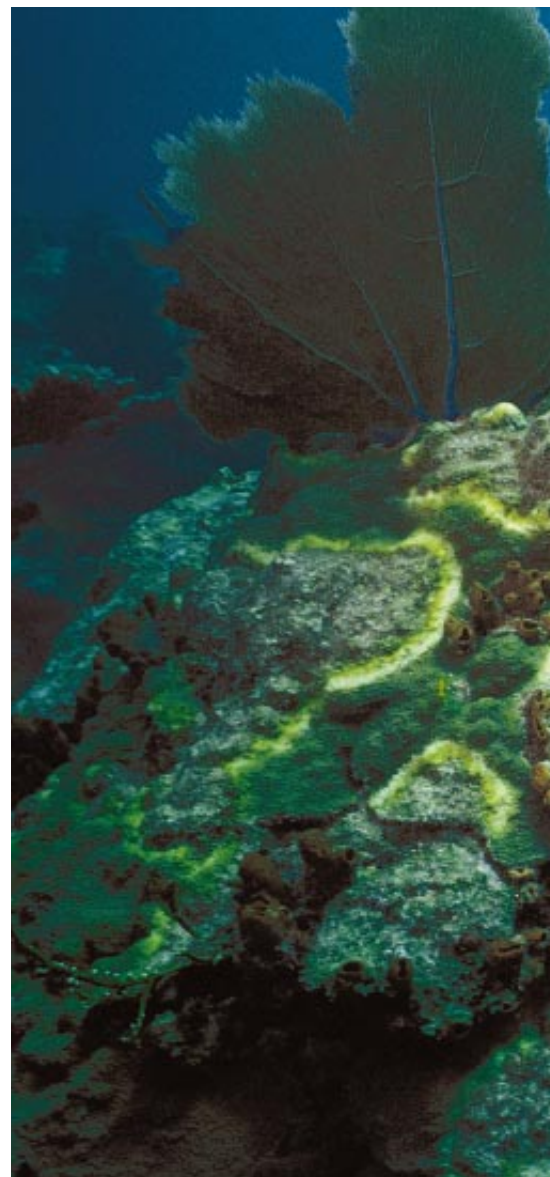
noted the same whitening. Nor was it the first occurrence of such bleaching. In 1982 and 1983, after the atmospheric and oceanographic disturbance called El Niño/Southern Oscillation (ENSO), corals in certain areas of the Florida Keys whitened and died, and off the coast of Panama mortality reached 50 percent. But it was only between 1987 and 1988, also an ENSO year, that reports of extensive bleaching became widespread. They have increased in frequency ever since.

The association of coral bleaching with ENSO, which ushers in warm water, and with water temperatures two to three degrees Celsius above normal has led some scientists to suggest that the bleaching is a manifestation of global warming. Others point out that coral reefs have been studied only for a few decades—too short a time to permit generalized conclusions about a poorly understood event.

Nevertheless, coral reefs around the world are suffering bouts of bleaching from which many do not recover. Although several factors can cause the process—including disease, excess shade, increased ultraviolet radiation, sedimentation, pollution and changes in salinity—the episodes of the past decade have consistently been correlated with abnormally high seawater temperatures. Understanding the complex pro-

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BOULDER CORAL has bleached only in parts—the rest remains healthy for now. Although several factors cause potentially lethal whitening, recent bouts have been consistently correlated with higher than average seawater temperatures.



cess of bleaching can help pinpoint, and perhaps eventually deter, this threat to the ecology of the reefs.

