

Global Loss of Coastal Habitats Rates, Causes and Consequences

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Offprint of Chapter

5. CONFRONTING THE GLOBAL DECLINE OF CORAL REEFS

by

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5.1. INTRODUCTION

HUMAN IMPACTS HAVE RESULTED in dramatic shifts in species composition in many marine and terrestrial ecosystems. These phase shifts are often long-lasting and difficult to reverse. Examples include the replacement of corals by sediment or algal blooms, changes caused by new diseases and invasions by exotic species, and the collapse of coastal and oceanic fisheries. Often these changes occur suddenly and emerge following a natural disturbance that is part of the ecosystem's normal dynamics. Instead of regenerating as they have done for millennia, many coral reefs have lost their capacity to recover from natural perturbations. A new approach to understanding the decline of ecosystems focuses on the concept of “resilience”—the extent to which ecosystems can absorb recurrent natural and human perturbations without switching suddenly or gradually into an alternative (usually degraded) state (Scheffer and Carpenter 2003). Anticipating and preventing unwanted phase shifts on coral reefs requires a better understanding of the processes that support or undermine resilience, and of the social and economic conditions that influence how people use and interact with reefs (Nyström, Folke, and Moberg 2000; Alcala and Russ 2006).

The world's coral reefs support the livelihoods of well over 250 million people, providing food and other resources and supporting a global tourism industry. Coral reefs also have enormous cultural, environmental, and aesthetic value. Yet the world's tropical reefs are in trouble. The Global Coral Reef Monitoring Network has produced summary reports from up to 97 countries in 17 regions, in 1998, 2000, 2002, 2004, and 2008. According to their most recent global assessment, an estimated 34% of the world's coral reefs have already been destroyed or are in imminent danger of collapse, with a further 20% assessed as being under threat of loss within 20-40 years (Wilkinson

◀ **Photo 5.1: Coral formation with individuals of the *Acropora* genus, Thailand.** Coral reefs support amazing diversity, including many species of hard and soft corals.

2008). Even for reefs that are isolated and relatively untouched, global warming and ocean acidification are growing concerns.

The principle human impacts on coral reefs are overfishing, declining water quality (from coastal development and land clearing), and climate change. Importantly, these are not separate issues, because they are highly interactive and they are occurring simultaneously on most reefs around the world. For example, reefs that are overfished and/or polluted often fail to recover after coral bleaching caused by global warming, instead becoming overgrown by blooms of seaweed or other weedy species (photo 5.2). These degraded reefs provide fewer economic options for sustaining coastal communities, especially in developing countries where most tropical reefs occur. Two case studies examined below, the Caribbean and the Great Barrier Reef, illustrate some of these issues from contrasting biogeographic and socioeconomic settings.

One way to view human impacts on coral reefs is to consider how overfishing and pollution affect the structure of foodwebs. The removal of species near the



Photo 5.2: Algal blooms. Promoted by added nutrients and overfishing, algal blooms are a major threat to coral reefs. Fleshy seaweed can outcompete corals, preventing recruitment by juveniles and overgrowing and shading adults.

top of a foodweb by fishing can lead to an increase in abundance of their prey (called a top-down effect). Many reefs worldwide have been severely overfished. Megafauna such as sharks and turtles are increasingly rare worldwide, and in many places fisheries have moved lower down the foodweb, targeting increasing numbers of herbivores such as parrotfish. Similarly, the addition of nutrients can stimulate growth of species at the bottom of the foodweb (primary producers such as phytoplankton and fleshy seaweed). This bottom-up effect can propagate upwards in a foodweb by providing more food for filter-feeders, herbivores and, in turn, for their predators. Top-down and bottom-up distortions of foodwebs typically happen simultaneously.

Natural disturbances (e.g., hurricanes or cyclones, floods, tsunamis, unusual low tides) play a role that is similar to fires in terrestrial systems, continually opening up space and maintaining the local diversity of reefs by preventing overcrowding. Corals and other reef organisms have evolved complex regenerative mechanisms which allow them to recover from a wide variety of natural sources of mortality such as storms, predation, and routine levels of disease. Therefore, human impacts are superimposed on the natural turnover and dynamics of coral reefs, causing elevated rates of mortality and—just as importantly—reduced rates of regeneration (e.g., due to sublethal impacts on reproduction, larval settlement, and survival of new recruits).

5.2. SHIFTING BASELINES, HISTORY, AND THE FOSSIL RECORD

In recent years, reef scientists have been taking a longer view of reef dynamics. Historical trajectories of reef degradation help to reveal the gradual erosion of ecological resilience that can lead to sudden ecosystem collapse, as well as providing insights into appropriate management interventions. Ignoring or denying trajectories of change leads to complacency and inaccurate perceptions that reefs are stable or “pristine”. A longer timeframe focuses attention on the cumulative and interactive effects of sequences of events, rather than concentrating solely on the most recent insult that can lead finally to ecosystem collapse (Jackson et al. 2001).

Most coral reefs today are highly altered ecosystems. In many countries, the current system of governance and management of coral reefs were instigated long after reefs became significantly degraded, with the goal of sustaining whatever remained. Typically, management targets slip lower and lower over time as reefs continue to decline and the memory of their former status fades, a scenario known as “the shifting baseline” (Pauly 1995). Today, for example,

younger Caribbean researchers and managers may never have seen a healthy thicket of Caribbean *Acropora* coral, a manatee, or a large shark. Shifting baselines such as these pervade coral reef science and management.

Corals and other calcifying organisms (e.g., coralline algae, mollusks, bryozoans) have an excellent fossil record which provides invaluable insights into the species composition and dynamics of reefs in the past. The same species alive today have dominated coral reefs for the past half million years, with one obvious exception, *Homo sapiens*. The fossil record, therefore, provides a unique baseline that long predates the influence of humans (Pandolfi et al. 2003). Historical analysis shows that reef megafauna (turtles, dugongs, sharks) declined before small animals and corals, and that Caribbean reefs declined earlier and to a much greater extent than reefs in the Red Sea and Pacific. The trajectories of decline and sequence of degradation were very similar worldwide, and nowhere can be considered today to be “pristine”. Many reefs were significantly degraded long before more recent outbreaks of coral disease and bleaching associated with contemporary global warming.

