Coral Reefs

Threats and Conservation in an Era of Global Change

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Coral reefs are iconic, threatened ecosystems that have been in existence for ~500 million years, yet their continued ecological persistence seems doubtful at present. Anthropogenic modification of chemical and physical atmospheric dynamics that cause coral death by bleaching and newly emergent diseases due to increased heat and irradiation, as well as decline in calcification caused by ocean acidification due to increased CO_2, are the most important large-scale threats. On more local scales, overfishing and destructive fisheries, coastal construction, nutrient enrichment, increased runoff and sedimentation, and the introduction of nonindigenous invasive species have caused phase shifts away from corals. Already ~20% of the world's reefs are lost and ~26% are under imminent threat. Conservation science of coral reefs is well advanced, but its practical application has often been lagging. Societal priorites, economic pressures, and legal/administrative systems of many countries are more prone to destroy rather than conserve coral-reef ecosystems. Nevertheless, many examples of successful conservation exist from the national level to community-enforced local action. When effectively managed, protected areas have contributed to regeneration of coral reefs and stocks of associated marine resources. Local communities often support coral-reef conservation in order to raise income potential associated with tourism and/or improved resource levels. Coral reefs create an annual income in S-Florida alone of over $4 billion. Thus, no conflict between development, societal welfare, and coral-reef conservation needs to exist. Despite growing threats, it is not too late for decisive action to protect and save these economically and ecologically high-value ecosystems. Conservation science plays a critical role in designing effective strategies.

Key words: **coral reef; conservation; global climate change; phase shift; overfishering; coral diseases; bleaching; ocean acidification; tourism; marine reserve**

Introduction

Coral reefs have been identified as an endangered ecosystem because they are subject to multiple natural, man-made and man-mediated stresses (Glynn 1996; Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007). Most crucially, they are being considered one of the most sensitive ecosystems to global climate change and are frequently likened to the proverbial canary in the coal mine. We, as the coal miners, have reason to be a bit more concerned about the canary's health.

Statistics vary according to source, but estimates suggest that 20% of the world's coral reefs are already lost, 24% under imminent risk of collapse, and another 26% in grave danger of irreparable damage (Fig. 1; Wilkinson 2006). Hardly any reef of the world is not overfished, and few have escaped degradation of their

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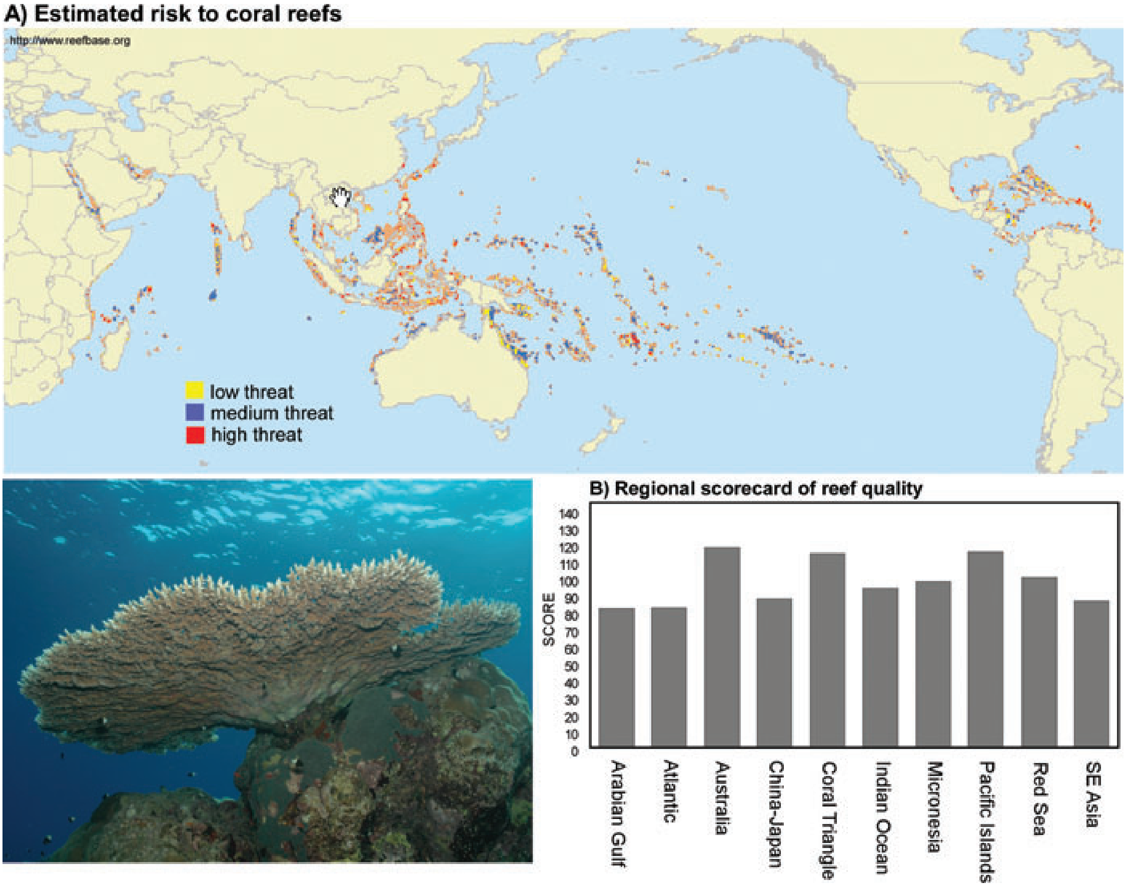