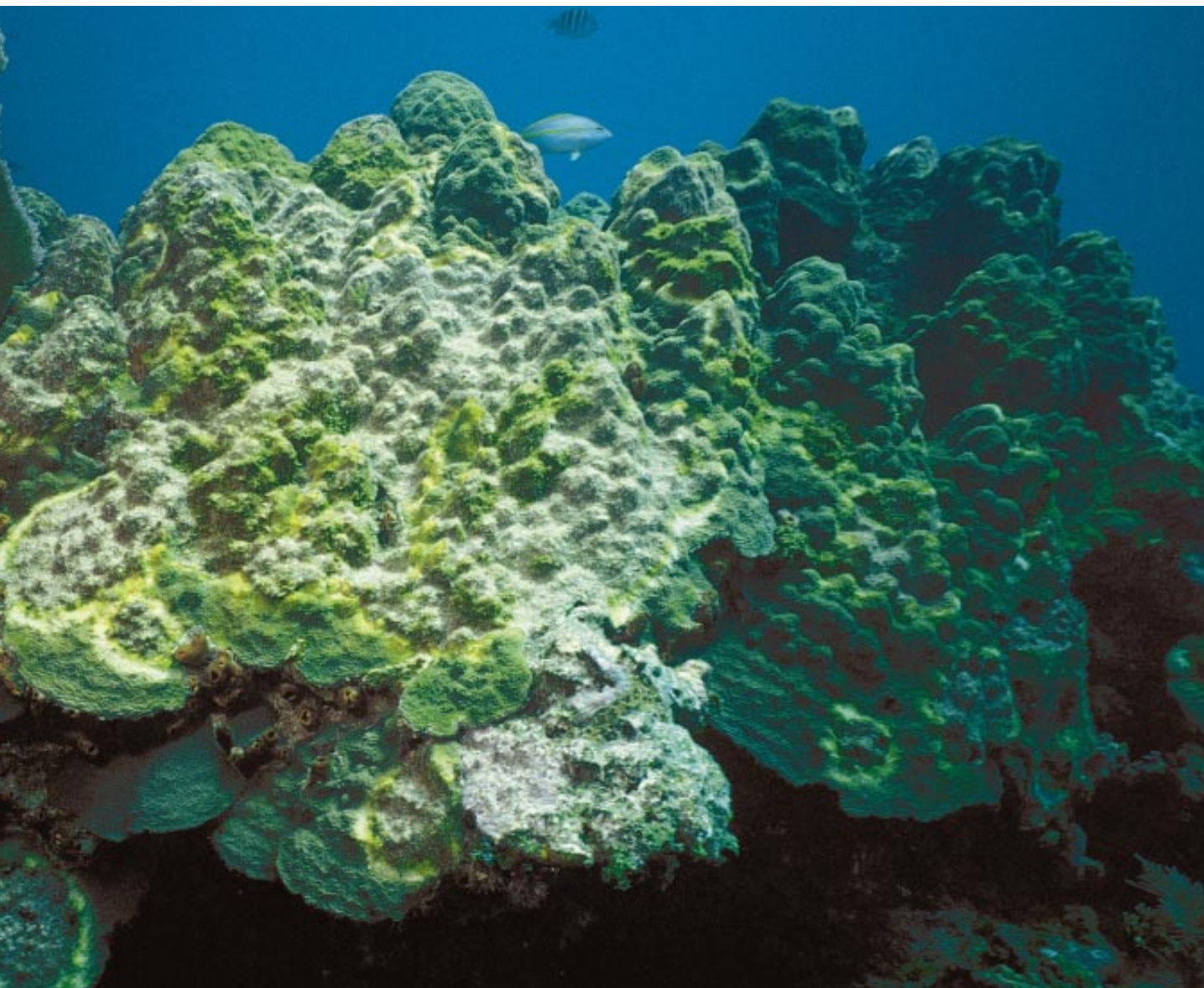
Tropical, shallow-water ecosystems, coral reefs are found around the world in the latitudes that generally fall between the southern tip of Florida and mid-Australia. They rank among the most biologically productive of all marine ecosystems. Because they harbor a vast array of animals and plants, coral reefs are often compared to tropical rain forests. Reefs also support life on land in several ways. They form and maintain the physical foundation for thousands of islands. By building a wall along the coast, they serve as a barrier against oceanic waves. And they sustain the fisheries and tourist diving industries that help to maintain the economies of many countries in the Caribbean and Pacific.

