environment

Coral reefs

& Global climate change

Potential Contributions of Climate Change to Stresses on Coral Reef Ecosystems

Robert W. Buddemeier
KANSAS GEOLOGICAL SURVEY

Joan A. Kleypas
NATIONAL CENTER FOR ATMOSPHERIC RESEARCH

Richard B. Aronson
DAUPHIN ISLAND SEA LAB

PEW CENTER
ON
Global CLIMATE CHANGE

Coral reefs

& Global climate change

Potential Contributions of Climate Change to Stresses on Coral Reef Ecosystems

Prepared for the Pew Center on Global Climate Change

by

Robert W. Buddemeier
KANSAS GEOLOGICAL SURVEY

Joan A. Kleypas
NATIONAL CENTER FOR
ATMOSPHERIC RESEARCH

Richard B. Aronson
DAUPHIN ISLAND SEA LAB

February 2004

Contents

+

i

Foreword *Eileen Claussen, President, Pew Center on Global Climate Change*

Coral reefs represent some of the most biologically diverse ecosystems on Earth, providing critical habitat to approximately 25 percent of marine species. In addition, these ecosystems provide economic benefits through tourism and fisheries. One recent estimate valued the annual net economic benefits of the world's coral reefs at $30 billion. However, human activities including development in coastal areas, over-fishing, and pollution have contributed to a global loss of over 10 percent of these valuable ecosystems. An additional 15 percent have been lost due to warming of the surface ocean, and climate change will further contribute to coral reef degradation in the decades ahead.

Coral Reefs and Global Climate Change is the tenth in a series of Pew Center reports examining the potential impacts of climate change on the U.S. environment. It details the likely impacts of climate change over the next century to coral reef ecosystems both in U.S. waters and around the world. Report authors Drs. Robert W. Buddemeier, Joan A. Kleypas, and Richard B. Aronson find:

• *Increases in ocean temperatures associated with global climate change will increase the number of coral bleaching episodes.* High water temperatures stress corals leading to "bleaching" — the expulsion of colorful, symbiotic algae that corals need for survival, growth, and reproduction. While coral species have some capacity to recover from bleaching events, this ability is diminished with greater frequency or severity of bleaching. As a result, climate change is likely to reduce local and regional coral biodiversity, as sensitive species are eliminated.

• *Increases in atmospheric concentrations of carbon dioxide (CO_2) from fossil fuel combustion will drive changes in surface ocean chemistry.* The higher the concentration of CO_2 in the atmosphere, the greater the amount of CO_2 dissolved in the surface ocean. Higher dissolved CO_2 increases ocean acidity and lowers the concentration of carbonate which corals and other marine organisms use, in the form of calcium carbonate, to build their skeletons. Thus, continued growth in human emissions of CO_2 will further limit the ability of corals to grow and recover from bleaching events or other forms of stress.

• *The effects of global climate change will combine with more localized stresses to further degrade coral reef ecosystems.* Although climate change itself will adversely affect coral reefs, it will also increase the susceptibility of reef communities to degradation and loss resulting from natural climate variability such as El Niño events as well as disease, over-fishing, disruption of food webs, and pollution from neighboring human communities.

• *Multiple environmental management strategies, from local to global, will be necessary to ensure the long-term sustainability of the world's coral reef ecosystems.* Efforts to reduce emissions of greenhouse gases that contribute to global climate change can reduce the risk of future bleaching events and moderate changes in ocean chemistry. Meanwhile, the establishment of marine protected areas may help protect coral reefs from non-climate stresses as well as enable coral reefs to better adapt to the effects of global climate change.

ii

Executive Summary

Coral reefs are striking, complex, and important features of the marine environment. Reefs are geologic formations constructed from the accumulated skeletons of limestone-secreting animals and plants. The intimately linked plant-animal communities that create them are representative of an ecosystem that occurs in tropical and subtropical waters across the planet, most commonly in shallow oceanic water, and often close to land. Coral reefs have the highest biodiversity of any marine ecosystem, and they provide important ecosystem services and direct economic benefits to the large and growing human populations in low-latitude coastal zones.

The natural habitat of coral reefs near the junction of land, sea, and air is both varied and variable, and is a potentially stressful environment. Reef organisms have evolved adaptations over hundreds of millions of years to cope with recurring disturbances: damage or destruction, followed by recovery or regrowth. These are natural features of coral reef history. However, recent global increases in reef ecosystem degradation and mortality (the "coral reef crisis") appear to be sending a clear message that the rate and nature of recent environmental changes are frequently exceeding the adaptive capacity of coral reef organisms and communities.

The coral reef crisis is almost certainly the result of complex and synergistic interactions among local-scale human-imposed stresses and global-scale climatic stresses. Both can produce direct and indirect chronic and acute stresses, leaving few, if any, parts of the ocean truly hospitable for healthy coral reef communities. Documented human stresses include increased nutrient and sediment loading, direct destruction, coastal habitat modification, contamination, and the very important chronic indirect effects of overfishing. The major climate change factor that is becoming increasingly important for coral reefs is rising ocean temperatures, which have been implicated in chronic stress and disease epidemics, as well as in the occurrence of mass coral bleaching episodes. Also of concern are the effects of increasing atmospheric carbon dioxide (CO_2) on ocean chemistry, which can inhibit calcification—the deposition of the calcium carbonate minerals that are the structural building materials of coral reefs.

Coral reef communities usually recover from acute physical damage or coral mortality if chronic environmental stresses (such as reduced water quality) are weak, and if the acute stresses are not strong or overly frequent. Coral reefs also withstand chronic stresses in the absence of acute stresses. The combination of acute and chronic stress, however, often results in the replacement of the coral reef community by seaweeds or some other nonreef system. Such ecosystem shifts are well advanced in the Caribbean region, where two of the major reef-building coral species have been devastated by disease. In the Indo-Pacific region, the repeated and lethal episodes of "bleaching" associated with unusually high water temperature raise concern that reefs cannot sufficiently recover between such events.

Whereas remote oceanic reefs will be affected primarily by climate change, reefs close to human populations will continue to be affected by combinations of additional stresses (e.g., reduced water quality, physical damage, and overharvesting) that must be considered together to be understood and managed. Predictions of the future of coral reefs are difficult because current environmental changes are leading to a combination of surface ocean chemistry and temperature conditions that have almost certainly never occurred over the evolutionary history of modern coral reef systems.

This report reviews the published literature in an effort to analyze the current state of knowledge regarding coral reef communities and the potential contribution of future climate change to coral reef degradation and loss. The major conclusions of the review are summarized as follows:

1) Climate and localized nonclimate stresses interact, often synergistically, to affect the health and sustainability of coral reef ecosystems. Stresses associated with climate change, such as high-temperature episodes that promote coral bleaching, reduced calcification, and changes in ocean and atmospheric circulation, present one set of challenges to coral reefs. However, these stresses may exacerbate other stresses not directly related to climate, such as disease, predation, and the cumulative effects of other nonclimate stresses. Thus, it is difficult to separate the effects of global climate and local nonclimate influences when considering reef condition or vulnerability.

2) Coral reef alteration, degradation, and loss will continue for the foreseeable future, especially in those areas already showing evidence of systemic stress. As we enter an unprecedented climatic state, recent geological and biological history gives us little on which to base predictions regarding the future of coral reef ecosystems. Key uncertainties include the extent to which human activities will continue to alter the environment, how climate variability such as the frequency and intensity of El Niño-Southern Oscillation (ENSO) events will change relative to global temperature, and the biological and ecological responses of coral reef communities to unprecedented future conditions. However, there is no realistic doubt that continued climate change will cause further degradation of coral reef communities, which will be even more devastating in combination with the continuing nonclimate stresses that will almost certain-ly increase in magnitude and frequency.

3) The effects of climate change on global coral reef ecosystems will vary from one region to another. Although climate change has the potential to yield some benefits for certain coral species in specific regions, such as the expansion of their geographic ranges to higher latitudes, most of the effects of climate change are stressful rather than beneficial. Reef systems that are at the intersection of global climatic and local human stresses will be the most vulnerable. Remote, deep, or well-protected reef communities are more likely to provide reserves and refuges for future generations of coral reef organisms, and aesthetic and scientific resources for future generations of humans.

iv

4) While the net effects of climate change on coral reefs will be negative, coral reef organisms and communities are not necessarily doomed to total extinction. The diversity of coral species comprising existing reefs, the acknowledged adaptation potential of reef organisms, spatial and temporal variations in climate change, and the potential for human management and protection of coral reef ecosystems all provide possibilities for survival. Nevertheless, coral reefs of the future will be fewer and probably very different in community composition than those that presently exist, and these changes will cause further ecological and economic losses.

5) Research into adaptation and recovery mechanisms and enhanced monitoring of coral reef environments will permit us to learn from and influence the course of events rather than simply observe the decline. Most local (and some regional) nonclimate stresses have the potential to be mitigated and managed more readily than global climate change itself. A significant step would be a distributed international network of coral reef refuges and marine protected areas, selected on the basis of biological and environmental diversity, connectivity, potential threats, and enforcement feasibility. Yet, even with such efforts, recent degradation of coral ecosystems combined with future climate change will still pose a significant challenge to the global sustainability of coral reefs.

vi

I. Introduction

A. Coral Reefs and Reef Organisms

Coral reefs, and the organisms and communities that build and live on them, are widely distributed in shallow tropical and subtropical waters of the world (Figure 1; Box 1). Coral reefs are unique ecosystems in that they are defined by both biological ("coral" community) and geological ("reef" structure) components. The reef is constructed of limestone (calcium carbonate) secreted as skeletal material by corals and calcareous algae. Reef-building corals are colonial animals that house single-celled microalgae, called zooxanthellae, within their body tissues (Box 1; Figure 2). This symbiotic relationship benefits both partners: the coral obtains food from the plant photosynthesis, the microalgae benefit from nutrients released as waste by the coral, and the two have complementary effects on carbon dioxide (CO_2) exchange that is believed to account for the rapid rates of skeletal growth.

Figure 1

Worldwide Distribution of Coral Reefs
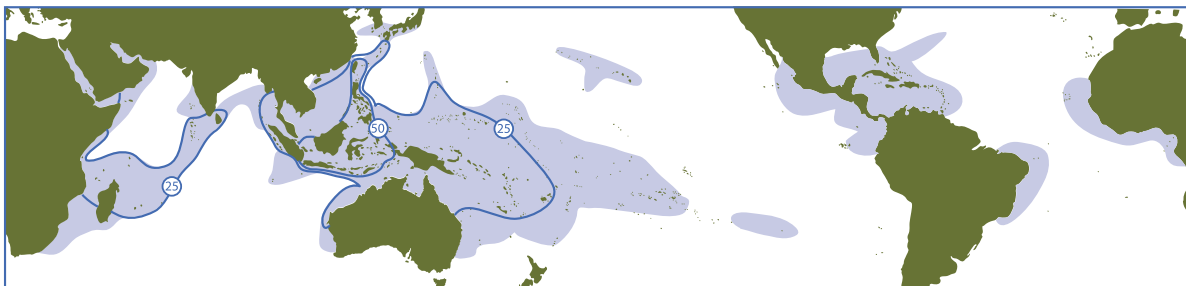
General worldwide distribution of coral reefs, with contours indicating the number of genera (clans of related species). The area inside the 50 genera contour is essentially the high diversity "coral triangle"—the Southeast Asian center of coral diversity. The blue area outside of the contour lines represents regions with at least 10 but fewer than 25 genera.
Source: based on Veron (1995).

Coral reefs offer many values to human society and to the health of the biosphere. Reefs support fisheries, and reef structures provide natural breakwaters that protect shorelines, other ecosystems, and human settlements from waves and storms. Humans use reefs and reef products extensively for food, building materials, pharmaceuticals, the aquarium trade, and other products. Due to their grandeur,

beauty, and novelty, reefs have become prime tourist destinations and, therefore, economic resources.

Less evident are the multiple "ecosystem services" of coral reefs, such as recycling nutrients and providing food, shelter, and nursery habitat for many other species. Many of these services are related to the geologic and biologic structures that create the spatial complexity necessary for the high biodiversity of reefs. The biodiversity is not all marine; humans, like many seabirds and other air-breathing species, have colonized island and coastal environments formed by coral reef communities.

All coral reef communities share the characteristics described in Box 1, but the range of variation makes generalization challenging and risky. The major biological provinces of reef corals are the Indo-Pacific and the Atlantic (of which the Caribbean is the best-known and most extensive example). These two ocean basins have very few reef species in common, and the Indo-Pacific accounts for about

---

Box 1

Corals and Reefs

"Coral reef" is a term used to describe both shallow limestone formations in tropical and subtropical waters and the biological communities that create them (Kleypas et al., 2001). Originally feared by mariners as a hazard to navigation, coral reefs are now valued for their beauty, biodiversity, and the products and services they provide to human society.

These values, like the reefs themselves, originate largely from the life histories of a remarkable group of organisms: reef-building corals. (Many other organisms are popularly called corals; we discuss only those that contribute substantially to reef building.) These organisms are distinct from most other animals in two important ways. First, most of them consist of multiple small, sea anemone-like organisms called polyps connected by living tissue into one sheet-like colony. Second, they have evolved an intimate symbiotic relationship with a group of microalgae: small plants, called zooxanthellae, that live in large numbers within the tissue of the coral animals. This fusion of plant and animal creates a composite organism: many coral polyps and a much larger number of algal cells all connected into a single living entity (see Figure 2). In most cases, the colony can be subdivided into pieces that will continue to live, much as plant cuttings can be propagated. Although reefs may be found in high-nutrient waters, the coral colony's ability to feed as an animal and

photosynthesize as a plant gives it great survival advantages in the nutrient-poor waters where they are often found: the tropical "deserts" of the ocean. However, this dependence on light restricts corals, and especially extensive reef-building activity, to shallow depths (from the intertidal zone to no more than 100 meters) and relatively clear waters. Most reefs, therefore, occur near land, making them particularly vulnerable to exploitation by humans, and to changes on nearby land masses.