Figure 1. Coral reefs around the world are threatened by a variety of natural and man-made factors. Threat is not contributed evenly, though. (**A**) from ReefBase online GIS (http://www.reefbase.org); (**B**) ReefCheck data from Wilkinson (2006), the lower the index, the more degraded the reefs of the area. (Photo by A. Hagan.)

biological components (Jackson *et al.* 2001; Sale 2008). Worldwide events, such as the 1998 El Niño Southern Oscillation (ENSO) that caused widespread coral bleaching and death (Baker *et al.* 2008), have led to indiscriminate damage in protected and unprotected systems (Fig. 1). Global climate change is potentially threatening every single coral, and its associated fauna worldwide (Hoegh-Guldberg *et al.* 2007). This leads to the question whether it is even possible to conserve coral reefs. What are the odds? Should we even bother?

Yet, despite this apparently gloomy outlook, coral reefs, similar to those we know today, have existed for approximately 215 million years (and, in another taxonomic guise, for about 500 million years). They have survived the extinction of the dinosaurs and the climate changes of the ice ages. This would suggest remarkable evolutionary resilience and would certainly suggest that there is scope for ecological resilience as well. The ultimate question is whether we need not worry about the survival of coral reefs or whether the upheavals of the Anthropocene (= the present era dominated by human activities; Crutzen 2002; Crutzen and Steffen 2003) will turn out to be more than these time-proven ecosystems can sustain.

To understand actions needed to conserve coral reefs and understand what will be lost if stresses continue unabated, we require an overview of their dynamics and the most important threats facing them. While many states and societies have been more or less active in coral-reef conservation, there have been mixed results, and reef stresses keep rising (Sale 2008). Is there more we should do? And if so, what?

On the following pages we will provide a condensed overview of what we consider to be the issues and we will show how they have been, and can, be addressed. This review should thus provide an easy entry point to the discussion about the why, when, where, and how of coral-reef conservation.

Coral Reefs in the Past: Crises and Renewed Evolution

When decrying the "coral reef crisis," losses of biodiversity, and threats to the ecosystem, we are well advised to read the pages of Earth history in order to put what is happening today into perspective. Crises and extinction are nothing new for coral reefs. They and analogous sedimentary systems have a very long geological history and have persisted through all major Phanerozoic (i.e., much of the entire fossil record, >600 Ma = million years) biotic crises (Fig. 2). Over time, many reef crises and innumerable extinctions have occurred, but coral reefs (in the widest sense) have persisted. Not only have reefs survived or arisen repeatedly after extirpation, they have been shown to be evolutionary focal points, with more organisms evolving within reefs and spreading to adjacent habitats than the other way around (Kiessling 2005, 2008). However, each crisis brought major extinctions and faunal turnovers, and in some cases it took evolution millions of years to compensate for the damages. The question is whether mankind has created the final crisis that will push these long-lived systems into extinction.