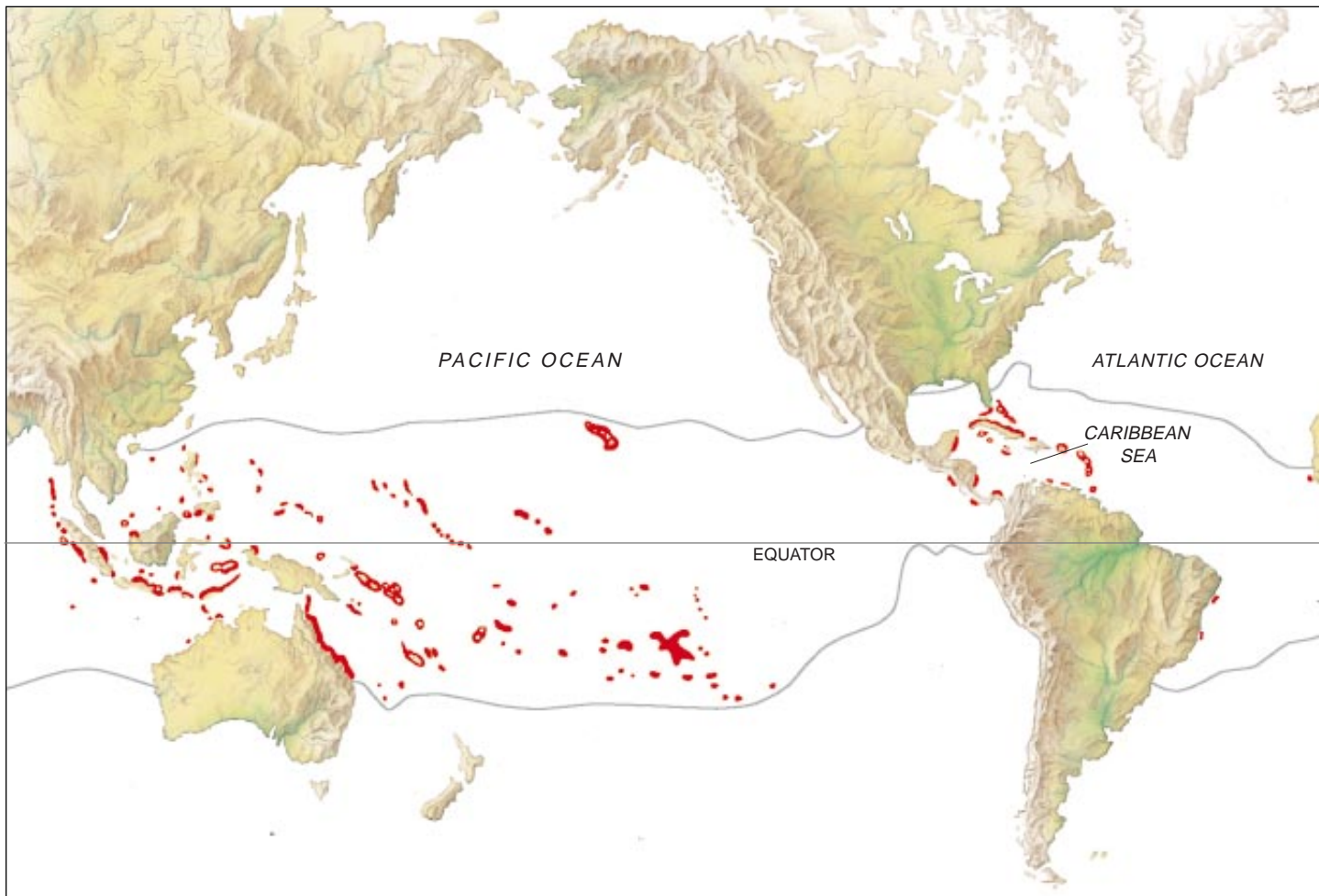
Although corals seem almost architectural in structure—some weigh many tons and stand between five and 10 meters high—they are composed of animals. Thousands of tiny creatures form enormous colonies: indeed, nearly 60 percent of the 220 living genera of corals do so. Each colony is made up of many individual coral animals, called polyps. Each polyp is essentially a hollow cylinder, closed at the base and interconnected to its neighbors by the gut cavity. The polyps have one or more rings of tentacles surrounding a central mouth. In this way, corals resemble sea anemones with skeletons. The soft external tissues of the polyps overlie a hard structure of calcium carbonate.

Many of the splendid colors of corals come from their symbionts, creatures that live in a mutually dependent relation with the coral. Symbiotic algae

called zooxanthellae reside in the often transparent cells of the polyps. There are between one and two million algae cells per square centimeter of coral tissue. Through photosynthesis the algae produce carbon compounds, which help to nourish the coral—some species receive 60 percent of their food from their algae. Algal photosynthesis also accelerates the growth of the coral skeleton by causing more calcium carbonate to be produced. The corals provide algae with nutrients, such as nitrogen and phosphorus, essential for growth, as well as with housing. The association enables algae to obtain compounds that are scarce in the nutrient-poor waters of the tropics (where warm surface waters overlie and lock in cold, nutrient-rich waters—except in restricted areas of upwelling).

When corals bleach, the delicate balance among symbionts is destroyed.





CORAL REEFS (red) thrive around the world in tropical, shallow waters—those areas falling between the lines. They are the most biologically productive of all marine ecosystems. Coral reefs also support life on land by providing a barrier

The corals lose algae, leaving their tissues so colorless that only the white, calcium carbonate skeleton is apparent. Other organisms such as anemones, sea whips and sponges—all of which harbor algae in their tissue—can also whiten in this fashion. Some of this loss is routine. A healthy coral or anemone continuously releases algae, but in very low numbers. Under natural conditions, less than 0.1 percent of the algae in a coral is lost during processes of regulation and replacement. When subject to adverse

changes, such as temperature increases, however, the corals release increased numbers of algae. For example, transferring coral from a reef to a laboratory can cause a fivefold elevation in the numbers of algae expelled.

The mechanism of algal release is not fully understood. Even defining bleaching remains tricky. The current definition has its basis in laboratory measurements of the loss of algae and the reduction in algal pigments. The laboratory approach, however, is rarely, if

ever, applied in the field. There judgment must rely on the naked eye's ability to detect loss of coloration. Although such methods may be reliable for instances of severe bleaching, a determination that pale colonies are bleached can be extremely arbitrary, given the natural variability of pigmentation.