Coral skeletons display a bewildering variety of geometries. The elaborate, three-dimensional structures of corals and reefs create a diversity of habitats, making coral reefs the most diverse shallow-water marine ecosystems known. As corals and other limestone-secreting organisms (especially calcifying, or calcareous, algae) grow, die, and are replaced, their mineral byproducts are compacted and cemented into the durable reef formations that are among Earth's largest biogenic features (i.e., features built by living organisms). Drilling on Enewetak Atoll in the tropical Pacific in 1952 penetrated 1,267 meters (4,158 feet) of coral reef materials and related carbonate deposits—literally an underwater coral reef mountain— which had accumulated over tens of millions of years and which is capped by living reef communities that are still producing carbonate minerals.

Figure 2

A Typical Reef-Building Coral

Cross-section diagram of a polyp and the skeleton of typical reef-building coral, illustrating the presence of symbiotic microalgae (zooxanthellae). The organism is colonial, with many polyps connected in a single living surface above the limestone skeleton. Inset figures show the relationships of the polyp to the colony and of the colony to the reef community.

TENTACLES

ZOOXANTHELLAE
(ALGAE)

GULLET

SKELETON
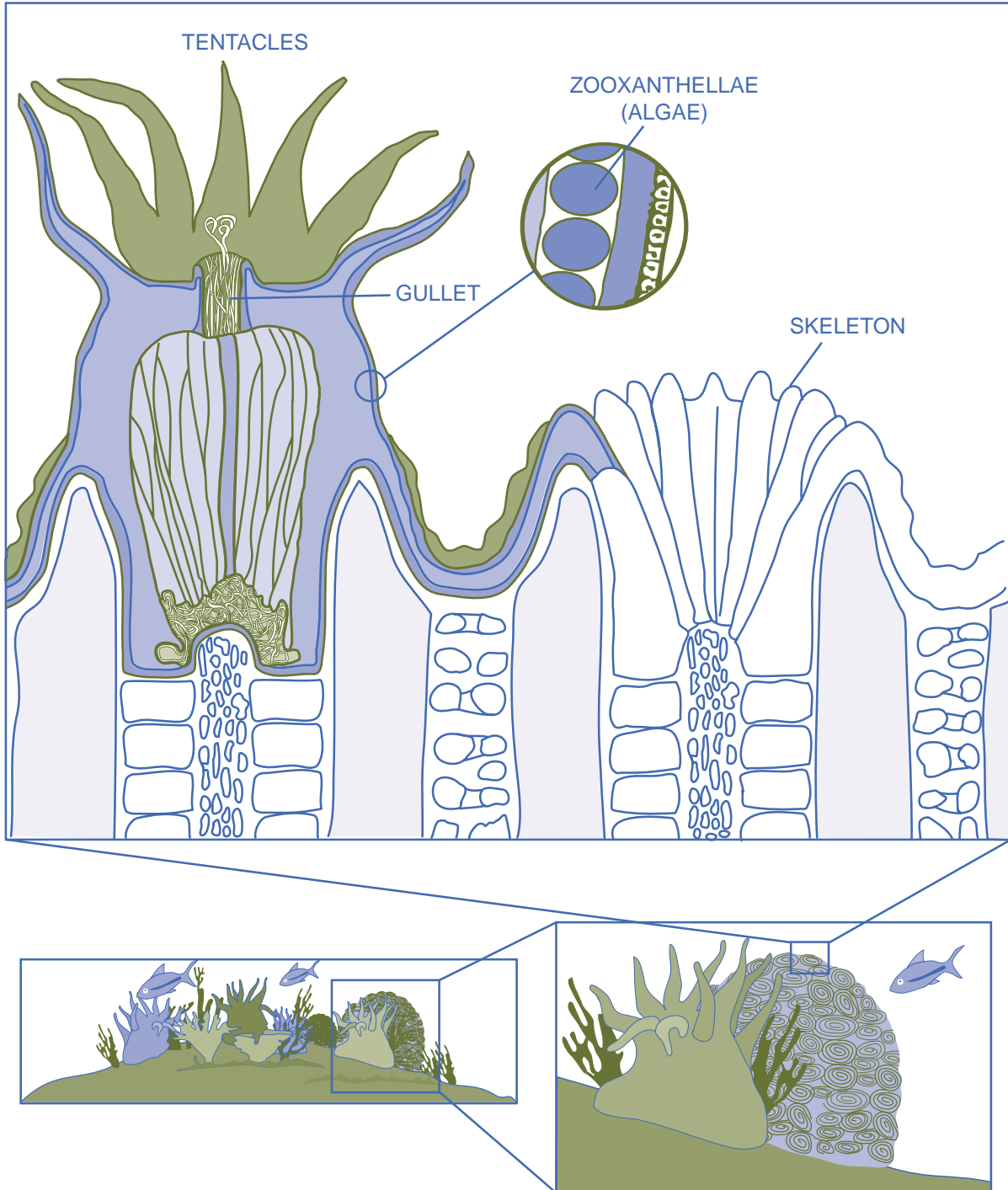
85 percent of the world's reefs and a similar proportion of reef biodiversity (Veron, 1995). The center of maximum coral diversity is in the Southeast Asian region (Figure 1). Reef communities vary across large-scale environmental gradients, as reflected in the diversity gradients across both latitude (North-South; e.g., Harriott and Banks, 2002) and longitude (East-West). At smaller scales, the makeup of reef communities differs according to the degree of land influence, storm frequency, and combination of other local and regional factors.

Reef communities produce limestone, which can be well-preserved in the geologic record. Because reefs and corals have existed in one form or another for hundreds of millions of years, this record provides a wealth of information about organism and ecosystem evolution and Earth's environmental changes through time. Corals have not, however, always been the main reef builders, and comparing ancient with present-day reefs can be confusing, because the terms "coral" and "reef" have been used to refer to a wide variety of things. Modern coral reef organisms and communities have evolved over the past 40-55 million years. Present-day reefs have accumulated during the last 10,000 years of the current interglacial period (the Holocene epoch). The modern reef community is the living veneer over these limestone accumulations that may be tens of meters thick.

B. The "Coral Reef Crisis"

Coral reefs have declined over the course of human history, culminating in the dramatic increase in coral mortality and reef degradation of the past 20-50 years (Pandolfi et al., 2003). This "coral reef crisis" is well-documented and has stimulated numerous publications on the future of coral reefs (e.g., Hoegh-Guldberg, 1999; Knowlton, 2001; McClanahan, 2002) and their vulnerability to environmental change (e.g., Bryant et al., 1998; Hughes et al., 2003). The causes of this crisis are a complex mixture of direct human-imposed and climate-related stresses, and include factors such as outbreaks of disease, which have suspected but unproven connections to both human activities and climate factors. By 1998, an estimated 11 percent of the world's reefs had been destroyed by human activity, and an additional 16 percent were extensively damaged in 1997–98 by coral beaching (Wilkinson, 2000, 2002). Widespread coral bleaching, unknown before the 1980s, has brought recognition that reefs are threatened by global-scale climate factors as well as by more localized threats, and that different types of stress may interact in complex ways.

Although the crisis is widespread, individual reefs and even whole regions exhibit considerable variation in both health and responses to stress. The Caribbean region has been particularly hard-hit by problems (Gardner et al., 2003), many of which are well-studied. Caribbean case studies and inter-ocean contrasts help to illustrate both the consistencies and the variations in coral reef responses to complex environmental changes.

C. Climate and Environmental Change

Over the past one to two centuries, human population growth and development have greatly altered not only local environments, but also the global environment as a whole. Major systematic changes include rising atmospheric concen-

---

Box 2

Climate Change Projections

The Earth's climate system consists of natural processes that redistribute the sun's energy that is absorbed and re-emitted by the planet. We tend to think of climate in terms of its physical manifestations—the temperature and movements of the oceans and atmosphere, and the hydrologic cycle that redistributes water across the earth's surface. However, chemical, biological, and geological processes are also integral features of the climate system.

The Third Intergovernmental Panel on Climate Change (IPCC) found that the average temperature of the earth has risen 0.4–0.8°C (approximately 1°F) since the late 19th century, and attributed a substantial part of that change to the concurrent increase in greenhouse gas concentrations; for example, atmospheric CO_2 has increased from about 280 parts per million by volume (ppmv) to nearly 370 ppmv (Houghton et al., 2001). Greenhouse gas concentrations will continue to increase over the next few decades to centuries—how much depends on future economic and technological developments. A range of scenarios that combined predictions of population growth, economic growth, and technological advances was used to arrive at the estimates in Table 1.

Table 1

IPCC global **average climate change** observations and projections[1]

Variable	Observed		Projected	
	1880	2000	2050	2100
CO_2 (ppmv)	280	367	463–623	478–1,099
Global mean temp (°C) (°F)	---	+0.4–0.8 (+0.7–1.4)	+0.8–2.6 (+1.4–4.7)	+1.4–5.8 (+2.5–10.4)
Tropical SST (°C) (°F)	---			~+1.0–3.0[2] (~+1.8–5.4)
Sea level (m) (ft)	---	+0.07[3]–0.15[4] (+0.23–0.49)	+0.05–0.32 (+0.16–1.0)	+0.09–0.88 (+0.29–2.88)

[1] Projected values are from Table TS-1 of the IPCC Working Group II Technical Summary (McCarthy et al., 2001) unless otherwise noted.

[2] Estimated from Figure 20 of IPCC Working Group I Technical Summary (Albritton et al., 2001)

[3] Cabanes et al., 2001

[4] Houghton et al., 2001

trations of greenhouse gases (GHGs) that influence the earth's energy budget and climate. Climate changes due to rising GHG levels (the enhanced greenhouse effect) are summarized in Box 2 (previous page). In addition, the global phosphorus and nitrogen cycles have accelerated because of artificial fertilizer use and massive changes in land use, the hydrologic cycle has been altered by river damming and water diversion as well as climate change, major natural ecosystems have been altered by fishing, forestry, and agriculture, and the ecological and biogeochemical implications of increased atmospheric CO_2 levels go well beyond the effects on global temperature (Steffen and Tyson, 2001).

Because coral reefs occur near the junction of land, sea, and atmosphere, their natural habitats experience both the marine and terrestrial results of any climatic change and are vulnerable to human activities. This report first summarizes the contributions of direct human stress to the coral reef crisis, then reviews the source and nature of climate change stresses, and finally summarizes the future prospects for coral reef ecosystems in a rapidly changing world.

We use "acute" and "chronic" to classify various stress factors, discuss their interactions, and integrate their probable combined effects. Acute stresses are those short-term events that cause rapid damage on a reef (such as from tropical storms), while chronic stresses act over longer terms and are generally associated with more gradual environmental degradation (such as sediment loading). Although some stresses are not clearly either acute or chronic, this approach allows us to discuss reef decline as a combination of stresses, and highlights the need to consider chronic (and usually less apparent) stress as much as acute stress.

6

II. Nonclimatic Stresses to Coral Reefs

A. Types and Categories of Stresses and Effects

A wide variety of environmental factors that are not directly related to changes in the climate system have the potential to stress coral reefs. Reef communities have been described as "disturbance-adapted" ecosystems (Connell, 1997; Hughes and Connell, 1999), but that adaptation is to natural rather than human-enhanced disturbances. Cycles of damage followed by recovery are natural aspects of reef persistence, and coral reefs have been described by Done (1999) as a "shifting steady-state mosaic"—a regional population of reef communities that are diverse and changing, but in which all of the important types and components are always represented. This pattern breaks down when reef communities are lost and fail to recover (as appears to be happening worldwide), or when critical components are lost on a regional scale (e.g., the loss of *Acropora* species—staghorn and elkhorn corals—in the Caribbean), causing fundamental change in the larger coral reef ecosystem.

Reef decline, as opposed to change or variation, has two components: the initial damage or mortality and the failure of the ecosystem to recover. Reefs can recover from acute stresses and tolerate chronic stresses, but chronically stressed reefs are far less likely to recover from acute stress (Kinsey, 1988). As disturbances (acute stresses) become more varied and frequent against a background of deteriorating conditions (chronic stresses), components of the original coral reef mosaic are progressively replaced by noncoral organisms. Environmental alteration and climate change need to be considered together to predict the future trajectory of coral reef ecosystems, since both can cause chronic and acute stresses; both also vary across time and space and are likely to have strong interactions.

Table 2 and the discussion that follows consider the main human-induced stresses on reefs, whether acute or chronic, and how they interact with climate change and each other. These stresses act over different spatial scales, which is important to understanding responses and possible remedies.

Table 2

Stresses on Coral Reef Ecosystems

Stresses are grouped into Chronic or Acute Categories; some factors occur in both categories. Within categories, listing is by the spatial scale at which the stress functions; G=global, R=regional, L=local, R+L = intermediate. Factors related to climate change appear in bold; others are of more direct human origin.