Recent glacial-interglacial cycles caused the sea to repeatedly flood and drain from continental shelves and oceanic islands. For example, the Great Barrier Reef in Queensland, Australia was high and dry at the end of the last ice age, when sea level was >100 meters lower than today. Heron Island, which today lies 70 km offshore from mainland Australia, was then a hill more than 100 km inland. The coastline was much more exposed to oceanic conditions than today, and the area of shallow water habitat was a small fraction of its current extent. Sea level rose rapidly from 14,000 years before the present, stabilizing at close to its current level 6,000 years ago. In the broadest parts of Queensland’s continental shelf, the water raced sideways at an average rate of more than 50 cm per week for several thousand years. Inshore habitats dominated by mangroves, seagrass, and oyster beds increased dramatically, and corals once more re-invaded the newly submerged shelf. Many marine species exhibit a genetic legacy of these substantial population fluctuations and range shifts caused by past climate change.

The anticipated rise in sea level over the next 50 years due to contemporary global warming is relatively tiny compared to the recent historical rises at the end of the last ice age, because today the world’s oceans are already at a high sea-level stand. Sea level rise and coastal flooding in the coming decades will be a much more serious issue for people in low-lying countries than it will be for coral reefs. Higher temperature due to global warming is a much more serious issue than sea-level rise for corals, because many species are already

close to their maximal thermal limits. The expected increases in temperature and atmospheric carbon dioxide over the next 50 years will substantially exceed the conditions under which coral reefs have flourished over the past half million years. There is one other major difference between the future and past responses to climate change by coral reefs: this time reefs will also have to cope with the activities of more than six billion people. Over the past few hundred years, accelerating human impacts have undermined the resilience of coral reefs, increasing their vulnerability to future climate change.

5.3. BIOGEOGRAPHY HOTSPOTS AND CONSERVATION PRIORITIES

Biodiversity hotspots, regions with exceptionally high species richness, are often identified as prime targets for the protection of marine ecosystems. However, there are several new lines of evidence to suggest that “cool spots”, areas of low species richness, are even more vulnerable. The major coral reef biodiversity hotspot is located in the central Indo-Pacific, a large triangular region centered on Indonesia, Malaysia, Papua New Guinea, and the Philip-



Photo 5.3: Coral reef covered with soft corals (*Sarcophyton trochelioporum*), Philippines, Pacific Ocean

piners (lying between 10°S-10°N and 100°-140°E). In general, the diversity of corals and other reef-associated species declines latitudinally away from the central Indo-Pacific hotspot (which straddles the equator), as well as longitudinally to the east across the Pacific and westwards across the Indian. Two secondary coral reef hotspots occur in the Red Sea and, to a lesser extent, in the Caribbean. The similarity in regional-scale biodiversity patterns among major groups such as corals, reef fishes, mollusks, and crustaceans points to a shared history and set of mechanisms that exert a broad influence on many taxonomic groups (Bellwood and Hughes 2001).

Widespread concerns over the loss of biodiversity and species extinctions have led many conservation groups and governments to focus on the preservation of hotspots as a priority. Protecting biodiversity hotspots may be the most cost-effective way to protect large numbers of species. In terrestrial systems, biodiversity hotspots generally contain large numbers of species with small geographic ranges (endemics) that are potentially vulnerable to global extinction, especially if they are also numerically rare and specialized. For corals and reef fishes, however, high diversity in the central Indo-Pacific hotspot arises primarily from the overlap of pandemic species, whose ranges stretch from the hotspot westwards across the Indian Ocean to East Africa and/or eastwards to the Central Pacific. Only 1% of 602 Indo-Pacific corals are endemic to the central Indo-Pacific hotspot. Among reef fishes, only 3% have geographic ranges that lie entirely within the hotspot boundaries. For these two crucial groups, corals and reef fishes, the proportion of endemics is highest at depauperate, peripheral regions such as Hawaii, the Eastern Pacific, and at high latitude sub-tropical reefs (Hughes, Bellwood, and Connolly 2002).

5.4. FUNCTIONAL GROUPS, REDUNDANCY, AND BIOGEOGRAPHY

A functional group is defined as a group of species that share a common ecological function, regardless of their taxonomic affinities. An example is reef herbivores, a diverse assemblage that includes many species of fish, echinoids, and other taxa. The depletion or loss of one species in a functional group can potentially be compensated for by other species that share a similar ecological role. Low-diversity coral reefs in the Caribbean and the Eastern Pacific, and at many high-latitude locations in the Indo-Pacific, have low disease, because functional groups there may be absent or represented by just

a single species. For example, in the Caribbean there are no weedy bushy corals with high rates of larval recruitment and growth. This functional group of corals is diverse and abundant throughout most of the Pacific and Indian Oceans and the Red Sea (photo 5.4). Caribbean reefs have only a small fraction, about 15%, of the total number of coral species found throughout most of the tropical Indo-Pacific oceans. The most striking taxonomic difference is the generic and species richness of the family Acroporidae. The four Indo-Pacific genera in this family, *Acropora*, *Anacropora*, *Astreopora*, and *Montipora*, are represented by over 120 species on the Great Barrier Reef. In marked contrast, only *Acropora*, represented by just two species (*A. palmata*, *A. cervicornis*, and a hybrid between them) are present today in the



Photo 5.4: A healthy coral reef at Lizard Islands on the northern Great Barrier Reef. Almost all of the corals shown are fast-growing staghorn, bushy, and tabular species of *Acropora*, the dominant genus of corals throughout most of the Indo-Pacific.