In some cases, normal coral undergoing an adaptive behavioral response can look bleached. In 1989, while working at the Phuket Marine Biological Center in Thailand, one of us (Brown) observed that some intertidal coral species—those that thrive in shallow water and are exposed to the air at low tide—

Some of the Species That Thrive on Coral Reefs



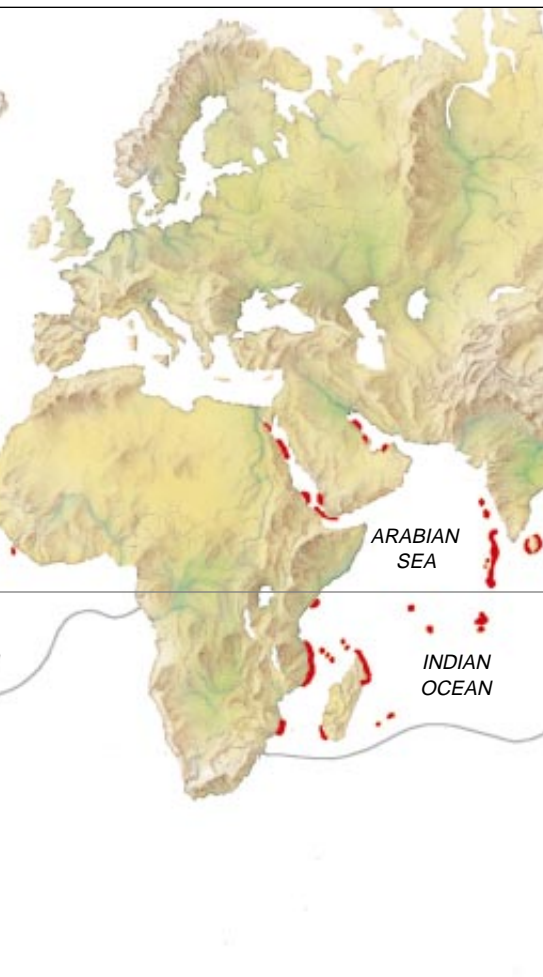
SPINY LOBSTER

QUEEN CONCH

LOGGERHEAD SPONGE

SEA ANEMONE

BUTTERFLY FISH



against oceanic waves and by forming the foundation for thousands of islands.

appear completely white during low spring tides. It became clear that these corals are able to pull back their external tissues, leaving their skeletons exposed; they do not lose their algae. This behavior should perhaps be more accurately described as blanching, a response that may reduce desiccation during exposure to air.

Despite the absence of an unassailable definition of the bleaching process, several mechanisms have been proposed that may be at work. In 1928 Sir Maurice Yonge and A. G. Nicholls, who participated in an expedition to the Great Barrier Reef, were among the first

to describe coral bleaching. They suggested that algae migrated through coral tissue in response to environmental stress, before being released into the gut and ultimately expelled through the mouth. The precise trigger for the release and the stimulus causing the algae to be so conveyed were unknown then and remain largely unknown today.

One of the several theories proposed by Leonard Muscatine of the University of California at Los Angeles is that stressed coral polyps provide fewer nutrients to the algae. According to this theory, the algae would not necessarily be directly affected by, say, high temperature, but the metabolism of the coral would be lowered. Supplies of carbon dioxide, nitrogen and phosphorus would become insufficient, and this rationing would in turn cause the algae to abandon their residence.

In addition, Muscatine, R. Grant Steen and Ove Hoegh-Guldberg, also at U.C.L.A., studied the response of anemones and corals to changes in temperature, light and salinity. They described the release of algae from the tissues into the gut cavity and hypothesized that the coral was actually losing animal tissue along with the algal cells. Work by Suharsono at the University of Newcastle upon Tyne supported this idea. He showed that anemones exposed to warmer temperatures in the laboratory lose their own cells and algal cells during bleaching. Thus, host tissue thinned significantly, perhaps reducing the space available for the algae.

The direct release of algae into the gut, however, may be a mechanism of algal loss that results only from the extreme shocks invoked in a laboratory. It is not yet clear that algae behave the same way in corals in situ. Under natural conditions, it is quite likely that algae are released by a variety of mechanisms. All experimental work carried out on bleaching has involved exposure to extreme temperature changes—that is, increases of six degrees C or more over a period of 16 to 72 hours. In nature the temperature increases that induce bleaching are much smaller, about two degrees C, and may occur over several months.

Another hypothesis suggests that algae emit poisonous substances when they experience adverse conditions and

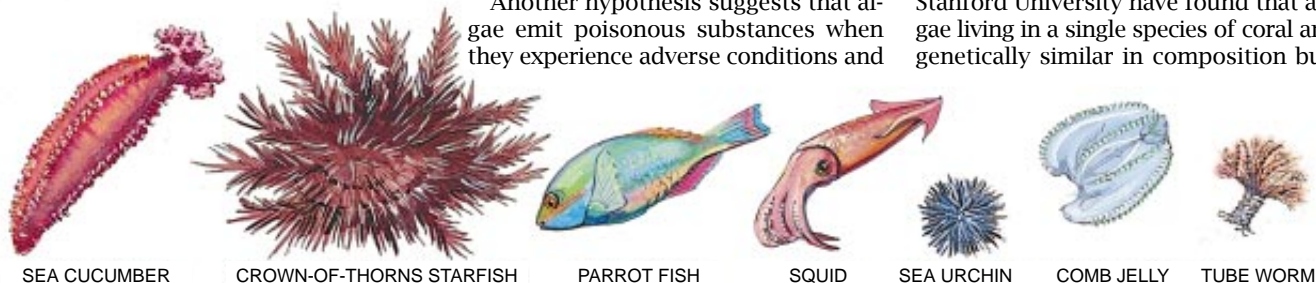
that these toxins may deleteriously affect the host. Algae produce oxygen compounds, called superoxide radicals, in concentrations that can damage the coral. (Molecular oxygen is relatively unreactive, but it can be chemically altered to form the superoxide radical.) An enzyme, superoxide dismutase, in the coral detoxifies the radicals.