Stress factor	Scale			Comments
Chronic Stresses	**G**	**R**	**L**	
Carbonate ion decrease and reduced calcification	•			Cooler areas will be stressed first, opposing possible warming benefit
Temperature increase	•			Gradual increase may be chronic stress in warm areas, benefit in cool
Overharvesting	•	•	•	Fishing – commercial, recreational; fin-fish, others; souvenir and aquarium trades
Nutrient loading		•	•	Land use – agriculture, sewage treatment, biomass burning, increased runoff
Introduced/invasive species; diseases[1]		•		Increased competition and debilitation by parasites, predators, or diseases
Ocean/atmospheric circulation change		•		Specific predictions are difficult
Coastal and watershed alteration		•	•	Alteration of circulation patterns, runoff, and land-ocean coupling
Sedimentation		•	•	Land use – agriculture, land clearing, construction, increased erosion and runoff
Acute Stresses				
Temperature increase	•	•		Transient high-temperature episodes are major stresses
ENSO[1]	•	•		Linkage to climate change uncertain; major factor in acute temperature stress
Diseases[1]; introduced or invasive species		•	•	Increased virulence and frequency of disease outbreaks may be linked to climate change
Storm frequency & intensity increase		•	•	Major factor in land-ocean coupling
Sedimentation		•	•	Land use – agriculture, land clearing, construction, increased erosion, and runoff
Urbanization, watershed modification		•	•	Increase in waste, other discharges, alteration of land-ocean coupling
Commercial and incidental destruction		•	•	Transportation, tourism and recreational use, mining, dredging, destructive fishing

[1]Natural factors that may be triggered or intensified by climate change

8

Regional stresses typically impact large areas (100-1,000 km) and thus are more likely to systematically interact with (and be harder to distinguish from) climate change effects. Regional-scale stresses include overfishing and selective removal of species; introduction or invasion of alien species; and changes in land use, water quality, and water and nutrient cycles.

Intermediate-scale stresses (10-100 km) may have manifestations at various levels from the local coral reef community to the region. Coastal development, land and water resource use (including modifications to runoff and sedimentation), tourism and recreation, and harvesting for the aquarium and live-fish trades often fall into this category.

Local stresses (0.1-10 km) have impacts primarily on specific reefs or parts of reefs, and may include point source and localized coastal pollution; anchorings and groundings of boats and ships; destructive fishing practices; and the marine impacts of offshore oil and gas production and transportation.

B. Terrestrial Inputs

Nutrient Loading and Contaminant Inputs

The symbiotic relationship between reef-building corals and zooxanthellae allows them to thrive in the nutrient-poor "marine deserts" of the tropical oceans. Addition of nutrients to the water may harm corals directly (if concentrations are sufficiently high) or make the environment less favorable for reefs by promoting growth of phytoplankton (which reduces water clarity and light availability) and of seaweeds (macroalgae) that compete with corals for space on the reef. Additional organic production resulting from nutrient loading can also increase populations of bioeroders that break down coral skeletons and reef structures.

Humans have altered the nitrogen (N) and phosphorous (P) cycles at least as extensively as they have the carbon cycle, greatly increasing N and P inputs to the world's oceans and coastal zone (Jickells, 1998; Moffat, 1998). The degree to which rising "background" levels of nutrients in coastal waters are affecting coral reefs is unclear, but heavy nutrient loading can have marked impacts. In a case study from Kaneohe Bay, Hawaii, nutrient-rich sewage discharge was clearly responsible for takeover of the coral communities by algae following storm-related coral kills (Smith et al., 1981; Jokiel et al., 1993).

Unlike nutrients, contaminants are generally human-produced toxic or bioactive materials, which have no natural source or are highly concentrated. They include heavy metals, pesticides and herbicides, solvents, fuels, and other compounds. These materials may be part of complex waste streams discharged to the ocean or adsorbed in sediment. Effects of individual contaminants are difficult to document, trace, or separate from combined effects.

Sediment Loading

Sediment deposited onto corals interferes with feeding by the polyps and costs the colonies energy to remove (Riegl and Branch, 1995). In the extreme, burial by rapid or prolonged sediment deposition is fatal to corals and other bottom-dwellers. Sediment accumulation also inhibits the establishment of new reefs, because coral communities require hard and stable surfaces. Sediment suspended in the water increases turbidity and reduces available light. Reefs that grow in naturally turbid environments, with organisms that are suited to such conditions, may experience low impacts from a moderately increased sediment supply (Larcombe and Woolfe, 1999), but sediment loading on reefs that are accustomed to low-sediment conditions imposes significant stress (e.g., Cortés, 1994).

Sediment on a coral reef can have two sources: transport of soil particles with freshwater runoff from land, or resuspension of sediment already on the seafloor. Human activities have reduced some sediment sources and increased others. Damming of major rivers has dramatically reduced their sediment discharge to the ocean (Meade et al., 1990; Vörösmarty and Sahagian, 2000), but large river outflows represent only a small proportion of the world's coastline and are usually not near reefs.

In smaller coastal watersheds and offshore, human activity has tended to increase sediment discharge and resuspension in coastal waters. In Southeast Asia, Burke et al. (2002) calculated that more than 21 percent of all coral reefs are threatened by sedimentation from land-based sources, primarily due to logging and poor agricultural practices. McCulloch et al. (2003) used coral skeletal records (1750–1998) to show that sediment delivery to the near-shore central Great Barrier Reef increased five- to ten-fold with the introduction of European agricultural practices. These findings support the contention that significant portions of the Great Barrier Reef suffer chronic anthropogenic sediment stress (Wolanski et al., 2003). Local dumping, dredging, land reclamation, mining, and construction activities can also result in increased sedimentation or resuspension of sediment in the marine environment.

The socioeconomic forces behind increased sediment runoff are difficult to reverse or control, particularly with rising coastal populations. Once there has been substantial influx of land-derived sediment to a reef region, the "new" sediment often remains in place, is subject to resuspension, and makes the substrate where it accumulates less hospitable to corals. Reefs closest to land masses will probably continue to experience the most intense chronic (and locally acute) sediment stress, and the effects will be magnified by climatic change in some areas.

C. Overfishing and Resource Extraction

Fishing for food and recreation removes fish and other organisms (e.g., giant clams and sea cucumbers), and with them, the ecosystem functions they perform. Many organisms of all types are also taken for use as souvenirs or decorations (mostly shells, but also corals), and for the aquarium trade.

Overfishing, the unsustainable fishing or collection of particular organisms, is a global problem with a long history of impacts across the entire marine ecosystem (Jackson et al., 2001; Pandolfi et al., 2003). Removal of plant-eating organisms (herbivores) from a reef upsets the competitive balance between corals and seaweeds, often leading to a fundamental change in the community (Box 3).

Box 3

Overfishing: Upsetting the Competitive Balance

Coral reefs are limited by the availability of hard seafloor areas of suitable depth. Corals and calcifying algae must compete with noncalcifying plants (macroalgae, or seaweeds) for this space, so anything that enhances the growth of plant material on reefs can also inhibit the growth of the reef-builders. Plant-eating animals (herbivores) are important controls on seaweeds, and both experimental studies (e.g., Lirman, 2001) and field comparisons of heavily and lightly fished areas have shown that reduced herbivore populations tend to result in enhanced seaweed growth at the expense of coral cover (Littler and Littler, 1997; Williams et al., 2001).

One of the most dramatic demonstrations of the effect of herbivory resulted from a gradual loss of herbivores due to overfishing, combined with an acute disease outbreak. Prior to the 1980s, the most important reef herbivores in the Caribbean were parrotfish, surgeonfish, and the black-spined sea urchin, *Diadema antillarum,* but in many areas the fish populations had been greatly reduced (Hughes, 1994). When a disease outbreak destroyed most of the *Diadema* populations throughout the Caribbean in 1983–84 (Lessios, 1988), acute episodes of coral mortality (due to hurricanes and other factors) combined with the absence of crucial herbivores to convert coral-dominated Caribbean reefs to seaweed-dominated communities (Hughes, 1994; Aronson and Precht, 2000; see also Carpenter, 1986; Lewis, 1986).

The chronic stress of overfishing is often hard to avoid on coral reefs. Although seemingly lush and teeming with life, reef communities generate only small amounts of sustainably harvestable biomass. Further, many reef organisms are long-lived and must reach a certain size or age before they reproduce. Removal of large individuals thus has a disproportionate impact on the species' reproduction.

Fishing operations also often have acute destructive effects beyond simple removal of target species. By-catch (incidentally captured nontarget species) is often wasted, and damage to other reef organisms and the reef structure itself is common (e.g., from boat anchors or nets). Blast fishing, widespread in the Southeast Asian region, destroys habitat and is extremely wasteful in terms of incidental kills. Muro-ami ("fishnet") fishers mechanically smash shallow patch reefs and net the fish that are driven out. In areas such as the South China Sea, the shallow sea floor is trawled, and chains are dragged to destroy corals that would snag the nets (Burke et al., 2002).

Box 4

Large-Scale Environmental Modification—the South Florida Example

The Florida Keys were originally a chain of islands separated by wide passages connecting ocean water with the waters of Florida Bay. Over the course of the 20th century, these islands were progressively connected by bridges and causeways that blocked or modified the original flow paths of water. This physical modification was accompanied by growing human population, exploitation of the reef resources, and major changes in land and water use on the Florida mainland. All of these changes interacted and probably contributed to the major decline of the reefs and other ecosystems in the area by slowing ocean water exchange and allowing the buildup of land-derived contaminants—and by facilitating population growth and human access.

Society faces the dilemma of deciding on targets for protection and remediation. Physical systems have been altered in ways unlikely to be reversed, and ecosystems have never come to any sort of equilibrium with an environment constantly undergoing modification by humans. This is a local equivalent of the global climate change problem: we are in an unprecedented state, without a baseline or any system with which to compare the changes that are occurring. The ecosystems of the Florida Keys, Florida Bay, and the Everglades can be regarded as the degraded remnants of their predecessors, subject to multiple chronic and acute stresses. From both a practical and a scientific standpoint, however, we might also look at them as defining new, modified baseline conditions for "the ecosystem as it is" (Jackson, 1997; Jackson et al., 2001).

12

D. Coastal Zone Modification and Mining

Human efforts to improve or maintain the coastal zone often have unintended ecological consequences. Dredging, land reclamation, shoreline protection, harbor and runway construction, and other similar activities can have direct, acute impacts by destroying coral reef habitats. The impacts of spoil dumping, sediment resuspension, or local contamination may become chronic and extend well beyond the immediate site. Less apparent is the potential long-term chronic stress imposed by altering patterns of both marine and fresh water movement, as has occurred in south Florida (Box 4).

Reef destruction can also result from deliberate mining of nonliving resources. On atolls, reef islands, and in other coastal areas, sand and reef-rock are the only readily and economically accessible building material. Although healthy reefs produce enough sand to supply reasonable uses, sustainable "harvesting" requires careful attention to where and how the material is removed.

E. Introduced and Invasive Species

Introduced or invasive species may be inadvertently brought to a reef through travel, shipping, or careless disposal (e.g., by the food and aquarium industries). The worst incidents of species introductions have occurred in terrestrial, fresh water, or estuarine environments, but there is growing evidence that coral reefs are not immune from the problem (Ruiz et al., 1997; Coles and Eldredge, 2002). A major concern is that pathogens or parasites will be transported across natural barriers to new and vulnerable host populations; a possible example is the *Diadema* sea urchin die-off in the Caribbean, discussed later (see also Box 3).

III. Climatic Change Stresses to Coral Reefs

Global climate change imposes interactive chronic and acute stresses, occurring at scales ranging from global to local, on coral reef ecosystems.

Table 2 summarizes what we know about present and future climate stresses, but prediction of coral reef response is difficult because there are no precedents for the expected changes and conditions in the evolutionary history of modern corals (~50 million years). Figure 3 illustrates the extraordinary nature of some of the changes now in progress.
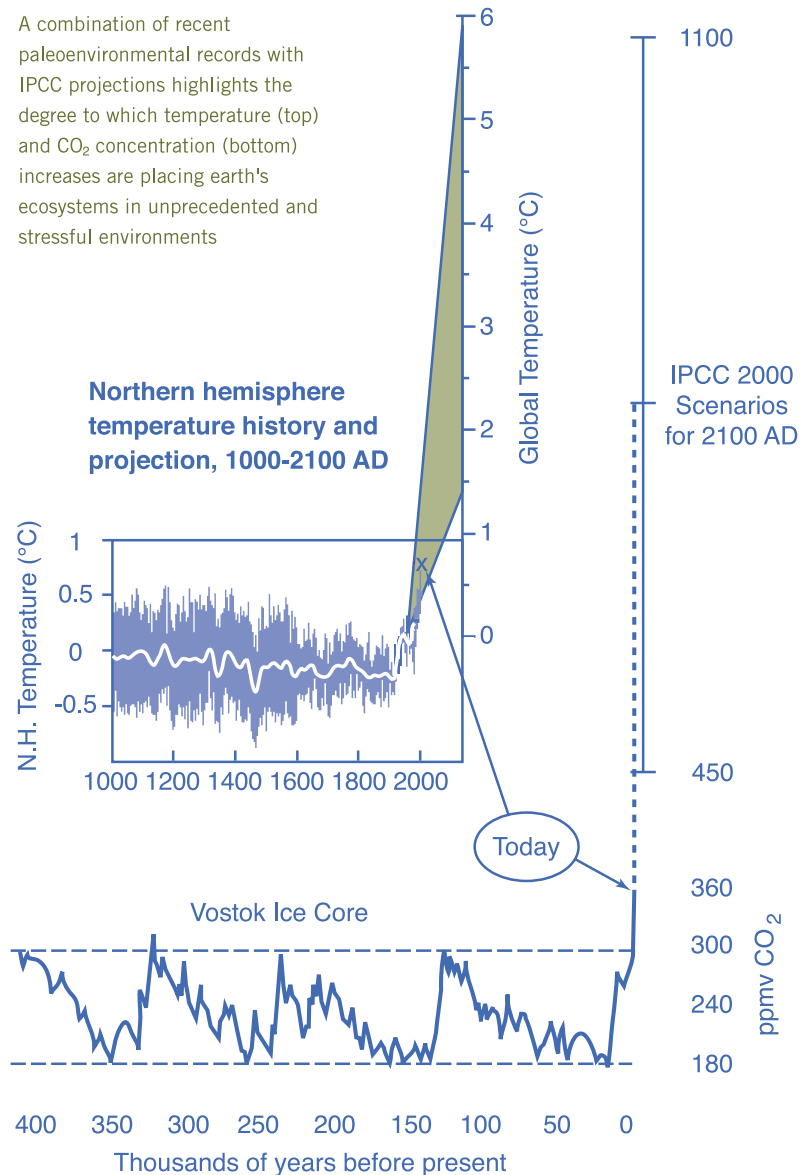
Gas bubbles preserved in polar ice caps show that atmospheric CO_2 concentrations over the past 400,000 years have oscillated between about 180 and 310 parts per million volume, or ppmv (Figure 3; Petit et al., 1999); past temperature and sea-level variations mimic the CO_2 fluctuations, with relatively constant minimum (glacial period) and maximum (interglacial) values. The human-caused increase in atmospheric CO_2 is the near-vertical line at the present-day end of Figure 3. Accompanying this CO_2 increase is an observed increase in temperature (see inset, Figure 3), and a