In the immediate past, the corals themselves record climate in their skeleton via variability in geochemistry. While much of this information is lost in older fossil corals that have been replaced by different types of calcium carbonate, the skeletons of recent or subfossil corals provide an excellent monitoring tool for climate variability, at least in the Holocene and Pleistocene (Eakin and Grottoli 2006) and perhaps even further back in time. Thus, looking back and observing patterns may indeed help us to look forward in anticipation of what might be forthcoming.

The earliest analogues to reefs were stromatolites, layered rocks formed by filamentous blue-green algae (Riding 1999), arising at the dawn of time in the Archaean Eon (~3.5 Ga = billion years ago; Walter *et al.* 1980). Stromatolites have persisted throughout the geological record into the present day. The rise of biodiversity was the demise of stromatolite dominance. As more grazers evolved, the algae making up the stromatolites were consumed, suppressing their formation (Copper 2001). Thus, we find them primarily in extreme habitats (as today in hypersaline western Australian lagoons, or in tidal passes with extreme currents in the Bahamas, Fig. 3A) or during extreme times (biotic crises of all ages; Wood 1999). Although many of today's remaining stromatolites need protection and could easily be destroyed, we probably need not worry about their future—evolutionary crises will recur, and stromatolites have demonstrated their ability to survive over billions of years. The first true reefs were built by spongelike organisms, archaeocyaths, in the lower Cambrian (~520 Ma). These reefs were ecologically complex and had zoned communities with niche separation (Zhuravlev 2001; Rowland and Shapiro 2002). They were wiped out by a mass mortality caused by a global transgression–regression couplet (Zhuravlev 2001) and were immediately followed in the Ordovician (500–440 Ma) by one of the most significant marine metazoan radiations in Earth history (Sepkoski 1990). This period saw the rise of corals with the appearance of the Tabulata and Rugosa (also called "Tetracorals," since they always had a multiple of four septa; modern "Hexacorals," which always have a multiple of six septa,

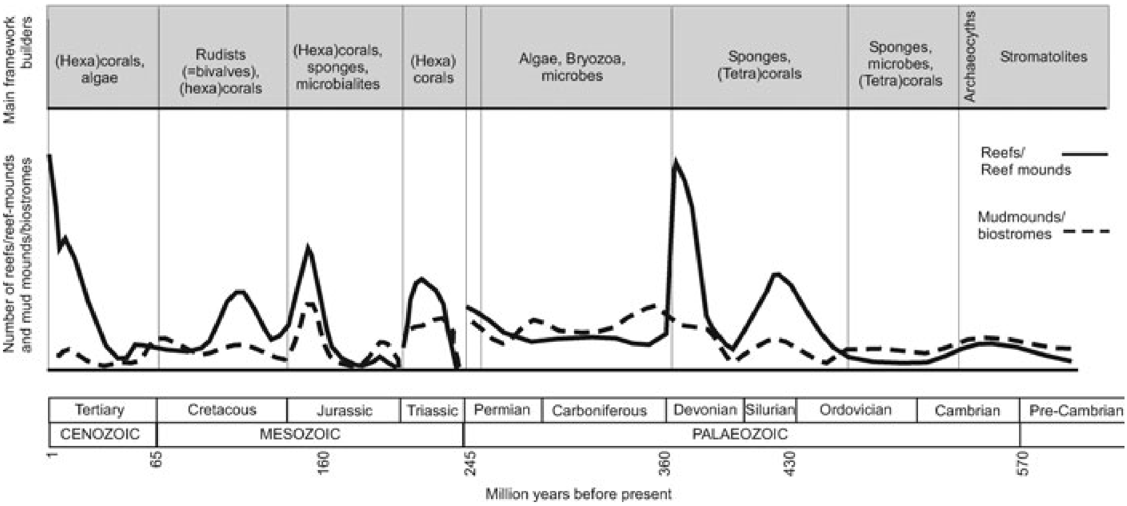

Figure 2. Reef abundances through time. (Modified from Fluegel 1997.) The *curve* shows the reconstructed number of reef sites in the geological record. Extinction events are plainly visible as strong downward dips in the number of reefs recorded. The dominant framebuilding taxa, that is, those that built the reef rock, are mentioned in the *gray bar* above the curves.