But Michael P. Lesser and his colleagues at the University of Maine noted that in certain cases oxygen toxicity could lead to bleaching. Although Lesser and his team were unable to measure the oxygen radicals directly, they followed the production of superoxide dismutase. They found that exposure to elevated temperatures and to increased ultraviolet radiation independently spurred enzymatic activity. The researchers concluded that oxygen toxicity could be responsible for bleaching because harmful oxygen radicals were exported from the damaged algae to the animal host.

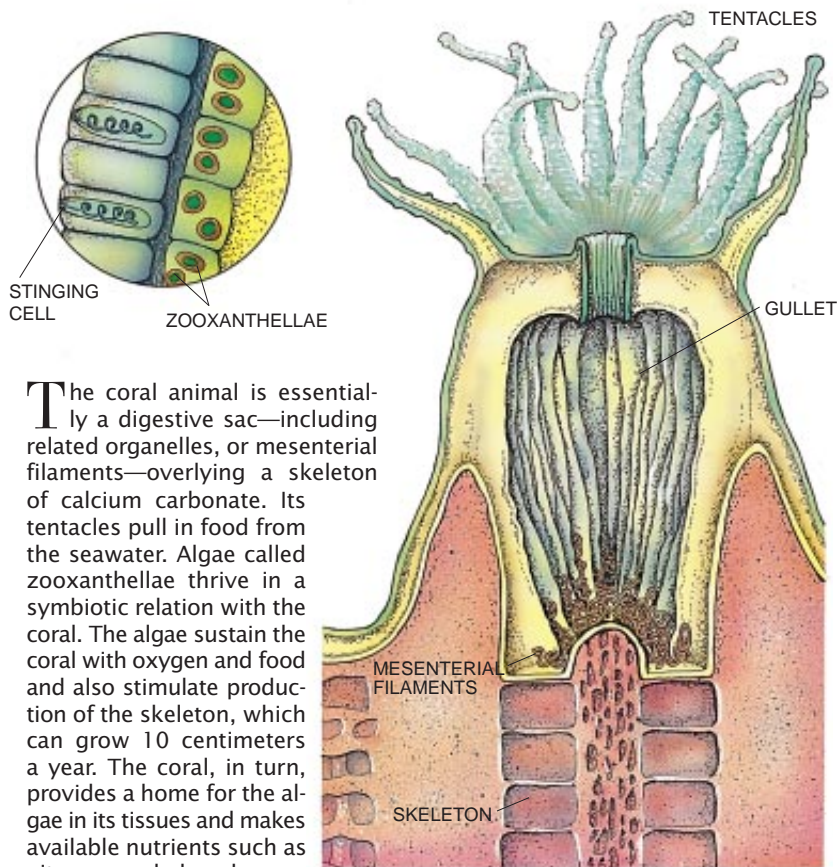
Other biochemical changes may take place as well. David Miller of the University of Leeds and students from Brown's laboratory suggest that alterations in gene expression occur as a response to deleterious environmental changes. These changes may involve the synthesis of heat-shock proteins—compounds found in all living systems subject to adversity that serve to protect cells temporarily from heat damage. Miller determined that these proteins are enhanced in anemones undergoing heat shock. Furthermore, in anemones that tolerate temperature increases, the presence of proteins appears to be correlated with reduced bleaching during heat shock.

Genetic variability also plays an important role in bleaching. Environmental factors may affect species of algae or coral in different ways. Of course, predicting the ability of corals and their algae to adapt to increases in seawater temperature or global climatic change may be possible by identifying the types of corals or algae at highest risk.

When working together at the University of California at Santa Barbara, Robert K. Trench and Rudolf J. Blank showed that different corals act as hosts to varied strains of algae. Subsequently, Rob Rowan and Dennis A. Powers of Stanford University have found that algae living in a single species of coral are genetically similar in composition but



Anatomy of a Coral Polyp



The coral animal is essentially a digestive sac—including digestive related organelles, or mesenterial filaments—overlying a skeleton of calcium carbonate. Its tentacles pull in food from the seawater. Algae called zooxanthellae thrive in a symbiotic relation with the coral. The algae sustain the coral with oxygen and food and also stimulate production of the skeleton, which can grow 10 centimeters a year. The coral, in turn, provides a home for the algae in its tissues and makes available nutrients such as nitrogen and phosphorus.

genetically different from algae in other coral species. Certain algae may prove to be particularly sensitive to temperature and may have varying temperature tolerances. If so, Rowan and Powers's findings would help explain why related, but not identical, corals exposed to warmer temperatures frequently show different susceptibilities to bleaching.