Figure 3

Global Temperature and Atmospheric CO₂
Projections for 1990-2100 Relative to Past Conditions

A combination of recent paleoenvironmental records with IPCC projections highlights the degree to which temperature (top) and CO_2 concentration (bottom) increases are placing earth's ecosystems in unprecedented and stressful environments

Northern hemisphere temperature history and projection, 1000-2100 AD

Coral reefs & Global climate change

decrease in pH of the surface ocean (Caldeira and Wickett, 2003). IPCC projections (Box 2 and Figure 3) show an even greater departure from geologically recent climates by the end of the present century.

A. Coral Bleaching

The atmosphere and the ocean have warmed since the end of the 19th century and will continue to warm into the foreseeable future, largely as a result of increasing greenhouse gas concentrations (Houghton et al., 2001; Levitus et al., 2000, 2001). El Niño-Southern Oscillation (ENSO) events have increased in frequency and intensity over the last few decades. This combination (warming and intense El Niño events) has resulted in a dramatic increase in coral bleaching (Glynn, 1993; Brown, 1997a; Wilkinson, 2000).

"Bleaching" describes the loss of symbiotic algae by the coral or other host. Most of the pigments in the usually colorful corals depend on the presence of these plant cells. The living tissue of coral animals without algae is translucent, so the white calcium carbonate skeleton shows through, producing a bleached appearance. Bleaching is a general stress response that can be induced in both the field and the laboratory by high or low temperatures, intense light, changes in salinity, or by other physical or chemical stresses. Bleaching is the extreme case of natural variation in algal population density that occurs in many corals (Fitt et al., 2000, 2001).

Three types of bleaching mechanisms are associated with high temperature and/or light: "animal-stress bleaching," "algal-stress bleaching," and "physiological bleaching" (Fitt et al., 2001). Although all are important to understanding climate-coral interactions, two are particularly relevant to present concerns: algal-stress bleaching, an acute response to impairment of photosynthesis by high temperature coupled with high light levels; and physiological bleaching, which reflects depleted reserves, reduced tissue biomass, and less capacity to house algae as a result of the added energy demands of sustained above-normal temperatures. A rising baseline in warm-season sea-surface temperatures on coral reefs (Fitt et al., 2001; Lough, 2001) suggests that physiological bleaching is at least partly to blame in some bleaching events (e.g., in the Caribbean in 1987 and on the Great Barrier Reef in 2001). Such chronic temperature stress may also underlie some less obvious causes of reef decline, such as low rates of sexual reproduction (Mendes and Woodley, 2002). Box 5 explains these relationships by analogy with drought in terrestrial forests.

A Coral Reef – Terrestrial Forest Analogy

Forests and reefs are very different, but both are complex ecosystems and both share enough similarities that the response of forests to severe drought can serve as a useful analogy for understanding coral reef stress responses.

Trees are the main photosynthesizers in a forest and provide the structural complexity that modifies the environment and creates many habitats on which other organisms depend. Similarly, corals and marine algae —the calcareous algae mentioned in Box 1, as well as the more familiar seaweeds—are the photosynthesizers that create the reef's structural and ecological complexity. Reefs, like tropical rainforests, grow in nutrient-poor conditions and have high biodiversity.

Under severe drought, photosynthesis of many trees is interrupted when they lose their leaves, and some or most of them may die. Other forest organisms will then die or migrate elsewhere. Most forests can recover with the return of suitable weather conditions. Some trees will regrow leaves, but the energy lost during the drought may make them vulnerable to disease and less likely to bear fruit (reproduce) in the short term. Recovery time depends on factors like the original state of the forest, the extent of damage, resistance to disease, and whether seeds for new growth are available in the soil or by wind or animal transport from nearby forests. The nature of some forests may change permanently if a different ecosystem (e.g., a grassland) takes its place.

Coral reef ecosystems have similar responses to bleaching; stress causes corals to expel their zooxanthellae, interrupting photosynthesis. Many corals can survive mild bleaching events, just as trees can recover from the loss of leaves. However, the longer corals remain bleached, the more susceptible they become to disease and other stresses. The 1997–98 mass bleaching event included extensive regions where corals and other species suffered high losses (> 90 percent mortality). Recovery, if it occurs, will depend on how many corals survive and reproduce, and whether the geographic placement of the reefs in relation to ocean currents provides larvae from elsewhere.

The temperature threshold for bleaching is not an absolute value, but is relative to other environmental variables (especially light) and to the duration and severity of the departure from the normal temperature conditions of a reef (Liu et al., 2003). Bleaching due to thermal stress is not, therefore, limited to areas of normally high water temperature. However, regions where higher temperatures are the norm seem likely to be more vulnerable to increased physiological bleaching (Fitt et al., 2001).

Coral bleaching events of greatest concern are acute episodes of high mortality and protracted debilitation of survivors in the form of diminished growth and reproductive rates (Omori et al., 2001). Corals with branching growth forms, rapid growth rates, and thin tissue layers appear to be most sensitive to bleaching, and usually die if seriously bleached. Slow-growing, thick-tissued, massive corals appear to be less sensitive and commonly recover from all but the most extreme episodes. Bleaching thus selectively removes certain species from reefs and can lead to major changes in the geographic distribution of coral species and reef community structures (Hughes et al., 2003).

B. Global Warming and Reef Distribution

The global distribution of reef-building corals is limited by annual minimum temperatures of ~18°C (64°F) (Veron, 1995; Kleypas et al., 1999b).

Although global warming might extend the range of corals into areas that are now too cold (Precht and Aronson, 2003), the new area made available by warming will be small, and the countervailing effects of other changes suggest that any geographic expansion of coral reefs will be very minor (see Box 6).

Box 6

Will Global Warming be Good for Reefs?

About 5,000–6,000 years ago, an earthquake lifted a coral community out of the sea at Tateyama, Japan, at the same latitude as Tokyo. That community contained at least 72 species of corals, compared to the 35 now found in the vicinity (Veron, 1992, 1995). Tateyama sea-surface temperature (SST) was 1.2–1.7°C warmer at that time than at present, because the earth was experiencing a warm period known as the Altithermal, or Middle Holocene High (Veron and Minchin, 1992). This suggests that corals and reef-building could migrate to higher latitudes in response to global warming. Geographic shifts of reefs would not mitigate the ecological and economic problems caused by the loss of tropical reefs, but it would partly alleviate concerns about global biodiversity loss.

The problem with comparing the effects of Altithermal warming and future warming is that little besides temperature would be comparable. Then, any human settlements in the area were small and primitive, and the coastline was essentially pristine. Today's corals would have to settle and survive in highly populated and developed areas with intensive agriculture, fishing, pollution, coastal construction, and other societal artifacts that make coastal waters inhospitable to coral communities. When Tateyama reaches the temperature levels of 5,000–6,000 years ago, the chemistry of the water will be less favorable to coral growth and reef building (Kleypas et al., 2001; Guinotte et al., 2003; see Box 7). With both suitable habitat and the potential for coral and reef growth reduced, future immigrant corals will face very different prospects than their predecessors.

Figure 4

Global Warming and the Distribution of Coral Reefs

At present, coral reefs (indicated by asterisks) are limited to the tropics and occur only in waters where temperature remains warmer than 18°C (64°F) (green). A 2°C (4°F) warming of the oceans will expand the range by a few degrees latitude (dark blue). Locations within this region that have suitable depth, substrate, and other environmental conditions could potentially support new coral reefs at the higher temperatures.
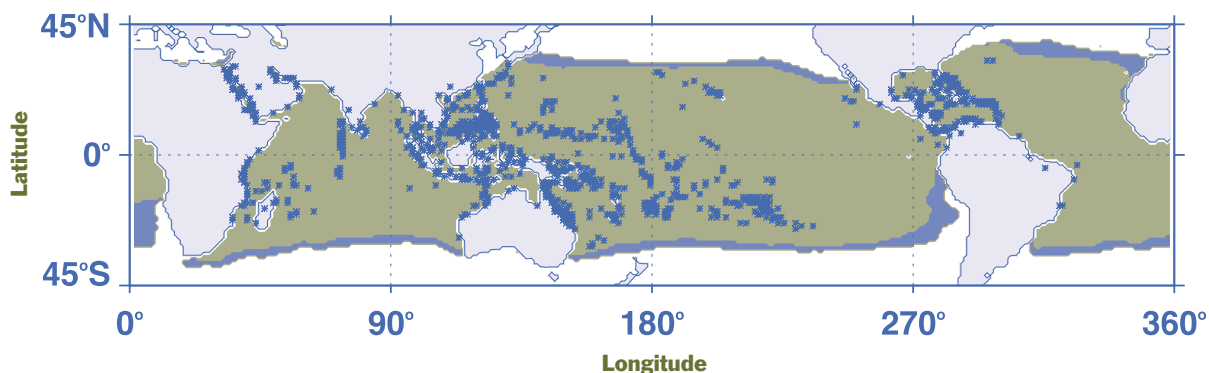
Coral reefs require shallow, clear water with at least some hard seafloor, and their propagation depends primarily on ocean currents. The west coasts of North and South America, Europe, and Africa experience cool water flowing toward the equator and are thus "upstream" from potential sources, causing restricted distributions of coral reefs (see Figure 4). In areas such as the southeastern United States and near the Amazon River, reef expansion along the coast is blocked by muddy coastal shelves, river deltas, and turbid water. Only southern China, Japan, Australia, and southern Africa present geographically realistic opportunities for reef expansion. Additionally, sea-surface temperature (SST) gradients are very steep in the vicinity of 18°C (the annual minimum temperature threshold for coral reef growth), and ocean model projections (shown in Figure 4) suggest that SST warming associated with doubled CO_2 will only move the 18°C contour by a few hundred kilometers, especially in the critical western boundary areas (Kleypas et al., 2001). The overall positive effects of warming on habitat availability and ecosystem distribution will be very minor compared to the overall negative effects.

Box 7

Effects of CO₂ on the Carbonate Chemistry of Seawater

The chemical behavior of CO_2 in water is well understood, but it is complex and counterintuitive. Burning fossil fuels increases the concentration of CO_2 in the atmosphere, which drives more of the gas into the surface layer of the ocean. The top 100 meters of the ocean has absorbed much of the anthropogenic increase in CO_2, while most of the deep ocean, which mixes with the surface water on about a thousand-year time scale, reflects primarily the older, unaltered CO_2 cycle. When CO_2 dissolves in water, it forms carbonic acid (H_2CO_3):

$$H_2O + CO_2 \leftrightarrow H_2CO_3$$

Carbonic acid is a weak acid that can lose a hydrogen ion to form bicarbonate (HCO_3^-):

$$H_2CO_3 \leftrightarrow H^+ + HCO_3^-$$

or further shed the remaining hydrogen ion to form carbonate (CO_3^{2-}):

$$HCO_3^- \leftrightarrow H^+ + CO_3^{2-}$$

Thus, carbon can occur simultaneously in several forms: CO_2 (dissolved CO_2 and carbonic acid), HCO_3^-, and CO_3^{2-}. Increasing atmospheric CO_2 drives more CO_2 into the ocean, lowering the pH (making the ocean more acidic) and changing the relative proportions of the three forms of carbon (Figure 5). In tropical water of normal salinity (35 Practical Salinity Units, or PSU), average temperature (25°C; 77°F), and preindustrial levels of CO_2 (280 ppmv), about 85 percent of the dissolved CO_2 in seawater exists as bicarbonate, and the remaining 15 percent exists as carbonate ion. Doubling the CO_2 concentration in seawater without changing the other conditions would increase bicarbonate ion concentration to 90 percent and decrease carbonate ion concentration to 10 percent. Calcifying organisms combine calcium and carbonate ions to build their skeletons ($Ca^{2+} + CO_3^{2-} \leftrightarrow CaCO_3$), so a reduction in carbonate ion concentration slows the calcification process.