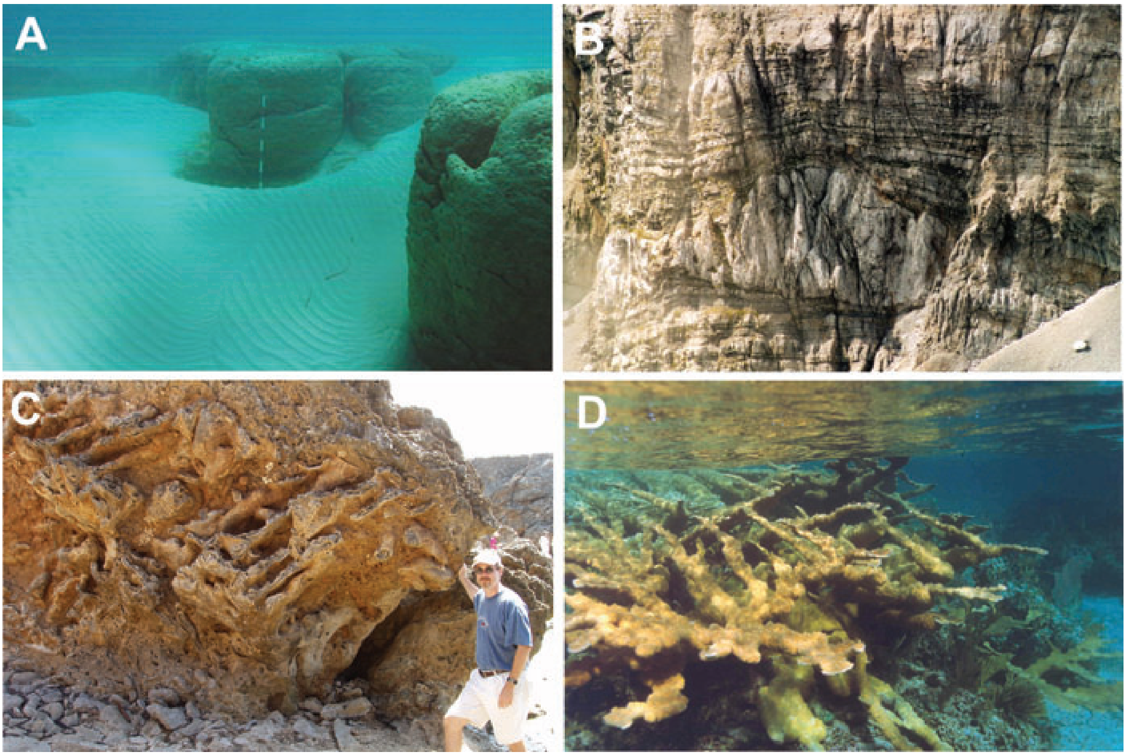

Figure 3. (**A**) Stromatolites, such as these at Lee Stocking Island in the Bahamas, were the first organisms that formed geological structures akin to reefs. (**B**) A Devonian coral reef in Austria. (**C** and **D**) Pleistocene/Holocene ecological constancy. The coral *Acropora palmata* dominated shallow Caribbean for the past few hundred-thousand years. (**C**) shows a Pleistocene *A. palmata* reef in Curacao, and (**D**) shows recent *A. palmata* in Andros, Bahamas. (Part (B) courtesy of Bernhard Hubmann.)