Alternatively, the variability may lie with the coral instead of the algae. Studies of several species of coral have indicated that genetically dissimilar strains exist within a species of coral. Such strains may have different environmental tolerances, which could account for the observation that one colony of a particular species appears to have been bleached while a nearby member of the same species has not been.

The reports of bleaching in the Caribbean in the 1980s seem to be related most consistently to elevated sea temperatures. Coral reefs normally thrive between 25 and 29 degrees C, depending on their location. When patterns depicting coral diversity are plotted on a globe, it is apparent that diversity declines as the reefs get farther away

from two centers—one in the Indo-Pacific and the other in the Caribbean. The outlines of a map marking plummeting diversity coincide with the contours of lower seawater temperatures.

The narrow temperature range for healthy coral is very close to its upper lethal temperature: an increase of one to two degrees above the usual summer maximum can be deadly. Paul Jokiel and Stephen Coles of the University of Hawaii have shown that bleaching and coral mortality are not induced by the shock of rapidly fluctuating temperatures but are a response to prevailing high temperatures and to significant deviations above or below the mean.

Many times during a 10-month period in 1982-1983, an unusually severe ENSO warmed the waters of the eastern Pacific three to four degrees C over the seasonal average. Peter W. Glynn and his colleagues at the University of Miami tracked the event and the subsequent developments in that region. As a result of elevated temperatures, coral reefs underwent bleaching. Between 70 and 90 percent

of the corals in Panama and Costa Rica perished several weeks later; more than 95 percent of the corals in the Galápagos were destroyed.

Glynn and Luis D'Croz of the University of Panama also linked coral mortality with high temperatures in a series of laboratory experiments that duplicated field conditions during ENSO. The major reef-building coral of the eastern Pacific, *Pocillopora damicornis*, took the same amount of time to die in the laboratory at 32 degrees C as it did in the field, indicating that the experiments had replicated the natural condition. Glynn and D'Croz also suggested that the temperature disproportionately affected types of coral that normally experienced seasonal upwelling of deep, cool water in the Gulf of Panama.

Evidence for the 1987 warming of the seawater in the Caribbean is not as definitive. Donald K. Atwood and his colleagues at the Atlantic Oceanographic and Meteorological Laboratory in Miami examined the National Oceanographic Data Center's sea-surface temperature records from 1932 to the present and found no discernible long-term increases in seawater temperature in the Caribbean. The monthly mean sea-surface temperature did not exceed 30.2 degrees C in any of the regions examined—in other words, the water remained well below the 32 degrees C required to induce bleaching in Glynn's laboratory experiments.

Atwood also examined the maps from the National Climate Data Center of the National Oceanic and Atmospheric Administration (NOAA). These records provide average monthly sea-surface temperature and track anomalies derived from satellite data that are validated by measurements taken from ships. The maps indicate that in 1987 the surface of the Caribbean was generally less than 30 degrees C. Other groups examined similar temperature records and concluded that the temperatures of some sectors of the Caribbean reached 31 degrees C or more during 1990, another year of bleaching.

The records, of course, are subject to interpretation based on the geographic scale of the satellite measurements and the integration of these data with in situ measurements. Unfortunately, there are no long-term temperature records taken at the small geographic scale needed to clarify the cause of damage to corals.

The 1987 reports of coral bleaching coincided with escalating concern about global warming. It was not surprising, therefore, that some scientists and other observers reached the conclusion that coral reefs served as the canary in the coal mine—the first indication of an increase in global ocean tempera-