Figure 5 illustrates how increases in atmospheric CO_2 levels change ocean pH and the relative abundance of the different inorganic carbon forms in water. The pH of shallow ocean waters was about 8.15 in the preindustrial period, when atmospheric CO_2 levels were 280 ppmv. Today, pH is about 8.05. This relatively small change in pH has caused a large shift in the balance of bicarbonate and carbonate ions.
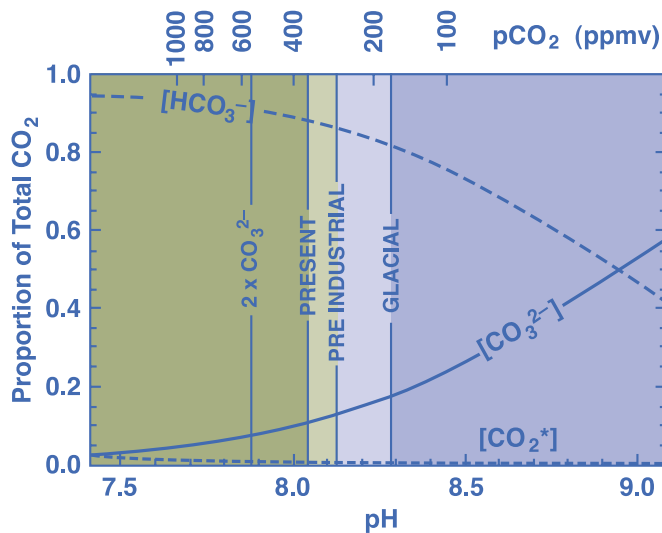
C. Reduced Calcification Potential

The oceans currently absorb about a third of the anthropogenic CO_2 inputs to the atmosphere, resulting in significant changes in seawater chemistry that affect the ability of reef organisms to calcify (Houghton et al., 2001). Photosynthesis and respiration by marine organisms also affect seawater CO_2 concentration, but the overwhelming driver of CO_2 concentrations in shallow seawater is the concentration of CO_2 in the overlying atmosphere. Changes in the CO_2 concentration of seawater through well-known processes of air-sea gas exchange alter the pH (an index of acidity) and the concentrations of carbonate and bicarbonate ions (Box 7; previous page). Surface seawater chemistry adjusts to changes in atmospheric CO_2 concentrations on a time scale of about a year. Projected increases in atmospheric CO_2 may drive a reduction in ocean pH to levels not seen for millions of years (Caldeira and Wickett, 2003).

Many marine organisms use calcium (Ca^{2+}) and carbonate (CO_3^{2-}) ions from seawater to secrete $CaCO_3$ skeletons. Reducing the concentration of either ion can affect the rate of skeletal deposition, but the carbonate ion is much less abundant than calcium, and appears to play a key role in coral calcification (Langdon, 2003). The carbonate ion concentration in surface water will decrease substantially in response to future atmospheric CO_2 increases (Box 7; Figure 5), reducing the calcification rates of some of the most important $CaCO_3$ producers. These include corals and calcareous algae on coral reefs and planktonic organisms such as coccolithophores (Riebesell et al., 2000) and foraminifera in the open ocean (Barker and Elderfield, 2002).

In laboratory experiments that simulate doubled atmospheric CO_2 conditions, coral calcification rates decrease by 11–37 percent, whereas calcareous algae appear to

Figure 5

The figure above depicts relative changes in carbonate ion species in response to changes in atmospheric CO_2 concentrations. Rising CO_2 levels cause a substantial reduction of the carbonate ion concentration (CO_3^{2-}), which affects the ability of organisms to build calcium carbonate skeletons. Note: pCO_2 refers to the partial pressure of CO_2 in the atmosphere, measured in parts per million by volume (ppmv).

show a stronger reduction of 16–44 percent (reviews by Gattuso et al., 1999 and Langdon, 2003, plus recent data of Marubini et al., 2003). Calcification of coral reef communities reflects whether the community is dominated by corals or calcareous algae: the Biosphere2 coral reef mesocosm, which is dominated by calcareous algae, showed a 40 percent reduction (Langdon et al., 2000), while coral-dominated mesocosms showed a 14–21 percent reduction in their calcification rates (Leclercq et al., 2000, 2002).

Calcification rates of corals also depend on other factors such as temperature. Kleypas et al. (1999a) estimated an average decline of reef calcification rates of 6–14 percent as atmospheric CO_2 concentration increased from preindustrial levels (280 ppmv) to present-day values (370 ppmv). However, studies have shown that calcification rates of large heads of the massive coral *Porites* increased rather than decreased over the latter half of the 20th century (Lough and Barnes, 1997, 2000; Bessat and Buigues, 2001). Temperature and calcification rates are correlated, and these corals have so far responded more to increases in water temperature (growing faster through increased metabolism and the increased photosynthetic rates of their zooxanthellae) than to decreases in carbonate ion concentration. In order to boost calcification, however, the temperature increase must remain below the corals' upper thermal limit.

A lowered calcification rate means that calcifying organisms extend their skeletons more slowly and/or form skeletons of lower density. Lower extension rates reduce the ability of corals to compete for space on a reef. Reduced skeletal density means less resistance to breakage (analogous to osteoporosis in humans) and greater susceptibility to both physical breakdown and bioerosion.

Reef-building occurs where calcium carbonate precipitation exceeds its removal. The structural components of reefs (skeletons of corals and algae) are glued together and made more resistant to physical breakdown by calcium carbonate cements that precipitate within the reef framework, and by the overgrowth of thin layers of calcareous algae. A reduction in $CaCO_3$ precipitation by whatever means (mortality of reef organisms, lowered calcification rates, or lowered cementation rates) reduces a reef's ability to grow and to withstand erosion (Kleypas et al., 2001). Some slow-growing or weakly cemented reefs may stop accumulating or shrink as carbonate deposition declines and/or erosion increases. Such effects have been observed in the Galápagos and elsewhere (Eakin, 1996; Reaka-Kudla et al., 1996).

Future changes in seawater chemistry will not only lead to decreases in calcification rates, but also to increases in $CaCO_3$ dissolution. Field experiments (Halley and Yates, 2000) indicate that the dissolution rate could equal the calcification rate once atmospheric CO_2 concentrations reach double the preindustrial levels. This points to a slow-down or reversal of reef-building and the potential loss of reef structures in the future.

D. Sea Level

The predicted rise of sea level due to the combined effects of thermal expansion of ocean water and the addition of water from melting icecaps and glaciers is between 0.1 and 0.9 meter (4-36 inches) by the end of this century (Houghton et al., 2001). Sea level has remained fairly stable for the last few thousand years, and many reefs have grown to the point where they are sea-level-limited, with restricted water circulation and little or no potential for upward growth. A modest sea-level rise would therefore be beneficial to such reefs. Although sea-level rise might "drown" reefs that are near their lower depth limit by decreasing available light, the projected rate and magnitude of sea-level rise are well within the ability of most reefs to keep up (Smith and Buddemeier, 1992). A more likely source of stress from sea-level rise would be sedimentation due to increased erosion of shorelines.

E. El Niño-Southern Oscillation (ENSO)

Mass bleaching of corals in the past two decades has been clearly linked to El Niño events (Hoegh-Guldberg, 1999; Glynn, 2000). For example, widespread bleaching events occurred during the El Niños of 1982-83, 1987-88, and 1997-98. During a typical El Niño event, regions of unusually warm water develop throughout the Pacific and Indian Oceans. When these warm water anomalies coincide with seasonal maximum water temperatures, coral bleaching is very likely. Mean sea level decreases in the western Pacific during an El Niño event, which can expose shallow reefs, and lead to mass mortalities (Eakin and Glynn, 1996; Eakin, 2001). Coral bleaching has also occurred during the cold phase of ENSO (La Niña) in regions that tend to have warmer-than-normal SSTs (e.g., South Pacific Convergence Zone; New Britain during 1998-99).

El Niño events have increased in frequency, severity, and duration since the 1970s (Stahle et al., 1998; Mann et al., 2000; Rayner et al., 2000), but longer-term records do not support a link to global warming (Cobb et al., 2003). Most global climate models do not predict significant changes in El Niño through the present century, although they do suggest an evolution toward a more "El Niño-like" state (Houghton et al., 2001). Nonetheless, the severity of bleaching events during El Niño years of the last two decades presents a "worst case scenario" in predicting the future of coral reef ecosystems, particularly when added to a background of warming sea-surface temperatures.

F. Ocean Circulation Changes

Circulation, from local (wind-driven upwelling) to global (thermohaline) scales, is likely to change with global climate. Virtually all coral reefs at high latitudes occur where boundary currents deliver warm waters from tropical regions (e.g., Bermuda near the Gulf Stream, Lord Howe Island in the East Australia Current, and the Ryukyus of Japan in the Kuroshio Current). Changes in the path or strength of these currents would impose different temperature regimes on these reefs. There has been concern that ocean thermohaline circulation (THC) will shut down in the future due to changes in ocean temperature and freshwater runoff (Manabe and Stouffer, 1993). Recent modeling predicts a 0–40 percent slowing of THC within this century, but most models do not predict a complete shutdown (Gent, 2001). A slowing of THC would lead to significant changes in oceanic circulation and upwelling patterns that could potentially affect coral reef ecosystems (Vellinga and Wood, 2002), but how THC will be affected by global climate change remains uncertain (Broecker, 2003).

G. Precipitation and Storm Patterns

Tropical precipitation has increased over the past century by 0.2-0.3 percent per decade in the $10^{\circ}S$-$10^{\circ}N$ region, and the frequency of intense rainfall events is "very likely" (90-99 percent chance) to increase over most areas (Houghton et al., 2001). Increases in precipitation can lower salinity and increase sediment discharge and deposition near river mouths, sometimes leading to mass mortalities on nearby coral reefs (van Woesik et al., 1991; Coles and Jokiel, 1992; Wolanski et al., 2003). The frequency and intensity of droughts are also expected to increase, which may cause changes in vegetation cover and land use that lead to erosion and sediment stress when rains return.

Tropical cyclones (including hurricanes and typhoons) are a fact of life in many tropical regions, and although they may limit reef development in a few instances (Macintyre and Adey, 1989), healthy coral reefs tend to recover from the infrequent damage caused by cyclones. Comprehensive observations of cyclone activity are limited to the last five or six decades, and these show few trends in cyclone frequency or intensity (Henderson-Sellers et al., 1998). Hurricane models and thermodynamic calculations indicate that the maximum potential intensity (MPI, or the theoretical limit of cyclone strength) of cyclones could increase 10-20 percent and surface winds could increase by about 3-10 percent (Knutson and Tuleya, 2001). There is little evidence that the frequency of cyclones or where they form is likely to change (Albritton et al., 2001).

IV. Synthesis and Discussion

The coral reef crisis is a global composite of various interactive problems and variable responses and cannot be understood, predicted, or mitigated on the basis of separate, individual categories of stresses. The effects of changes in predator/prey relationships, and especially coral disease, do not fit conveniently into either the climate change or human stress categories, and they therefore provide an opportunity for considering interactions and synergism. Outbreaks of disease or intense attacks upon corals by predators can occur naturally, but they can also result wholly or in part from climate change or human interventions that modify the natural balance of ecosystems. Recent outbreaks of disease and predation on reefs have been attributed to both human activities and climate change.

The following sections consider coral disease, predation, and synergistic stresses; compare conditions and responses in the Caribbean and the Indo-Pacific; and briefly discuss the potential for adaptation of the organisms to altered conditions.

A. Infectious Diseases

Disease outbreaks and consequent mortality among corals and other reef organisms have been a major cause of the recent increase in coral reef degradation (Epstein et al., 1998; Harvell et al., 1999; Bruckner, 2002a; Rosenberg and Ben-Haim, 2002). Although diseases and syndromes of corals and other reef organisms remain incompletely characterized (Richardson and Aronson, 2002), they are known to be caused by both bacterial and fungal agents. These diseases are commonly lethal, but they exhibit a wide range of rates of progression. Most appear to affect some species more than others, but few, if any, are species-specific.

Two specific outbreaks have radically altered the ecology of Caribbean coral reefs (Richardson and Aronson, 2002). One disease killed more than 97 percent of the black-spined sea urchin, *Diadema antillarum* (Lessios, 1988), some populations of which are now beginning to recover (Aronson and Precht, 2000; Miller et al., 2003). This sea urchin is an herbivore, and its removal contributed substantially to the transition from coral-dominated to seaweed-dominated surfaces on Caribbean reefs (see Box 3). Another disease, white band disease (WBD), has killed much of the elkhorn (*Acropora palmata*) and staghorn (*A. cervicornis*) coral throughout the Caribbean. These were dominant reef-building corals in the Caribbean for tens of thousands to hundreds of thousands of years (Jackson, 1992; Aronson and Precht, 1997; Aronson et al., 2002), but since 1972 WBD has helped reduce these species to candidacy for listing under the Endangered Species Act (Aronson and Precht, 2001a, 2001b; Bruckner, 2002b). Cores taken from the Belizean barrier reef show that *A. cervicornis* dominated this coral reef community continuously for at least 3,000 years, but was killed by WBD and replaced by another species after 1986 (Aronson and Precht, 1997; Aronson et al., 2002). WBD caused a similar, unprecedented change in community structure in the Bahamas (Greenstein et al., 1998).

Other bacterial diseases of Caribbean corals, including black-band disease, "plague," and "white pox," have caused significant coral mortality (Richardson, 1998; Richardson et al., 1998; Patterson et al., 2002). A disease caused by a fungus of terrestrial origin, *Aspergillus sydowii* (Geiser et al., 1998), has killed large numbers of sea fans and sea whips (Kim and Harvell, 2001).