Caribbean (photo 5.5). These two species are now increasingly uncommon, due to their failure to recover from mass mortalities caused by hurricanes, algal blooms, sedimentation and runoff, disease, and climate change (Gardener et al. 2003). Loss of species from low-diversity locations affects a disproportionately large proportion of an already depauperate fauna. The widespread decline of *Acropora palmata* and *A. cervicornis*, the only tall three-dimensional corals in the Caribbean, provides a graphic example of the vulnerability of depauperate regions that have little or no disease.

An important issue is whether high species richness confers greater resilience to marine ecosystems. Comparisons of species-rich and naturally depauperate marine systems indicate that higher biodiversity can, in some circumstances, afford a degree of ecological insurance against ecological uncertainty. However, if all species within a functional group respond similarly to pressures such as overfishing or pollution, then higher biodiversity will not afford additional protection. Low-diversity coral reefs of the Caribbean undoubtedly have lower disease than most reefs in the Indo-Pacific, but nevertheless even the most diverse reefs in the world are increasingly threatened by severe overfishing, pollution, and climate change.



Photo 5.5: A Caribbean reef in the 1970s. The image shows the dominance of the robust elkhorn coral, *Acropora palmata*, and the more slender staghorn coral, *Acropora cervicornis*. These two species are increasingly rare due to their vulnerability to coastal runoff, hurricanes, disease, and algal blooms.

5.4.1. Overfishing: impacts on foodwebs and the functioning of ecosystems

Overfishing is a major environmental and economic problem facing virtually all marine ecosystems, including most coral reefs. Typically, overexploitation of a mixed reef fishery first depletes stocks of megafauna and large predators (e.g., turtles, dugongs, sharks, groupers), and subsequently smaller herbivorous and planktivorous fishes become a more prevalent component of the overall catch. For example, in most parts of the Caribbean, parrotfish are a major component of reef fisheries, especially where their predators have long been depleted. Comparisons of lightly and heavily fished coral reefs (e.g., inside and outside of no-take areas) provide compelling evidence for top-down alterations to foodwebs (also called trophic cascades) following the depletion of predators. In the Caribbean and the eastern Pacific, the depletion of fish predators and competitors of echinoids is likely to have played a key role in generating unsustainably high densities of sea urchins. In 1983-4, the abundant Caribbean sea urchin *Diadema antillarum* suffered 99% mortality from disease, which in turn led to dramatic algal blooms that have persisted for the past 25 years. Similarly, the widespread declines of herbivorous and predatory turtles have led to increases in the biomass of seagrasses and sponges (Jackson et al. 2001).

Until recently, fishing on most coral reefs has been largely artisanal, providing a much-needed and cheap source of protein. Even in locations with relatively small human populations, traditional fishing has reduced the abundance of targeted species and changed ecosystem function. For example, the dugong and many species of turtles are ecologically extinct throughout most of their former geographic ranges and are locally abundant only in remote pockets. Similarly, the Indo-Pacific humphead parrotfish, *Bolbometopon muricatum*, has been overfished through most of its geographic range. *Bolbometopon* grows to more than a meter in length, with each adult fish consuming five tonnes of coral per annum (Bellwood, Hoey, and Choat 2003). Its depletion has removed the major external bioeroder from many Indo-Pacific reefs, with poorly understood long-term consequences.

In recent decades, there has been a dramatic increase in fishing effort on coral reefs, and the export of both live and dead coral reef fishes is expanding rapidly. The unprecedented demand for live reef fishes in Southeast Asia is exerting additional fishing pressure on reefs throughout vast areas of the Indo-Pacific. With retail prices of up to US\$250 per kg, exploitation of remote reef systems has become financially viable for the first time, overcoming previous cost-barriers. Herbivorous fishes are an increasingly significant component of the live fish

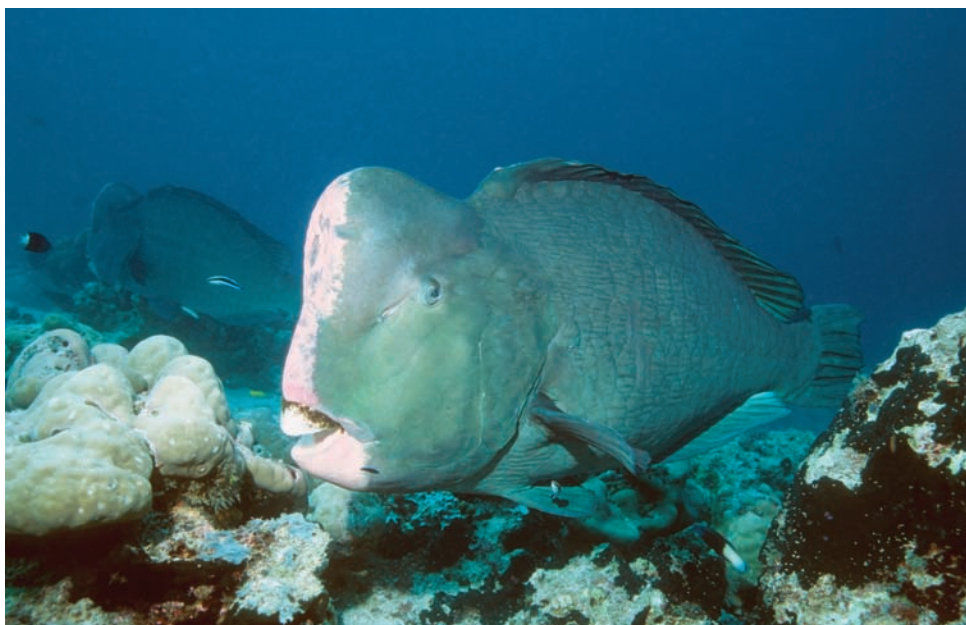


Photo 5.6: The humphead parrotfish (*Bolbometopon muricatum*) has been severely depleted by spear-fishing

trade, ranking currently as the second largest group targeted for exploitation (based on biomass). These new markets for reef fishes have greatly augmented both the intensity and scale of exploitation, and are set to increase as fish stocks elsewhere continue to decline. The depletion of herbivorous fishes combined with runoff of nutrients and increasingly frequent bleaching events is an ominous combination that has led to corals being replaced by blooms of seaweed on numerous reefs around the world (e.g., Hughes 1994; Mumby et al. 2006).