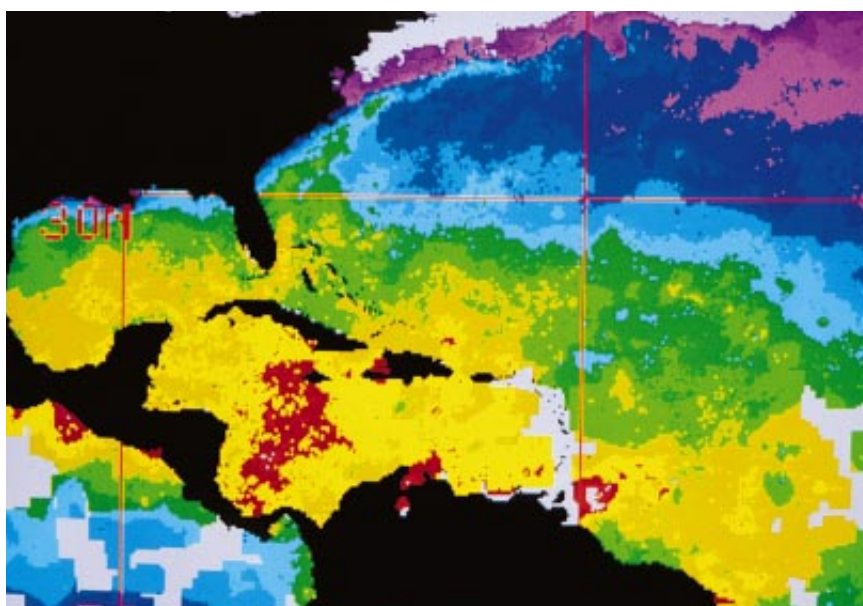
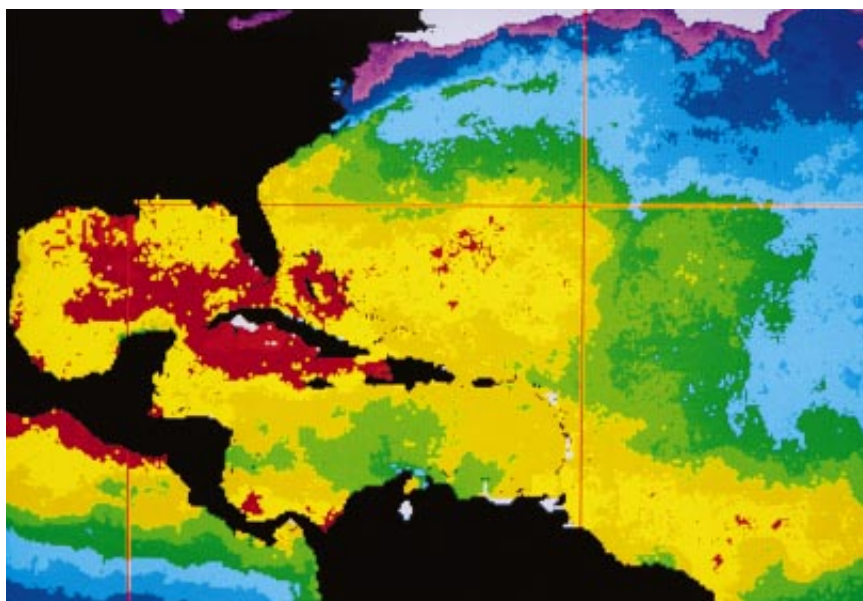
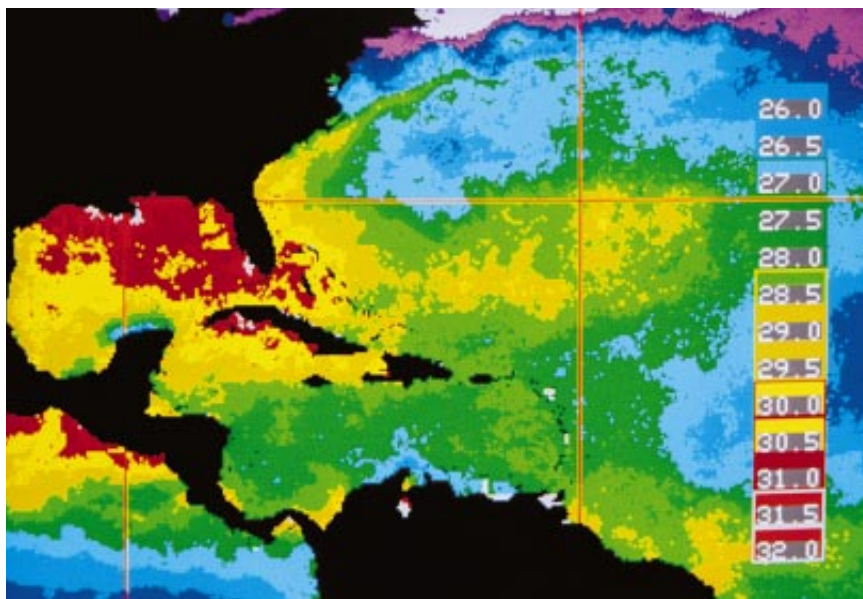
tures. Although it appears that elevated local seawater temperatures caused bleaching, linking this effect to global warming cannot be conclusive at this time. With the support of the National Science Foundation, NOAA and the Environmental Protection Agency, reef scientists and climatologists convened in Miami in June 1991 to discuss coral reefs and global climatic change. The workshop determined that reports of coral bleaching were indicative of threats to the ecosystem and that bleaching did appear to be associated with local temperature increases. But the paucity of knowledge about the physiological response of corals to stress and temperature, the inadequacy of seawater temperature records and the lack of standardized protocol for field studies made it impossible to decide whether bleaching reflects global climatic change in the ocean.

Several international monitoring efforts are now in progress or are planned so that the appropriate data can be gathered. For example, the Caribbean Coastal Marine Productivity Program, a cooperative research network of more than 20 Caribbean marine research institutions in 15 countries, was founded in 1990 and began systematic observations of coral reefs in 1992. Other networks of marine laboratories have been proposed in the central and western Pacific Ocean.

Whatever its cause, bleaching has important implications for the community structure, growth and accretion of coral reefs. Developing countries are particularly dependent on coral reefs for food resources and have made heavy investments in reef-related tourism. Bleaching, added to the accumulated toll taken by pollution and overfishing, may seriously burden the future economies of many nations.