B. Predation

Although coral diseases appear to be increasing in the Indo-Pacific region (Richardson and Aronson, 2002), a more significant biological stress in parts of the western Pacific has been outbreaks of the crown-of-thorns starfish, an intense coral predator (Carpenter, 1997). These outbreaks may be natural events in the crown-of-thorns starfish *(Acanthaster planci)* population cycle, perhaps associated with river floods in wet years, but it has been argued that overfishing of starfish predators or elevated nutrients in freshwater runoff have aided the survival of different life stages of the animal. Like bleaching, *Acanthaster* outbreaks are acute stresses on reefs and probably result from a combination of human and natural factors. Mortality and recovery rates vary among coral species, resulting in shifts in community structure.

C. Connections with Global Climate Change and Human Activity

Multiple, concurrent chronic stresses may interact to weaken the resistance of corals and other reef organisms to agents that they might otherwise withstand. This subtle synergy is nearly impossible to demonstrate conclusively, but it is an explanation for the apparent downward spiral of coral reef ecosystems that seems to involve many causes and agents.

Climatic warming can increase the virulence of pathogens, since optimal water temperatures for those infectious agents for which data are available are at least 1°C (2°F) higher than the optima of their coral hosts (Harvell et al., 2002). Recent increases in the frequency and virulence of disease outbreaks on coral reefs are consistent with this prediction, suggesting that the trend of increasing disease will continue and strengthen as global temperatures increase. Elevated temperatures thus can enhance disease effects by both strengthening the pathogen and weakening the host, and can inhibit recovery by suppressing reproduction (see section III.A). This provides a strong example of potential synergy—and of the difficulty in diagnosing it conclusively.

Two other possible climatic connections to increased coral disease have been proposed. Dust transported from Africa to the Caribbean is a possible source of pathogens, nutrients, and contaminants (Shinn et al., 2000; Garrison et al., 2003). Also, land-derived flood plumes from major storms transport materials from the Central American mainland to reefs that are normally considered remote from such influences (Andréfouët et al., 2002). Although dust transport and storms are not new phenomena, they now may be acting as vectors for a greater variety of contaminants.

Human actions can also spread disease to coral reefs. Increasing sediment and waste input to many coastal areas enhances the potential for introducing pathogens to coral reefs (the *Aspergillus sydowii* fungus, for example, is of terrestrial origin), and the alteration of nutrient and salinity regimes of coastal waters by human activity may facilitate the propagation of pathogens (Bruno et al., 2003). Human involvement is suspected in the spread of the pathogen that killed Caribbean *Diadema;* the disease began in Panama, suggesting a possible link to shipping through the Panama Canal (i.e., dumping of ballast water by ships from the Pacific). Travel, shipping, and the importation of marine species for food or the aquarium trade all have the potential to cross-contaminate regions with pathogens not previously present.

D. Regional Comparison

The structure and biodiversity of coral reef communities vary from one region to another. The vast, environmentally and biologically diverse Indo-Pacific (Figure 1) contrasts markedly with the much more compact and less diverse Caribbean. The Indo-Pacific has approximately 750 species of reef-building corals with 170 in the genus *Acropora,* compared to about 50 coral species and only two bona fide species of *Acropora* in the Caribbean (Veron, 2000). The Caribbean has been recognized as a potentially vulnerable region for these and numerous other reasons (Smith and Buddemeier, 1992). This vulnerability has been manifested as a decline in live coral cover on many reefs in the Caribbean from an average of 50 percent 30 years ago to an average of 10 percent at present (Gardner et al., 2003).

Recovery times for reefs severely affected by storms and *Acanthaster* vary from a decade to centuries, depending on the frequency of disturbance and the growth and recruitment rates of the affected corals. Caribbean reefs generally recover more slowly than Indo-Pacific reefs (Sammarco, 1985; Kojis and Quinn, 1994; Done, 1999). This may reflect the lower success rate of sexual reproduction in Caribbean corals, or the small size of the Caribbean; where disturbances have regional-scale effects, availability of replacement larvae from neighboring reefs upstream will be limited (Connell, 1997; Roberts, 1997).

If Caribbean reef-building corals are unable to recover from their currently depressed state, reduced herbivory (Box 6), and possibly nutrient loading, will prolong the ability of seaweeds to monopolize space. Under such circumstances, bioerosion—the breakdown of reef framework by limestone-consuming sponges, clams, and other organisms—and dissolution will exceed the buildup of reef mass. Vertical and lateral reef growth has probably already slowed or possibly changed to net shrinkage (Lewis, 2002), resulting in a reduction in the extent and variety of reef community habitats.

In the Indo-Pacific, the reefs of Southeast Asia (Indonesia, the Philippines, and surrounding areas) have been degraded by pollution, sediment-laden runoff from deforested land, destructive fishing practices, including explosives and cyanide, and other human impacts (Burke et al., 2002). As in the Caribbean, the added effects of climate change compound these local stresses. However, the Southeast Asian reefs have several characteristics more favorable for recovery: high levels of biodiversity (Figure 1), a pattern of large-scale throughflow of Pacific Ocean water, and neighboring reef systems that can supply coral larvae in close proximity.

Reefs elsewhere in the Indo-Pacific have generally sustained less intense local and regional damage (e.g., Connell, 1997; Wilkinson, 2000), and climate change is more likely to be the primary source of stresses affecting these. By contrast, the Caribbean can probably be expected to continue on the course already started: climate change will reinforce a broad spectrum of stresses resulting in shifts and declines not attributable to any single cause (Knowlton, 2001).

E. Adaptation

The environmental adaptability of the symbiotic corals is well-documented over time scales ranging from weeks to tens of thousands of years (Brown, 1997b; Buddemeier and Lasker, 1999; Coles and Brown, 2003). Populations and pigment concentrations of symbiotic algae within the coral tissues adjust to accommodate a wide range of light levels. Corals and reef communities in areas such as the Arabian Gulf tolerate salinity and temperature conditions in excess of any average near-term climate change predictions, conditions that would be lethal if imposed rapidly on the same species in more equable environments (Kleypas et al., 1999b). The pressing question is not, "can corals adapt?" but rather, "how fast and to what extent can they adapt?" The recent increases in the frequency and intensity of conditions that contribute to bleaching (e.g., higher surface ocean temperatures, higher light intensities, and calmer water) may have outpaced the compensating mechanisms of many corals. In this discussion, we use the word adaptation in its more general sense, rather than in its strict evolutionary sense of genetic change in populations. We combine the more narrowly defined scientific usages of "adaptation," "acclimation," and "acclimatization" (Coles, 2001; Coles and Brown, 2003) to make the usage relevant to the processes that may operate on decadal time scales of climate change.

One example of a potential adaptive mechanism is known as the adaptive bleaching hypothesis (ABH; Buddemeier and Fautin, 1993). Corals may host different types of zooxanthellae, either sequentially or at the same time, and different coral-algal combinations have different environmental tolerances (Baker, in press). Bleaching may result in the loss of those ill-suited to the applied stress, providing an opportunity for other, less vulnerable zooxanthellae to dominate in individual hosts and/or the coral community.

28

Over the past 5–10 years, evidence for the diversity of zooxanthellae and environmentally correlated coral-algal partnerships has expanded rapidly, and experiments have shown that the processes required for adaptation driven by bleaching occur in nature (Baker, 2001; Kinzie et al., 2001). Buddemeier et al. (in press) review the evidence and conclude that adaptive bleaching is real, but its operational significance will not be fully known until we have a better understanding of the detailed mechanisms and of the functional taxonomy of the zooxanthellae (Coles and Brown, 2003).

Field data indicate that coral bleaching on some eastern Pacific reefs was much worse during the 1982-83 El Niño than in 1997-98, although temperature extremes during the two events were similar (Glynn et al., 2001; Guzmán and Cortés, 2001; Podestá and Glynn, 2001). The difference in responses to these two comparable events offers some support for the idea that corals or communities can adapt to higher temperatures over decades, either through adaptive bleaching (Baker, 2003) or through evolutionary selection for more heat/irradiance-tolerant corals that survive bleaching events (Glynn et al., 2001).

V. Resources at Risk

A. Socioeconomic Impacts

Coral reefs benefit human society in many ways, but placing an economic value on the goods and services provided by reefs is difficult. While estimating direct economic benefits from fishing and tourism is relatively straightforward, estimating values of services such as shoreline protection, biodiversity, and aesthetic value is not (e.g., Costanza et al., 1997), and these services are often omitted from reef valuations. Two recently completed socioeconomic studies of U.S. reef areas differed in their accounting: a study of reefs of southeast Florida assessed spending and incomes related to reef use, while a study of Hawaiian reefs focused on economic benefits from fisheries, the aquarium trade, tourism, and property values. The reef-related economic contributions to four Florida counties (Palm Beach, Broward, Miami-Dade, and Monroe) totaled US$4.3 billion in sales and $2 billion in annual income (Johns et al., 2001). Hawaiian reefs produced an estimated total annual economic benefit of US$363 million (Cesar et al., 2002). Cesar et al. (2003) estimated the global net economic benefit from reefs to be about US$30 billion/year.

The worldwide coral bleaching events of 1997–98 stimulated a number of socioeconomic evaluations of coral reefs in affected regions (Schuttenberg and Obura, 2001). For example, in the Maldives, coral bleaching led to an estimated loss in 1998–99 tourism-related revenues of US$0.5–3.0 million (Westmacott et al., 2001). Palau (an island in western Micronesia), where many reefs suffered at least 50 percent coral mortality in the 1997–98 bleaching event, experienced a 5–10 percent drop in tourism in the years following the event (Graham et al., 2001).

Nearly 40 percent of the people on Earth live within 100 km (60 mi) of the coastline, and many local and regional economies are based on goods and services provided by coastal ecosystems. Environmental degradation both on land (e.g., land clearing, agricultural and urban waste disposal) and in the ocean (unsustainable and destructive fishing practices) reduces the ability of reefs to support local economies. This economic loss can lead to even more destructive methods (e.g., blast fishing, cyanide

fishing) to extract increasingly scarce resources from the reef and adjacent environments (Cesar et al., 2003), just as the pressures of climate change may cause even more unsustainable land use. In turn, decreased socioeconomic value of the reef reduces the standard of living of the society that depends on it. Similarly, unmanaged increases in scuba diving and other tourist-related activities on reefs (including coastal development to support tourism) can lead to degradation of the very environment that attracts the tourists.

B. Biological and Ecological Impacts

Coral reefs, which support more biodiversity than any other marine ecosystem, also alter water energy and circulation in many near-shore environments. This shapes other habitats and protects them from wave impact and coastal erosion. Mangrove systems, for example, often develop in quiet near-shore environments protected by reefs and are highly productive nurseries for many important marine species. Loss of reefs as both biological and structural entities would impoverish the marine biota and potentially reduce the large-scale resilience of tropical and subtropical marine ecosystems.

C. Protection and Conservation

Growing concerns with human impacts on oceanic ecosystems in general have focused attention on the use of marine protected areas (MPAs) as potentially important practical management tools (Lubchenco et al., 2003). MPAs can provide refuges for living organisms and serve as sources of larvae for replenishment of harvested areas outside of the reserve. Such reserves minimize local human impacts and, in the case of coral reefs, there is growing attention to the concept of siting reserves in locations where the stresses associated with climate change (especially thermal bleaching) are likely to be less severe (West and Salm, 2003). Successful implementation of MPAs will require conservation efforts across larger spatial and temporal scales that match the biogeographic scales of species distributions and life-histories (Hughes et al., 2003), and this will require design and cooperation at the international level (Wilkinson, 2002).

VI. Summary and Conclusions

Global climate change poses a broad range of challenges, both acute and chronic, to coral reef ecosystems, particularly when climate change is integrated with the more localized nonclimate stresses coral reefs are currently experiencing. Table 2 summarizes the stress factors in terms of origin (locally human-induced or global climate change), spatial scale (global, regional, or local), and whether they are predominantly acute or chronic. Most (but not all) of the global factors are of climatic origin, but many stresses have manifestations at a variety of spatial scales. We have emphasized the ways in which the various types of stresses interact, as well as the geographic and temporal diversity of reefs, reef organisms, reef habitats, and environments. Future changes in coral reef condition will reflect this diversity of stresses, present conditions, and biota, but will almost certainly be in the direction of further loss and degradation.

Drawing on the information assembled, we offer the following major conclusions:

1) Climate and localized, nonclimate stresses interact, often synergistically, to affect the health and sustainability of coral reef ecosystems. Stresses associated with climate change, such as high-temperature episodes that promote coral bleaching, reduced calcification, and changes in ocean and atmospheric circulation, present one set of challenges to coral reefs. However, these stresses may exacerbate other stresses not directly related to climate, such as disease, predation, and the cumulative effects of other nonclimate stresses. Thus, it is difficult to attempt to separate the effects of global climate and local nonclimate influences when considering reef condition or vulnerability.

2) Coral reef alteration, degradation, and loss will continue for the foreseeable future, especially in those areas already showing evidence of systemic stress. As we enter an unprecedented climatic state, recent geological and biological history gives us little on which to base predictions regarding the future of coral reef ecosystems. Key uncertainties include the extent to which human activities will continue to alter the environment, how climate variability such as the frequency and intensity of El Niño-Southern Oscillation (ENSO) events will change relative to global temperature, and the

biological and ecological responses of coral reef communities to unprecedented future conditions. However, there is no realistic doubt that continued climate change will cause further degradation of coral reef communities, which will be even more devastating in combination with the continuing nonclimate stresses that will almost certainly increase in magnitude and frequency.

3) The effects of climate change on global coral reef ecosystems will vary from one region to another. Although climate change has the potential to yield some benefits for certain coral species in specific regions, such as the expansion of their geographic ranges to higher latitudes, most of the effects of climate change are stressful rather than beneficial. Reef systems that are at the intersection of global climatic and local human stresses will be the most vulnerable. Remote, deep, or well-protected reef communities are more likely to provide reserves and refuges for future generations of coral reef organisms and aesthetic and scientific resources for future generations of humans.