5.4.2. No-take areas

No-take areas, where fishing is prohibited, are important tools for managing foodwebs, ecosystem function, and the resilience of reefs. Traditionally, proponents of no-take areas have focused on their utility for managing targeted fisheries, rather than their potential to regulate the ecosystem functions of harvested stocks, their prey, and the resilience of reef ecosystems. More recently, there has been a growing awareness of the role of no-take areas in maintaining the ecosystem functions provided by reef fishes. In particular, herbivorous fishes play several key roles in the dynamics of tropical reefs: they graze fleshy seaweeds that compete with juvenile and adult corals for space; they erode

dead coral skeletons and generate reef sediments; and they support subsistence fisheries on many coral reefs around the world (photo 5.7).

Because most no-take areas on coral reefs were established very recently, only a few studies have been conducted for long enough to demonstrate their long-term effects. The best available time series on the build-up of fish in coral reef no-take areas comes from long-term studies of no-take reserves in the Philippines, where the biomass of large predatory fish has increased at an average annual rate of 12%, to more than six times the biomass of adjacent non-reserves (Russ, Stockwell, and Alcala 2005). Importantly, the build-up of fish stocks showed no sign of leveling off after 19 years of protection. It is sobering to consider that in the timeframe required for comprehensive regeneration of fish stocks in coral reef no-take areas (>20 years), the human population size of developing countries is likely to double. In the Bahamas, scientists have focused on the number and size of grazing parrotfish and their predators and on the abundance of seaweed, both inside and outside a no-take area which was censused after 20 years of protection (Mumby et al. 2006). The biomass of predatory fishes (groupers, barracuda, moray eels, and large snappers) inside the no-take area was double that of adjacent reefs. The biomass of parrotfishes within the no-take area was also significantly higher than in adjacent areas

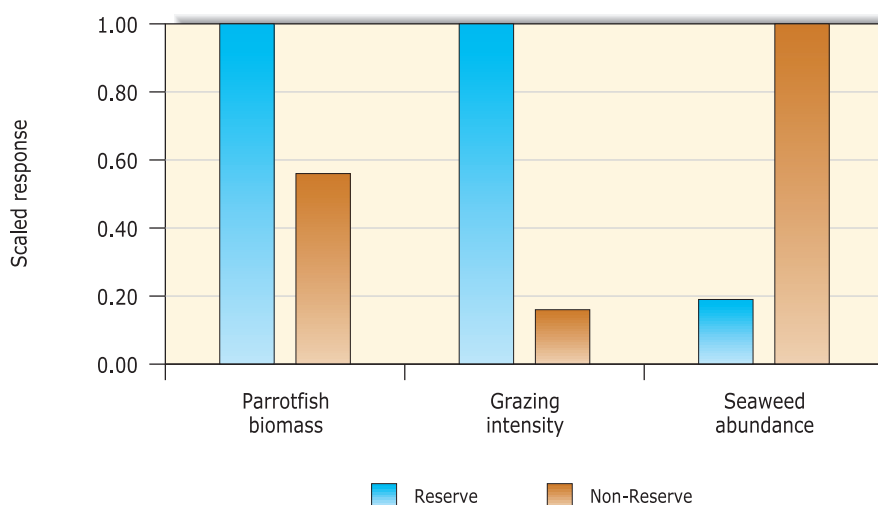


Photo 5.7: An endangered Caribbean parrotfish, *Scarus gaucamaia*, grazing on small tufts of macroalgae

that support a mixed-species reef fishery. The estimated grazing intensity of parrotfishes was six times higher inside the no-take area, and the cover of seaweed was five times lower compared to adjoining reefs (figure 5.1). This study demonstrates that no-take areas can regulate herbivory; a key ecosystem process for maintaining reef resilience.

Most no-take areas are very small, typically a few hectares. Even the largest ones, such as the Great Barrier Reef Marine Park (which is 33% no-take), are too small to be completely self-sustaining or to fully protect mobile species such as sharks and turtles that are targeted outside the no-take area. Similarly, the flow of larvae of most species across the boundary of no-take areas is extensive and multi-directional, and in many cases the replenishment of local populations within protected areas (including fishes, corals, algae, and pathogens) relies on an *influx* of propagules from outside habitats. Clearly, the success or failure of any no-take area will depend on outside areas that are part of the same highly connected reef system. While no-take areas are an important element in the global response to the coral reef crisis, they are not a panacea, and coordinated management of both no-take and harvested areas is crucial for their long-term sustainability (Hughes et al. 2003; Sale et al. 2005).

Figure 5.1: The effect of protection of herbivorous fishes afforded by no-take areas. The blue bars show the biomass of parrotfish, their grazing intensity, and the abundance of fleshy seaweed inside a no-take area in the Bahamas. The brown bars show lower fish biomass, less grazing, and more seaweed outside the no-take area



Source: Redrawn from Mumby et al. 2006.

5.5. WATER QUALITY

Runoff from land causes elevated nutrient loads and increased turbidity from suspended sediments. Excessive levels of sedimentation are caused by activities such as soil erosion from agriculture, dredging, coral mining, coastal development, and drilling for oil and gas. The most widespread of these is soil erosion, due to widespread changes in land use practices, increasing the sediment and nutrient levels in rivers that flow onto coastal reefs. Throughout the tropics, there has been widespread deforestation and land clearing for agriculture, aquaculture, and urbanization. Increased turbidity influences the physiology, growth, and survival of corals in several ways. Firstly, corals need to expend energy cleaning themselves of sediment to prevent smothering. Secondly, the amount of light reaching a coral colony is reduced by increased turbidity, slowing their growth. High rates of sedimentation are especially damaging to juvenile corals, which are easily smothered by silt, affecting the ability of reefs to regenerate after disturbances such as cyclones or coral bleaching.