The death of coral over such a wide geographic range in the eastern Pacific during the 1982-1983 ENSO had severe biological repercussions. Before the widespread bleaching, Glynn and his colleagues noticed that large fields of *Pocillopora* served to protect more massive coral species from the coral-feeding crown-of-thorns sea star (*Acanthaster planci*). The starfish did not venture across the dense coral stands, because

SEAWATER TEMPERATURE fluctuations in the Caribbean Sea in 1990 were tracked by satellite. Temperatures reached between 31 and 32 degrees Celsius (red) in certain areas during the months of August (top), September (middle) and October (bottom). Such unusually warm water is believed to cause coral reefs to bleach.





INTERTIDAL CORALS in Thailand “blanch” when exposed to the air. Unlike bleaching, this phenomenon appears to be adaptive: the coral polyps retract their soft tissues during low tide, leaving the calcium carbonate skeleton exposed. When water washes over again, the polyps and tentacles expand to cover the skeleton.

Pocillopora repelled it with the stinging cells of its tentacles. In addition, several species of symbiotic shrimp and crab in the *Pocillopora* attacked the sea stars, driving them away. As a result of warmer water, however, *Pocillopora* suffered higher mortality and lower fecundity, and large corals were consequently open to attack by the sea star. The predatory crustaceans were also affected. Because they normally feed on the lipid-rich mucus produced by the *Pocillopora* coral, a decline in the quantity and lipid content of the mucus brought about by the thermal stress triggered a decrease in the crustacean population.

The massive reduction in coral cover on the reefs of Panama and the Galápagos in 1982 and 1983 also restricted the range of one species of hydrocoral called *Millepora* and caused the apparent extinction of another species of the same genus. Glynn and W. H. de Weerd, now at the University of Amsterdam Zoological Museum, speculate that these species of corals were most severely affected because of their limited range and extreme sensitivity to increases in temperature. The disturbance also caused a nearly complete interruption in the long-term accumulation of calcium carbonate on the reefs of the region.

The fact that healthy reefs flourished in the eastern Pacific Ocean before 1982 indicates that an event of this magnitude is rare. Glynn estimated the age of two species of corals that were killed or heavily damaged in the Galápagos by multiplying their radius by their an-

nual growth rate of approximately one centimeter. He concluded that an ENSO like that of 1982–1983 had not occurred in the Galápagos for at least 200 years, possibly 400. The estimate is similar for corals in Panama. Interestingly, even at their most healthy, the coral reefs of the eastern Pacific are less well developed than those of the Caribbean. Their comparatively meager development may be partly explained by the relatively frequent high- and low-temperature disturbances over thousands of years.

The coral frameworks of the reefs of Panama and the Galápagos have changed dramatically as a result of the bleaching. Large areas of dead coral have become colonized by benthic algae, which in turn support increased populations of herbivores, particularly sea urchins. Sea urchins are grazers; they scrape the coral rock surface of the reef as they feed, contributing to the erosion of the reef structure.

Glynn and Ian Macintyre of the Smithsonian Institution and Gerard M. Wellington of the University of Houston have estimated the rates of calcium carbonate accretion and erosion on the reef. The rates of erosion after the 1982–1983 ENSO attributable to sea urchins alone are greater than the rates of accumulation on the healthy reefs before 1983. This finding suggests that without recovery of coral populations, these reefs will soon be reduced to carbonate sediments. Because the grazers erode the reef surface, they may also interfere with the recruitment

of new coral colonies, prolonging, or even preventing, their recovery.

Coral became bleached at many other places in the Indo-Pacific during the 1982–1983 ENSO, including the Society Islands, the Great Barrier Reef, the western Indian Ocean and Indonesia. Brown and Suharsono noted widespread bleaching and loss of as much as 80 or 90 percent of the coral cover on the shallow coral reefs of the Thousand Islands in the Java Sea. The corals most affected were on the shallow reef tops. Five years later coral cover was only 50 percent of its former level.

The extent of bleaching, environmental tolerances and the life-history characteristics of the dominant corals determine whether a reef recovers from the loss of most of its living coral. So do the nature and timing of other disturbances, such as predation and grazing. When bleaching is severe or prolonged, the coral may die. If the bleaching episode is short, the coral can rebuild its algal population and continue to live, but biological processes such as growth and reproduction may be impaired.

Because we are only now forming networks of sites that will conduct cooperative observations, the extent of coral reef damage brought about by bleaching has not been globally assessed. In 1987 Ernest H. Williams, Jr., of the University of Puerto Rico collected reports of bleaching from nearly every tropical ocean region. But until we have an adequate definition of coral bleaching in the field and have standardized our observations, the global impact of coral bleaching will remain a mystery.

If the temperature increase of one or two degrees C, predicted by the Intergovernmental Panel on Climate Change, does take place over the next 50 years in the tropical latitudes, the consequences for coral reefs could be disastrous. Unlike the miners with the canary, we cannot yet link bleaching to a clear cause. But that does not mean we should ignore the coral’s message.

FURTHER READING

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- CORAL BLEACHING. Edited by Barbara E. Brown. Special Issue of *Coral Reefs*, Vol. 8, No. 4; April 1990.
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