4) While the net effects of climate change on coral reefs will be negative, coral reef organisms and communities are not necessarily doomed to total extinction. The diversity of existing coral species, the acknowledged adaptation potential of reef organisms, the spatial and temporal variations in climate change, and the potential for human management and protection of coral reef ecosystems all provide possibilities for survival. Nevertheless, coral reefs of the future will be fewer and probably very different in community composition than those that presently exist, and these changes will cause further ecological and economic losses.

5) Research into adaptation and recovery mechanisms and enhanced monitoring of coral reef environments will permit us to learn from and influence the course of events rather than simply observe the decline. Most local (and some regional) nonclimate stresses have the potential to be mitigated and managed more readily than global climate change itself. A significant step would be a widely distributed international network of coral reef refuges and marine protected areas, selected on the basis of biological and environmental diversity, connectivity, potential threats, and enforcement feasibility. Yet, even with such efforts, recent degradation of coral ecosystems combined with future climate change will still pose a significant challenge to the global sustainability of coral reefs.

References

Albritton, D.L., L.G. Meira Filho, U. Cubasch, X. Dai, Y. Ding, D.J. Griggs, B. Hewitson, J.T. Houghton, I. Isaksen, T. Karl, M. McFarland, V.P. Meleshko, J.F.B. Mitchell, M. Noguer, B.S. Nyenzi, M. Oppenheimer, J.E. Penner, S. Pollonais, T. Stocker and K.E. Trenberth. 2001. *Technical Summary of the IPCC Working Group I Report.* Cambridge University Press, Cambridge, UK, 83 pp.

Andréfouët, S., P.J. Mumby, M. McField, C. Hu, and E. Muller-Karger. 2002. Revisiting coral reef connectivity. *Coral Reefs* 21: 43-48.

Aronson, R.B., and W.F. Precht. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23: 326-346.

Aronson, R.B., I.G. Macintyre, W.F. Precht, T.J.T. Murdoch, and C.M. Wapnick. 2002. The expanding scale of species turnover events on coral reefs in Belize. *Ecology* 72: 233-249.

Aronson, R.B., and W.F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology and Oceanography* 45: 251-255.

Aronson, R.B., and W.F. Precht. 2001a. Evolutionary paleoecology of Caribbean coral reefs. In: *Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change,* edited by W.D. Allmon and D.J. Bottjer. Columbia University Press, New York, NY, pp. 171-233.

Aronson, R.B., and W.F. Precht. 2001b. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460: 25-38.

Baker, A.C. 2001. Reef corals bleach to survive change. *Nature* 411: 765-766.

Baker, A.C. 2003. Flexibility and specificity in coral-algal symbiosis: Diversity, ecology and biogeography of *Symbiodinium. Annual Review of Ecology and Systematics* 34: 661-689.

Baker A.C. In press. Diversity, distribution and ecology of *Symbiodinium* on coral reefs and its relationship to bleaching resistance and resilience. In: *Coral Health and Disease,* edited by E. Rosenberg. Springer-Verlag, Berlin.

Barker, S., and H. Elderfield. 2002. Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO_2. *Science* 297: 833-835.

Bessat, F., and A.D. Buigues. 2001. Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): A response of ocean-atmosphere variability from south central Pacific. *Paleogeography, Paleoclimatology, Paleoecology* 175: 381-392.

Broecker, W.S. 2003. Does the trigger for abrupt climate change reside in the ocean or the atmosphere? *Science* 300: 1519-1522.

Brown, B.E. 1997a. Coral bleaching: Causes and consequences. *Coral Reefs* 16: S129-S138.

Brown, B.E. 1997b. Adaptations of reef corals to physical environmental stress. *Advances in Marine Biology* 31: 221-299.

Coral reefs & Global climate change

Bruckner, A. 2002a. *Priorities for Effective Management of Coral Diseases.* NOAA Technical Memorandum NMFS-OPR-22, Silver Spring, MD, 54 pp.

Bruckner, A. 2002b. *Proceedings of the Caribbean Acropora Workshop: Potential Application of the U.S. Endangered Species Act as a Conservation Strategy.* NOAA Technical Memorandum NMFS-OPR-24, Silver Spring, MD, 184 pp.

Bruno, J.F., L.E. Petes, C.D. Harvell, and A. Hettinger. 2003. Nutrient enrichment can increase the severity of coral diseases, *Ecology Letters* 6: 1056-1061.

Bryant, D., L. Burke, J. McManus, and M. Spalding. 1998. *Reefs at Risk: A Map-Based Indicator of Threats to the World's Coral Reefs.* Washington, DC: World Resources Institute, 56 pp.

Buddemeier, R.W., A.C. Baker, D.G. Fautin, and J.R. Jacobs. In press. The adaptive hypothesis of bleaching. In: *Coral Health and Disease,* edited by E. Rosenberg. Springer-Verlag, Berlin.

Buddemeier, R.W., and D.G. Fautin. 1993. Coral bleaching as an adaptive mechanism – A testable hypothesis. *BioScience* 43: 320-326.

Buddemeier, R.W., and H.R. Lasker (eds). 1999. Coral reefs and environmental change – Adaptation, acclimation, or extinction. *American Zoologist* 39, Number 1, 183 pp.

Burke, L., E. Selig, and M. Spalding. 2002. *Reefs at Risk in Southeast Asia.* World Resources Institute, Washington, DC, 72 pp.

Cabanes, C., A. Cazenave, and C. Le Provost. 2001. Sea level rise during the past 40 years determined from satellite and in situ observations. *Science* 294: 840-842.

Caldeira, K., and M.E. Wickett. 2003. Anthropogenic carbon and ocean pH. *Nature* 425: 365.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56: 345-363.

Carpenter, R.C. 1997. Invertebrate predators and grazers. In: *Life and Death of Coral Reefs,* edited by C. Birkeland. Chapman and Hall, New York, NY, pp. 198-229.

Cesar, H., L. Burke, and L. Pet-Soede. 2003. *The Economics of Worldwide Coral Reef Degradation.* Cesar Environmental Economics Consulting (CEEC), 6828GH Arnhem, The Netherlands, 23 pp.

Cesar, H., P. van Beukering, S. Pintz, and J. Dierking. 2002. *Economic Valuation of the Coral Reefs of Hawaii.* Final report to National Oceanic and Atmospheric Administration Coastal Ocean Program. Cesar Environmental Economics Consulting, Arnhem, The Netherlands.

Cobb, K.M., C.D. Charles, H. Cheng, and R.L. Edwards. 2003. El Niño/Southern Oscillation and tropical Pacific climate during the last millennium. *Nature* 424: 271-276.

Coles, S.L. 2001. Coral bleaching: What do we know and what can we do? In: *Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design,* May 29-31, 2001, Honolulu, HI, pp. 25-35.

Coles, S.L., and Brown, B.E. 2003. Coral bleaching – Capacity for acclimatization and adaptation. *Advances in Marine Biology* 46:183-223.

Coles, S.L. and L.G. Eldredge. 2002. Nonindigenous species introductions on coral reefs: A need for information. *Pacific Science* 56: 191-209.

Coles, S.L., and P.L. Jokiel. 1992. Effects of salinity on coral reefs. In: *Pollution in Tropical Aquatic Systems,* edited by D.W. Connell and D.W. Hawker. CRC Press, Boca Raton, Ann Arbor, pp. 147-166.

Connell, J.H. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16: S101-S113.

Cortés, J. 1994. A reef under siltation stress: A decade of degradation. In: *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993,* edited by R.N. Ginsburg. RSMAS, University of Miami, Miami, FL, pp. 240-246.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystems services and natural capital. *Nature* 387: 253-260.

Done, T.J. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist* 39: 66-79.

Eakin, C.M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15: 109-119.

Eakin, C.M. 2001. A tale of two ENSO events: Carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science* 69: 171-186.

Eakin, C.M., and P.W. Glynn. 1996. Low tidal exposures and reef mortalities in the eastern Pacific. *Coral Reefs* 15: 120.

Epstein, P.R., K. Sherman, E. Spanger-Seigfried, A. Langston, S. Prasad, and B. McKay. 1998. *Marine Ecosystems: Emerging Diseases as Indicators of Change.* Health Ecological and Economic Dimensions (HEED), NOAA Global Change Program, 85 pp.

Fitt, W.K., B.E. Brown, M.E. Warner, and R.P. Dunne. 2001. Coral bleaching: Interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20: 51-65.

Fitt, W.K., F.K. McFarland, M.E. Warner, and G.C. Chilcoat. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnology and Oceanography* 45: 677-685.

Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant, and A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301: 958-960.

Garrison, V.H., E.A. Shinn, W.T. Foreman, D.W. Griffin, C.W. Holmes, C.A. Kellogg, M.S. Majewski, L.L. Richardson, K.B. Ritchie, and G.W. Smith. 2003. African and Asian dust: From desert soils to coral reefs. *Bioscience* 53: 469-480.

Gattuso, J.-P., D. Allemand, and M. Frankignoulle. 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *American Zoologist* 39: 160-183.

Geiser, D.M., J.W. Taylor, K.B. Kitchie, and G.W. Smith. 1998. Cause of sea fan death in the West Indies. *Nature* 394: 137-138.

Gent, P.R. 2001. Will the North Atlantic Ocean thermohaline circulation weaken during the 21st century? *Geophysical Research Letters* 28: 1023-1026.

Glynn, P.W. 1993. Coral-reef bleaching – Ecological perspectives. *Coral Reefs* 12: 1-17.

Glynn, P.W. 2000. El Niño-Southern Oscillation mass mortalities of reef corals: a model of high temperature marine extinctions? In: *Carbonate Platform Systems: Components and Interactions,* edited by E. Insalaco, P.W. Skelton, and T.J. Palmer. Geological Society of London, Special Publications 178: 117-133.

Glynn, P.W, J.L. Maté, A.C. Baker, and M.O. Calderón. 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982-1983 event. *Bulletin of Marine Science* 69: 79-109.

Graham T., N. Idechong, and K. Sherwood. 2001. The value of dive-tourism and the impacts of coral bleaching on diving in Palau, In: *Coral Bleaching; Causes, Consequences and Response,* edited by H.Z. Schutenberg. Coastal Management Report No. 2230, Coastal Resources Center, Univ. Rhode Island, pp. 59-71.

Greenstein, B.J., H.A. Curran, and J.M. Pandolfi. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the Western Atlantic and Caribbean province: A Pleistocene perspective. *Coral Reefs* 17: 249-261.

Guinotte, J.M.. R.W. Buddemeier, and J.A. Kleypas. 2003. Future coral reef habitat marginality: Temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* 22: 551-558.

Guzmán, H.M., and J. Cortés. 2001. Changes in reef community structure after fifteen years of natural disturbances in the eastern Pacific (Costa Rica). *Bulletin of Marine Science* 69: 133-149.

Halley, R.B., and K.K. Yates. 2000. Will reef sediments buffer corals from increased global CO_2? In: *Ninth International Coral Reef Symposium.* Bali, Indonesia, 23-27 October 2000, Abstract.

Harriott, V.J., and S.A. Banks. 2002. Latitudinal variation in coral communities in eastern Australia: A qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21: 83-94.

Harvell, C.D., K. Kim, J.M. Burkholder, R.R. Colwell, P.R. Epstein, D.J. Grimes, E.E. Hofmann, E.K. Lipp, A.D.M.E. Osterhaus, R.M. Overstreet, J.W. Porter, G.W. Smith, and G.R. Vastra. 1999. Emerging marine diseases–climate links and anthropogenic factors. *Science* 285: 1505-1510.

Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfield, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158-2162.

Henderson-Sellers, A., H. Ahang, G. Berz, K. Emanuel, W. Gray, C. Landsea, G. Holland, J. Lighthill, S.-L. Shieh, P. Webster, and K. McGuffie. 1998. Tropical cyclones and global climate change: A post-IPCC assessment. *Bulletin of the American Meteorological Society* 79: 19-38.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50: 839-866.

Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, and D. Xiaosu (eds.) 2001. *IPCC Third Assessment Report: Climate Change 2001: The Scientific Basis.* Cambridge University Press, Cambridge, UK, 944 pp. [http://www.grida.no/climate/ipcc_tar/wg1/index.htm] [Also see: Summary for Policymakers and Technical Summary, 98 pp.]

Hughes, T.P. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Hughes, T.P., A.H. Baird, D.R. Bellwood, M. Card, S.R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J.B.C. Jackson, J. Kleypas, P. Marshall, M. Nyström, S.R. Palumbi, J.M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts and the resilience of coral reefs. *Science* 301: 929-933.

Hughes, T.P., and J.H. Connell. 1999. Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* 22: 932-940.

Jackson, J.B.C. 1992. Pleistocene perspectives of coral reef community structure. *American Zoologist* 32: 719-731.

Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16: S23-S32.

Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, C.B. Lange, H.S. Lenihan, J.S. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-638.

Jickells, T.D. 1998. Nutrient biogeochemistry of the coastal zone. *Science* 281: 217-222.

Johns, G.M., V.R. Leeworthy, F.W. Bell, and M.A. Bonn. 2001. *Socioeconomic Study of Reefs in Southeast Florida.* Final Report submitted to Broward County, Palm Beach County, Miami-Dade County, Monroe County, Florida Fish and Wildlife Conservation Commission, and National Oceanic and Atmospheric Administration, as revised April 18, 2003.