Inputs from sewage and runoff of fertilizers can potentially alter foodwebs (bottom-up effects) and damage coral reefs. The iconic example of sewage effects on a coral reef comes from Kaneohe Bay, Hawaii (Maragos, Evans, and Holtus 1985). The bay is very shallow, connected to the ocean by a narrow opening (i.e., it has a very low flushing rate compared to most coral reefs), and the land area surrounding it is densely populated. Kaneohe Bay has a long history of other impacts such as dredging and overfishing and has a high proportion of pest species introduced by shipping. Sewage was discharged into Kaneohe Bay in the 1960s and 1970s from three outfalls at a rate of up to 20,000 m³ per day. Several streams also enter the bay, carrying urban and suburban runoff. These conditions increased nutrients and sediment loads, leading to blooms of phytoplankton. Coral patch reefs were colonized by benthic macroalgae and suspension feeders (bivalves and sponges), while coral cover declined sharply. These effects exhibited a gradient away from the sewage outfalls. However, when the nutrient input was reduced, water clarity improved, the filter feeders and algae declined, and the corals slowly increased.

Population explosions of the coral-feeding crown-of-thorns starfish, *Acanthaster planci*, may also be related to widespread nutrient enrichment of coastal waters. These outbreaks were first observed in the late 1950s and 1960s, when many coral reefs in Australia, Guam, Japan, the Red Sea, and elsewhere were badly damaged by enormous densities of starfish. Since then, repeated outbreaks have occurred throughout most of the starfish's geographic range, and they have become a chronic issue on many reefs. Out-



Photo 5.8: The crown-of-thorns starfish (*Acanthaster planci*), a major predator of corals

breaks are initiated by heavy recruitment of juvenile starfish, leading to two theories that propose a link to human activities. One suggests that a top-down alteration of foodwebs has released *Acanthaster* from predation. This seems unlikely since there are very few fisheries for the predators of juvenile or adult starfish. The other theory hypothesizes that added nutrients have led to more phytoplankton food for starfish larvae. This bottom-up effect may have significantly reduced the development time of juvenile starfish, allowing many more of them to survive to settlement, potentially resulting in destructive outbreaks.

5.6. CLIMATE CHANGE

Climate change is not some distant future threat to reefs that may or may not come to pass. Global warming has already caused one or more bouts of coral bleaching on many reefs—roughly half of the world’s total—in the past 25 years or so. Some of these reefs appear to be recovering well, but many are not. The projected increases in water temperature, changes in the frequency and intensity of severe storms, and the rising acidity of the oceans all pose profound environmental and socioeconomic challenges, particularly for those

reefs that are already stressed due to more local pressures of overfishing and pollution (Hughes et al. 2003)

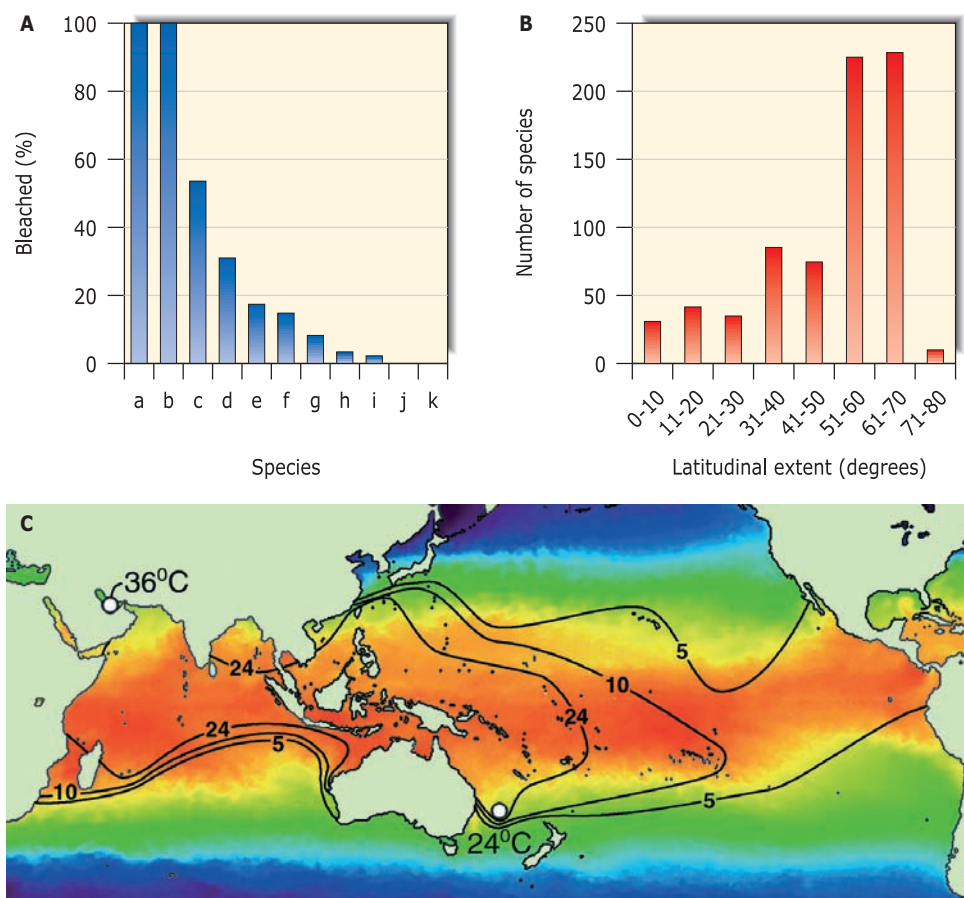
Coral bleaching occurs when corals become physiologically stressed and lose most of the symbiotic algae (zooxanthellae) that give them most of their color (photo 5.9). Small-scale bleaching has been widely described in older coral reef scientific literature following hot or cold weather and floods. However, regional-scale bleaching is a new phenomenon driven by global warming. In 1998, elevated sea surface temperatures associated with an extreme El Niño event resulted in the largest and most destructive bleaching event yet documented, causing widespread damage that extended from the western Pacific across the Indian Ocean to Africa and severely degrading an estimated 16% of the world's coral reefs (Wilkinson 2000).