arose in the Triassic, ~240 Ma) and calcareous sponges that dominated reefs throughout the Paleozoic. Despite several crises (Ashgill and Ludlow extinctions; Copper 1994), reefs flourished until the mid-Devonian (~480 Ma), one of the acmes of Phanerozoic reef building. Huge barrier-reef systems extended over 2000 km in Australia and Canada, and reefs were common throughout the world (Copper 2002; Fig. 3B). At about 470 Ma (Frasne/Famenne crisis), these spectacular ecosystems were wiped out by a complex series of sea-level rises, falls, and oceanic anoxia. Interestingly, while we currently fear for the future of reefs due to increased atmospheric CO_2 levels and anticipated effects on ocean chemistry (Guinotte and Fabry 2008), the Frasne/Famenne extinctions occurred during a time of the largest drop in pCO_2 in the Phanerozoic (Berner 1998, 1999), which also shifted the oceans from a calcite to an aragonite mode (Hardie 1996). This is in direct juxtaposition of scenarios for a near-future reef crisis of increasing CO_2 (Hoegh-Guldberg *et al.* 2007). Paleozoic reefs never recovered to their former glory. In the Mississippian, phylloid algae reefs existed and in the Permian, reef complexes were built in North America (e.g., the famous Permian reefs of Texas/New Mexico)—only to be wiped out for good during the greatest marine mass extinction on Earth at the Permian/Triassic boundary (Newell 2001), caused by a multitude of factors, worldwide cooling being among them (Wood 1999).

After an ~10 Ma interval with no reefal record, the modern corals stormed onto evolution's stage in about the mid-Triassic (~230 Ma) and rapidly built major reef complexes. It is uncertain whether these corals contained zooxanthellae or whether they functioned exactly like the modern ones, but some authors suggest that this is likely (Stanley and Swart 1995; Stanley and van de Schootbrugge 2009). The calcareous Alps are peppered with well-developed reefal limestones of impressive dimension built by scleractinian corals that were closely related to today's reef-builders. In the Rhaetian (~210 Ma) the reef period collapsed during a brief ice-house (Fluegel and Senowbari-Daryan 2001), but reefs subsequently diversified throughout the Jurassic (~203–135 Ma; Leinfelder *et al.* 2002). Many more and different types of reef than today (microbial, siliceous and calcareous sponges, corals) occupied and built frameworks in more environments. This rich reef age came to an end due to sea-level regression, leaving reefs high and dry. The following Cretaceous (~135–65 Ma) saw spectacular reef building during a time of much higher average temperatures, far higher atmospheric pCO_2 (2–10 times today's levels; Berner 1994), and a more sluggish ocean circulation than today. Counterintuitive to today's CO_2 discussion, the Cretaceous was a time of prolific carbonate deposition and reef building (Kiessling 2002). During this period, corals moved more and more into the oligotrophic realm at the shelf edge—a trend that had begun in the late Jurassic (Leinfelder *et al.* 2002)—with the inner shelf regions dominated by giant reef-building bivalves called Rudists. During the Createceous calcite sea, which presumably made skeletal formation difficult for scleractinia, some corals lost their skeleton altogether and became the Corallimorpharia ~110–133 Ma (Medina *et al.* 2006). The great end-Cretaceous cataclysm (~65 Ma) caused by a bolide impact exterminated this reef period.

The end-Cretaceous cataclysm wrought by the famous Chicxulub bolide impact terminated the reign of the dinosaurs, rain forests, and coral reefs. But within only a million years, rain forests covered the Earth again (Johnson and Ellis 2002) and coral reefs, of surviving Cretaceous species and new Cenozoic species reformed in the Danian (65–61 Ma; Perrin 2001). The Paleocene (65–53 Ma) and the Eocene 53–33.7 Ma) were characterized by some of the warmest temperatures ever, the Paleocene–Eocene Temperature Maximum (PETM), during which coral reefs expanded and diversified spectacularly. However, most of these reefs were in shallow water, and few existed in deep water (Perrin 2001). This is an interesting parallel to what has been proposed as future scenarios for