Jokiel, P.L., C.L. Hunter, S. Taguchi, and L. Watarai. 1993. Ecological impact of a fresh-water "reef kill" in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs* 12: 177-184.

Kim, K., and C.D. Harvell. 2001. Aspergillosis of sea fan corals: Disease dynamics in the Florida Keys. In: *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook,* edited by J.W. Porter and K.G. Porter. CRC Press, Boca Raton, Florida, pp. 813-824.

Kinsey, D.W. 1988. Coral reef system response to some natural and anthropogenic stresses. *Galaxea* 7: 113-128.

Kinzie, R.A. III, M. Takayama, S.R. Santos, and M.A. Coffroth. 2001. The adaptive bleaching hypothesis: Experimental tests of critical assumptions. *Biological Bulletin* 200: 51-58.

Kleypas, J.A., R.W. Buddemeier, D. Archer, J.-P. Gattuso, C. Langdon, and B.N. Opdyke. 1999a. Geochemical consequences of increased atmospheric CO_2 on coral reefs. *Science* 284: 118-120.

Kleypas, J.A., R.W. Buddemeier, and J.-P. Gattuso. 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences* 90: 426-437.

Kleypas, J.A., J.W. McManus, and L.A.B. Meñez. 1999b. Environmental limits to coral reef development: Where do we draw the line? *American Zoologist* 39: 146-159.

Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences of the U.S.A.* 98: 5419-5425.

Knutson, T.R., and R.E. Tuleya. 2001. Impact of CO_2-induced warming on hurricane intensities as simulated in a hurricane model with ocean coupling. *Journal of Climate* 14: 2458-2468.

Kojis, B.L., and N.J. Quinn. 1994. Biological limits to Caribbean reef recovery: a comparison with western South Pacific reefs. In: *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993,* edited by R.N. Ginsburg. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, pp. 353-359.

Langdon, C. 2003. Review of experimental evidence for effects of CO_2 on calcification of reef builders. *Proceedings of the 9th International Coral Reef Symposium*. Bali, Indonesia, 23-27 October 2000, Vol. 2: 1091-1098.

Langdon, C., T. Takahashi, C. Sweeney, D. Chipman, J. Goddard, F. Marubini, H. Aceves, H. Barnett, and M.J. Atkinson. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* 14: 639-654.

Larcombe. P., and K.J. Woolfe. 1999. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* 18: 163-169.

Leclercq, N., J.-P. Gattuso, and J. Jaubert. 2000. CO_2 partial pressure controls the calcification rate of a coral community. *Global Change Biology* 6: 329-334.

Leclercq, N., J.-P. Gattuso, and J. Jaubert. 2002. Primary production, respiration, and calcification of a coral reef mesocosm under increased CO_2 partial pressure. *Limnology and Oceanography* 47: 558-564.

Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19: 371-393.

Levitus, S., J.I. Antonov, T.P. Boyer, and C. Stephens. 2000. Warming of the world ocean. *Science* 287: 2225-2229.

Levitus, S., J.I. Antonov, J. Wang, T.L. Delworth, K.W. Dixon, and A.J. Broccoli. 2001. Anthropogenic warming of Earth's climate system. *Science* 292:267-270.

Lewis, J.B. 2002. Evidence from aerial photography of structural loss of coral reefs at Barbados, West Indies. *Coral Reefs* 21: 49-56.

Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56: 183-200.

Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19: 392-399.

Littler, M.M, and D.S. Littler. 1997. Epizoic red alga allelopathic (?) to a Caribbean coral. *Coral Reefs* 16: 168-168.

Liu, G., A.E. Strong, and W. Skirving. 2003. Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos, Transactions, American Geophysical Union* 84: 137,141.

Lough, J.M. 2001. Unprecedented thermal stress to coral reefs? *Geophysical Research Letters* 27: 3901-3904.

Lough, J.M., and D.J. Barnes. 1997. Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability against which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology* 211: 29-67.

Lough, J.M., and D.J. Barnes. 2000. Environmental controls on growth of the massive coral *Porites. Journal of Experimental Marine Biology and Ecology* 245: 225-243.

Lubchenco, J., S.R. Palumbi, S.D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. *Ecological Applications* 13: S3-S7.

Macintyre, I., and W.G. Adey. 1989. Buck Island Bar, St. Croix – A reef that cannot catch up with sea level. *Atoll Research Bulletin* 336: 1-7.

Manabe, S., and R.J. Stouffer. 1993. Century-scale effects of increased atmospheric CO_2 on the ocean-atmospheric system. *Nature* 364: 215-218.,

Mann, M.E., R.S. Bradley, and M.K. Hughes. 2000. Long-term variability in the El Niño Southern Oscillation and associated teleconnections. In: *El Niño and the Southern Oscillation: Multiscale Variability and its Impacts on Natural Ecosystems and Society,* edited by H.F. Diaz and V. Markgraf. Cambridge University Press, Cambridge, UK, pp. 357-412.

Marubini, F., C. Ferrier-Pages, and J.-P. Cuif. 2003. Suppression of growth in scleractinian corals by decreasing ambient carbonate ion concentration: A cross-family comparison. *Proceedings of the Royal Society B-Biological Sciences* 270: 179-184.

McCarthy, J.J., O.F. Canziani, N.A. Leary, D.J. Dokken, and K.S. White (eds). 2001. Climate Change 2001: *Impacts, Adaptation, and Vulnerability, Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC).* Cambridge University Press, 1042 pp.

McClanahan, T.R. 2002. The near future of coral reefs. *Environmental Conservation* 20: 460-483.

McCulloch, M., S. Fallon, T. Wyndham, E. Hendy, J. Lough, and D. Barnes. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421: 727–730.

Meade, R.H., T.R.Yuzyk, and T.J. Day. 1990. Movement and storage of sediment in rivers of the United States and Canada, In: *Surface Water Hydrology, Geology of North America,* O-1, edited by M.G. Wolman and H.C. Riggs. Geological Society of America, Boulder, CO, pp. 255-280.

Mendes, J.M., and J.D. Woodley. 2002. Effect of the 1995-1996 bleaching event on polyp tissue depth, growth, reproduction and skeletal band formation in *Montastraea annularis. Marine Ecology – Progress Series* 235: 93-102.

Miller, R.J., A.J. Adams, N.B. Ogden, J.C. Ogden, and J.P. Ebersole. 2003. *Diadema antillarum* 17 years after mass mortality: Is recovery beginning on St. Croix? *Coral Reefs* 22: 181-187.

Moffat, A.S. 1998. Global nitrogen overload problem grows critical. *Science* 279: 988-989.

Omori, M., H. Fukami, H. Kobinata, and M. Hatta. 2001. Significant drop of fertilization of *Acropora* corals in 1999. An after-effect of heavy coral bleaching? *Limnology and Oceanography* 46: 704-706.

Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R.R. Warner, and J.B.C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301: 955-958.

Patterson, K.L., J.W. Porter, K.B. Ritchie, S.W. Polson, E. Mueller, E.C. Peters, D.L. Santavy, and G.W. Smith. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata. Proceedings of the National Academy of Sciences of the U.S.A.* 99: 8725-8730.

Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.-M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V.M. Kotlyakov, M. Legrand, V.Y. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman, and M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429-436.

Podestá, G.P., and P.W. Glynn. 2001. The 1997-98 El Niño event in Panama and Galápagos: An update of thermal stress indices relative to coral bleaching. *Bulletin of Marine Science* 69: 43-59.

Precht, W.F., and R.B. Aronson. 2003. Climate flickers and range shifts of corals. *Geological Society of America Abstracts with Programs* 35: 84.

Rayner, N.A., D.E. Parker, P. Frich, E.B. Horton, C.K. Folland, and L.V. Alexander. 2000. SST and sea-ice fields for ERA40. In: *Proceedings of the Second International WCRP Conference on Reanalyses.* Wokefield Park, Reading, UK, 23-27 August 1999. WCRP-109, WMO/TD-No. 985.

Reaka-Kudla, M.L., J.S. Feingold, and P.W. Glynn. 1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. *Coral Reefs* 15: 101-107.

Richardson, L.L. 1998. Coral diseases: what is really known? *Trends in Ecology and Evolution* 13: 438-443.

Richardson, L.L., and R.B. Aronson. 2002. Infectious diseases continue to degrade coral reefs. In: *Implications for coral reef management and policy: relevant findings from the 9th International Coral Reef Symposium,* edited by B. Best, R.S. Pomeroy, and C.M. Balboa. U.S. Agency for International Development, Washington, DC. pp. 30-32.

Richardson, L.L., W.M. Goldberg, K.G. Kuta, R.B. Aronson, G.W. Smith, K.B. Ritchie, J.C. Halas, J.S. Feingold, and S.L. Miller, 1998. Florida's mystery coral killer identified. *Nature* 392: 557-558.

Riebesell, U., I. Zondervan, B. Rost, P.D. Tortell, R.E. Zeebe, and F.M. Morel, 2000: Reduced calcification of marine phytoplankton in response to increased atmospheric CO_2. *Nature* 407: 364-367.

Riegl B., and G.M. Branch. 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology* 186: 259-275.

Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278: 1454-1457.

Rosenberg, E., and Y. Ben-Haim. 2002. Microbial diseases of corals and global warming. *Environmental Microbiology* 4: 318-326.

Ruiz, G.M., J.T. Carlton, E.D. Grosholz, and A.H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent and consequences. *American Zoologist* 31: 621-632.

Sammarco, P.W. 1985. The Great Barrier Reef vs. the Caribbean: Comparisons of grazers, coral recruitment patterns and reef recovery. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 4: 391-397.

Schuttenberg, H.Z., and Obura D. 2001. Ecological and socioeconomic impacts of coral bleaching: A strategic approach to management, policy and research responses. In: *Coral Bleaching; Causes, Consequences and Response,* edited by H.Z. Schutenberg. Coastal Management Report No. 2230, Coastal Resources Center, Univ. Rhode Island, pp. 1-11.

Shinn, E.A., G.W. Smith, J.M. Prospero, P. Betzer, M.L. Hayes, V. Garrison, and R.T. Barber. 2000. African dust and the demise of Caribbean coral reefs. *Geophysical Research Letters* 27: 3029-3032.

Smith, S.V., and R.W. Buddemeier. 1992. Global change and coral reef ecosytems. *Annual Reviews of Ecology and Systematics* 23: 89-118.

Smith, S.V., W.J. Kimmerer, E.A. Laws, R.E. Brock, and T.W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35: 279-402.

Stahle, D.W., M.K. Cleaveland, M.D. Therrell, D.A. Gay, R.D. D'Arrigo, P.J. Krusic, E.R. Cook, R.J. Allan, J.E. Cole, R.B. Dunbar, M.D. Moore, M.A. Stokes, B.T. Burns, J. Villanueva-Diaz, and L.G. Thompson. 1998. Experimental dendroclimatic reconstruction of the Southern Oscillation. *Bulletin of the American Meteorological Society* 79: 2137-2152.

Steffen, W., and P. Tyson (eds). 2001. *Global Change and the Earth System: A Planet Under Pressure.* Global Environmental Change Programme, International Geosphere-Biosphere Programme, IGBP Science Series No. 4, Stockholm, 32 pp.

Van Woesik, R. 1991. Immediate impact of the January 1991 floods on the coral assemblages of the Keppel Islands. Great Barrier Reef Marine Park Authority Research Publication No. 23, 30 pp.

Vellinga, M., and R.A. Wood. 2002. Global climatic impacts of a collapse of the Atlantic thermohaline circulation. *Climatic Change* 54: 251-267.

Veron, J.E.N. 1992. Environmental control of Holocene changes to the world's most northern hermatypic coral outcrop. *Pacific Science* 46: 405-425.

Veron, J.E.N. 1995. *Corals in Space and Time.* University of New South Wales Press, Sydney, 321 pp.

Veron, J.E.N. 2000. *Corals of the World.* Australian Institute of Marine Science, Townsville, Queensland, Australia (3 volumes).

Veron, J.E.N., and P.R. Minchin. 1992. Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. *Continental Shelf Research* 12: 835-857.

Vörösmarty, C.J., and D. Sahagian. 2000. Anthropogenic disturbance of the terrestrial water cycle. *BioScience* 50: 753-765.

West, J.M., and R.V. Salm. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. *Conservation Biology* 17: 956-967.

Westmacott, S., H. Cesar, L.P. Soede, and O. Lindén. 2001. Assessing the socioeconomic impacts of the coral bleaching event in the Indian Ocean, In: *Coral Bleaching; Causes, Consequences and Response,* edited by H.Z. Schutenberg. Coastal Management Report No. 2230, Coastal Resources Center, Univ. Rhode Island. pp. 31-39.

Wilkinson, C. (ed.) 2000. *Status of Coral Reefs of the World: 2000.* Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville, Queensland, Australia, 363 pp.

Wilkinson, C. (ed.) 2002. *Status of Coral Reefs of the World: 2002.* Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville, Queensland, Australia, 378 pp.

Williams, I.D., N.V.C. Polunin, and V.J. Hendrick. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222: 187-196.

Wolanski, E., R. Richmond, L. McCook, and H. Sweatman. 2003. Mud, marine snow, and coral reefs. *American Scientist* 91: 44-51.

notes

This report, which analyzes the current state of knowledge about the potential effects of climate change on U.S. and global coral reef ecosystems, is published by the Pew Center on Global Climate Change. The Pew Center was established with a grant from the Pew Charitable Trusts and has been charged with bringing a new cooperative approach to the debate on global climate change. The Pew Center continues to inform the debate by publishing reports in the areas of policy (domestic and international), economics, environment, and solutions.