Like most forms of disturbance, bleaching affects some species of corals more than others (figure 5.2.A). For example, some coral genera, such as slow-growing, massive or encrusting *Porites* and *Leptastrea*, bleach less readily than faster-growing, branching and tabular *Acropora* (Loya et al. 2001; Marshall and Baird



Photo 5.9: Coral bleaching on the reef slope of Raiatea, French Polynesia. Note that bleaching is selective, with some corals affected more than others (see figure 5.2.A.). Selectivity is important, because it is already altering the species composition of coral assemblages, in favor of species that are relatively resistant to bleaching. Susceptible species are likely to become increasingly rare in the future as further bleaching events occur.

Figure 5.2: Coral bleaching by latitude and temperature. **A:** Different species of corals (here labeled a-k) show varying susceptibilities to bleaching. 100% represents bleaching by every coral in populations at Raiatea, French Polynesia, during May 2002. **B:** Latitudinal extents of all Indo-pacific reef corals, measured from the northern to the southernmost point in their range. Most species have a latitudinal span of 50-70 degrees, straddling the equator. **C:** Geographic range boundaries of 24 pandemic species of Indo-Pacific corals that are found in the Persian Gulf and at Lord Howe Island off Australia, where average maximum summer temperatures differ by 12°C. The coloring shows temperatures in the Southern Hemisphere summer of 1997/1998, when unprecedented mass bleaching occurred.



Source: Reproduced with permission from Hughes et al. 2003.

2000). Similarly, recolonization after disturbances such as cyclones or bleaching events varies greatly among coral species, depending on their life histories and the scale of stock-recruitment relationships (how far larvae travel from their source). Therefore, over coming decades some susceptible species may decline or disappear, while others may increase. The long-term impact of rapid temperature rises will depend critically on the ability of corals to acclimatize and/or

adapt, and on their capacity to migrate. The fossil record shows dramatic expansions and contractions in the geographic ranges of corals during past periods of warming and cooling, in the Pleistocene and Holocene. Along the coast of western Australia, for example, the geographic boundaries of staghorn corals extended up to 500 km further south (to 33°S) of their current range (27°S). In the past, some species migrated faster than others, producing rapid shifts in species composition, especially near faunal boundaries. This historical evidence suggests that contemporary climate change will also influence the geographic boundaries of species, via changes in their physiology, altered hydrodynamics and dispersal of larvae, and in response to a new mix of species interactions.

Most corals bleach when the sea water temperature exceeds the average summer level of a particular location by about 2°C for more than a few weeks. Importantly, average temperatures often differ by 10°C or more within the geographic range of most coral species, which typically straddle the equator and extend to cooler sub-tropical areas (figure 5.2. B and C). A higher bleaching threshold in warmer locations implies that there is strong selection for corals and their zooxanthellae to evolve thresholds that are near the expected upper temperature at that location. How long this adaptation takes to evolve is unknown, and so a major issue is whether coral and zooxanthellae species can adapt quickly to the rapid climate changes that are now underway.

Corals and their algal symbionts have high levels of genetic diversity, which could promote rapid evolution. Although it is clear that mortality rates from bleaching events are often very high, and the fecundity of surviving corals is often reduced, very little is known about how much selection this exerts or about the heritability of physiological traits. Aquarium studies of the upper thermal tolerances of corals have shown they have some capacity for phenotypic change, or acclimation. Past experience of thermal stress and bleaching can also substantially reduce the susceptibility of corals to subsequent bleaching episodes. Corals on geographically isolated, oceanic reefs are likely to be extremely vulnerable to global warming, even where local threats are minimal, because of their small population size, increased inbreeding, and the near absence of long-distance dispersal by larvae to the sites they occupy.

5.7. TWO CASE STUDIES

Two large-scale cases studies from the Caribbean and the Great Barrier Reef further illustrate the impact of human activities on the condition and dynamics of coral reefs, and the challenges for managing overfishing, pollution, and climate change in different social and economic settings.

5.7.1. The Caribbean

A recent analysis of coral abundance in the Caribbean, based on 65 studies at 263 sites, shows that average cover has declined from 54% in 1977 to just 9% in 2001 (Gardener et al. 2003). This recent collapse was preceded by dwindling stocks of fishes and increased nutrient and sediment runoff from land over the past century and longer. The depletion of fishes led to population explosions of the sea urchin *Diadema antillarum*. In the 1960s and 1970s, the recorded densities of *Diadema* on overfished reefs throughout the Caribbean were extraordinarily high, commonly averaging >20 individuals per m² in shallow waters (photo 5.10). On many reefs, this one species had replaced a suite of herbivorous fishes as the main grazer of algae. Consequently, it was the last abundant member of a crucial function group that controlled the abundance of seaweed. At high densities, *Diadema* were small and food-limited, and their grazing activities bulldozed coral recruits and removed more carbonate from live and dead corals than the reef could generate by calcification. The crowded condition of *Diadema* populations may have contributed to their eventual



Photo 5.10: The sea urchin *Diadema antillarum*. The most important herbivore and bioeroder of Caribbean reefs prior to its mass mortality from disease in 1983-4. The disease epidemic prompted blooms of fleshy seaweed, especially on reefs where fish herbivores such as parrotfish were over-exploited. The seaweed prevented recruitment by juvenile corals and slowly smothered and replaced adults. More than 30 years later, only a limited recovery of *Diadema* has occurred, and many reefs remain choked with seaweed.

demise in 1983-4, when a disease outbreak spread throughout the Caribbean, reducing their numbers by 99%.

The trajectory of coral cover over the past 30 years has varied from place to place around the Caribbean, depending on which locations were affected by hurricanes, bleaching events, and disease outbreaks in different years. The fact there has been so much debate about what killed the corals reflects these different sequences of events. In Jamaica, for example, the initial loss of coral cover occurred in 1980 due to Hurricane Allen, which destroyed most of the dense growths of staghorn and elkhorn corals, *Acropora cervicornis* and *A. palmate*. Other locations lost most of their *Acropora* from other hurricanes, runoff of sediments or, more recently, through disease or bleaching events. The debate on mortality, however, misses the crucial point that Caribbean reefs have lost their capacity to regenerate following the recurrent hurricanes these species have experienced for hundreds of thousands of years. The die-off of *Diadema* in Jamaica precipitated blooms of macroalgae that have prevented recovery of corals by inhibiting larval settlement and by smothering juveniles. All species of corals in Jamaica have declined in abundance over the past 30 years, through a combination of elevated mortality, declining brood stocks, and recruitment failure (photo 5.11).

In the past few years, *Diadema* has shown a modest recovery at some locations in the Caribbean. However, it remains an order of magnitude less abundant than

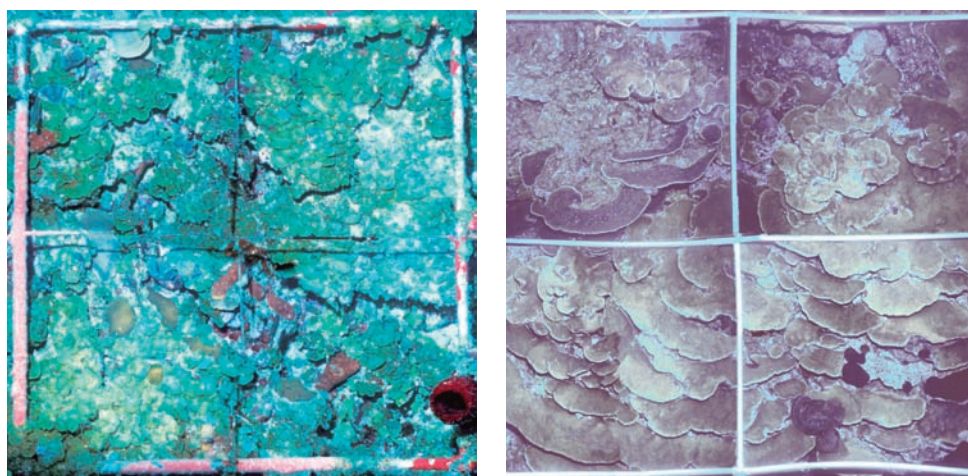


Photo 5.11: Phase shift from a healthy coral assemblage to a persistent algal bloom. This shift is illustrated by a before and after picture of the same 2x2 m quadrant located at a depth of 35 m off Jamaica. The left image records abundant corals in 1981, while the right image shows the same spot twelve years later, in 1993, by which time virtually all of the original corals were smothered by fleshy seaweed and almost no new coral recruits survived.

before the die-off in 1983-4 and is restricted to the shallow end of its former depth range. In 2006, the U.S. Fish and Wildlife Service added the two Caribbean species of *Acropora* to the List of Endangered and Threatened Wildlife. The continued slow recovery of *Diadema* may help to control algal blooms, but it is uncertain whether it will return to dangerously high densities or extend to its former depth range. Chronic overfishing continues throughout most of the Caribbean, and fish stocks remain severely depleted in most regions.

5.7.2. The Great Barrier Reef

Australia's Great Barrier Reef system is in relatively good condition, due in part to its large size, relative isolation, and a long-term investment by governments in reef science and management. Unusually among coral reef nations, Australia has a low population density and is relatively very wealthy. However, the Great Barrier Reef is showing symptoms of change and increased vulnerability that warrant concern. Fisheries that flourished following European colonization (e.g., sea cucumbers, pearl shell, *Trochus* snails, dugongs, whales,



Photo 5.12: An aerial photograph of one of the nearly 3000 reefs that collectively comprise Australia's Great Barrier Reef, the world's largest coral reef system. The Great Barrier Reef has the world's biggest network of no-take areas (where fishing is prohibited) and supports a major international tourism industry.

and turtles) have collapsed or are no longer commercially viable. Runoff of sediment and nutrients from land has increased greatly since the mid-1800s, affecting nearshore reefs and seagrass beds. In the past 40 years, large-scale outbreaks of crown-of-thorns starfish, *Acanthaster planci*, have occurred three times, reducing coral cover on roughly 200 reefs (out of the total number of 2,900 comprising the Great Barrier Reef system). Major bleaching events from climate change struck the Great Barrier Reef in 1998 (during the same El Niño event that damaged reefs elsewhere in the western Pacific and Indian Ocean) and again in 2002, damaging close to 600 individual reefs. Coral cover remains low on reefs affected by runoff, crown-of-thorn starfish, and coral bleaching. Rapid growth in recreational and commercial fishing has reduced the biomass of targeted fish species by more than 80% in heavily fished inshore areas, compared to adjacent no-take reserves (Williamson, Russ, and Ayling 2004). Herbivorous fishes remain abundant and are protected by regulations on fishing gear.

From July 1, 2004, the proportion of the Great Barrier Reef Marine Park closed to fishing (i.e., no-take fishing reserves) was increased from 5% to 33%, encompassing at least 20% of all major habitat types (Fernandes et al. 2005). Simultaneously, a new ten-year program, the Reef Water Quality Protection Plan, was formulated in an attempt to curb future nutrient and sediment runoff. These management changes exemplify a new ecosystem-based approach that arose from a shift in perceptions about the increasing risks to the “once pristine” Great Barrier Reef. The changes in zoning were undertaken to build ecological resilience and to cope proactively with the risk associated with human population growth, rising fishing pressure, future bleaching events, and other uncertainties. Australia belatedly ratified the Kyoto Protocol in 2008, following a change of national government.

5.8. FUTURE PROSPECTS

Building the resilience of coral reefs to avoid phase shifts provides a new framework for preserving and managing these important ecosystems. There is growing awareness among reef managers of the functional role of fishes, the effects of overfishing on the dynamics of foodwebs, and the bottom-up influence of pollution. In particular, preserving stocks of fishes and reducing runoff of nutrients and sediment are increasingly seen as ways to maximize the resilience of coral reefs. Local controls on fishing and water quality can also provide some insurance against larger-scale ecological surprises (such as coral bleaching) that are impractical to manage directly in the short term. Preventing coral bleaching is

not a tractable management goal at a local level (because it will require global reductions of greenhouse gases). On the other hand, building and supporting resilience in anticipation of bleaching and other recurrent disturbances can be achieved locally by changing destructive human activities (e.g., overfishing and pollution). However, local action will not be enough on its own to prevent the ongoing destruction of reefs due to rapid climate change. An urgent reduction in the world's greenhouse gas emissions is essential for reducing the severe impact of thermal stress and ocean acidification on coral reefs.

Predicting and preventing unwanted phase shifts (or, conversely, promoting desirable ones) is a major challenge for future research, which will require a much better understanding of the complex processes that support or erode resilience. The focus needs to shift from the conventional monitoring and mapping of biodiversity and species abundances towards active management of key functional groups that support important processes and sustain ecosystem services. Monitoring programs urgently need to be improved, to gain a clearer understanding of critical thresholds and feedbacks, and of the capacity of coral reefs to continue to provide ecological services such as fisheries and tourism. Developing and testing new metrics for the stewardship of coral reef resilience (e.g., stock sizes of herbivorous fishes, rates of coral recruitment and regeneration, disease) is critical for coping with uncertainty and future ecological surprises.

Restoring coral reef ecosystems after they have undergone a phase shift is much more difficult than maintaining them in good condition, as shown above by the two case studies. The timeframe for recouping depleted fish stocks and for improving regional water quality is typically decades not months, and indeed may not always be socially, economically or biologically feasible. Some severely degraded coral reefs have changed to the extent that they are unlikely to recover and regain their original configuration, because a new set of feedbacks have locked them into a new state. For example, regeneration of coral reefs can be inhibited by a surfeit of coral predators, by recruitment failure following the loss of brood stocks, by blooms of resilient algae that resist herbivory and smother juvenile corals, or by persistent layers of sediment. Similarly, because of their slow growth, a complete reversal of the ecological extinction of megafauna on most coral reefs would take centuries, even if hunting pressure disappeared and all lost habitat was restored. Clearly, it is easier to sustain a resilient ecosystem than to repair it after a phase shift has occurred.

Recovery of degraded coral reefs that are chronically impacted by people will not be possible unless the major ongoing drivers (e.g., greenhouse gas emissions, runoff of sediment, excess nutrients, and fishing pressure) are first



Photo 5.13: Coral community in the Philippines. Reefs provide critical ecosystem goods and services to local people, principally through fisheries and tourism. As a consequence, sustaining coral reefs is not just a goal for conserving biodiversity. It is also a social and economic imperative.

reduced. No-take areas can play an important role in rebuilding fish stocks and the structure of foodwebs. However, there is also an urgent need to improve management measures for the vast majority of reefs that are heavily impacted by people, because no-take areas are tightly linked to the broader seascape. Establishing appropriate multi-scale systems of governance that are strongly supported by local, national, and international communities is undoubtedly the major challenge for the future of coral reefs.

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LIST OF PHOTOGRAPHS

Photo 5.1:	Coral formation with individuals of the <i>Acropora</i> genus, Thailand. © Juan Carlos Calvín	140
Photo 5.2:	Algal blooms	142
Photo 5.3:	Coral reef covered with soft corals (<i>Sarcophyton trochelioporum</i>), Philippines, Pacific Ocean. © J. W. Alker/age fotostock	145
Photo 5.4:	A healthy coral reef at Lizard Islands on the northern Great Barrier Reef	147
Photo 5.5:	A Caribbean reef in the 1970s. © Conservation International	148
Photo 5.6:	The humphead parrotfish (<i>Bolbometopon muricatum</i>) has been severely depleted by spear-fishing. © Georgette Douwma/naturepl.com	150
Photo 5.7:	An endangered Caribbean parrotfish, <i>Scarus gaucamaia</i> , grazing on small tufts of macroalgae	151
Photo 5.8:	The crown-of-thorns starfish (<i>Acanthaster planci</i>), a major predator of corals. © Juan Carlos Calvín	154
Photo 5.9:	Coral bleaching on the reef slope of Raiatea, French Polynesia. © Jurgen Freund/naturepl.com	155
Photo 5.10:	The sea urchin <i>Diadema antillarum</i> . © Fred Bavendam/Minden Pictures	158
Photo 5.11:	Phase shift from a healthy coral assemblage to a persistent algal bloom	159
Photo 5.12:	An aerial photograph of one of the nearly 3000 reefs that collectively comprise Australia's Great Barrier Reef. © ARCO/Schulz/age fotostock	160
Photo 5.13:	Coral community in the Philippines. © Juan Carlos Calvín	163

LIST OF ILLUSTRATIONS

Figure 5.1:	The effect of protection of herbivorous fishes afforded by no-take areas	152
Figure 5.2:	Coral bleaching by latitude and temperature	156

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