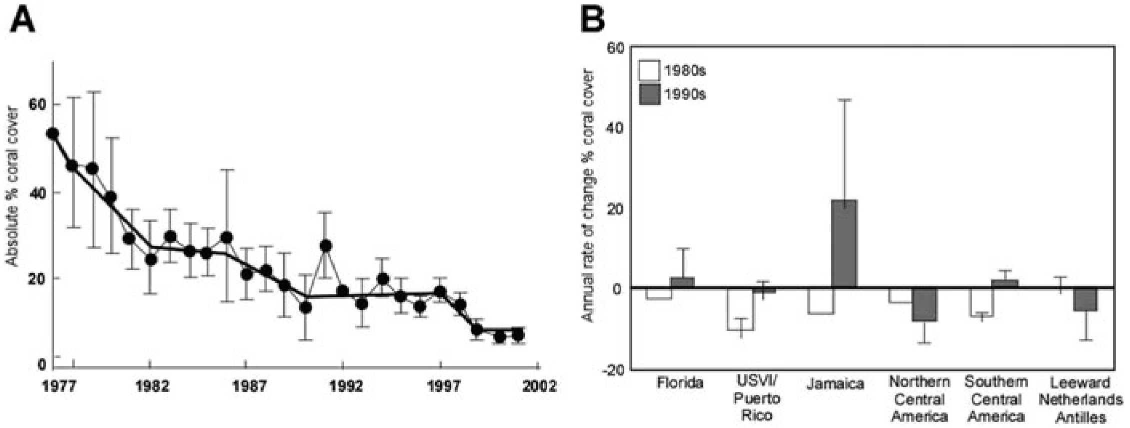

Figure 4. Coral cover has decreased on many reefs around the globe, but rarely as spectacularly as across the Caribbean basin. (**A** and **B**) From a meta-analysis by Gardner *et al.* (2003); a spectacular decline is shown, but also, in (**B**) some regional recovery. Thus, there is reason for hope.

modern deepwater reefs. It is feared that higher atmospheric pCO_2 and concomitant acidification will make calcification impossible for about 70% of today's deepwater reefs (Guinotte *et al.* 2006; Turley *et al.* 2007; Guinotte and Fabry 2008) and might lead to their demise. Maybe the situation during the PETM is indeed a valid analog—barring the fact that anthropogenic CO_2 input has no parallel during the PETM.

During the Oligocene (~30 Ma), reefs expanded more, but at its end, the western Atlantic–Caribbean area lost about half its genera (Edinger and Risk 1994). In the Micoene (~20 Ma), reefs started to look very much like today, which is not surprising, since the configuration of the continents and ocean circulation were similar. The Mediterranean had extensive reef systems, but it evaporated, ending its era of reef building. Increasing isolation of the Mediterranean basin had already led to a decrease in species diversity until reefs were almost entirely dominated by the genus *Porites* (Braga *et al.* 1990; Pomar 1991; Perrin 2001). A similar situation, loss of biodiversity and a shift toward *Porites* dominance has also been predicted to occur in the Caribbean (Aronson *et al.* 2004), which is similarly isolated today as the Mediterranean was in the Miocene.

After the closure of the Isthmus of Panama, a new fauna emerged over the past ~3 Ma in the Caribbean via a gradual step-down of the old Indo-Pacific fauna and a progressive step-up of newly evolved purely Caribbean taxa (Budd and Johnson 1999; Budd 2000). By the Pleistocene (<1 Ma), a fauna had evolved that was very similar to today's and showed remarkable constancy even throughout the major upheavals of the ice ages (Fig. 3D, 3E). Throughout much of the Caribbean, a community pattern similar to that observed until the early 1980s (i.e., *Acropora palmata* dominance in the shallows, *Montastraea*-group dominance in the deeper areas) showed ecological persistence through time. Beginning in the late 1970s, in the matter of only a few decades, the shallow *Acropora* zone was lost on most reefs in the Caribbean (Hughes 1994; Gardner *et al.* 2003). The near-total disappearance of this well-established zonation pattern in such a short time raised considerable alarm (Pandolfi and Jackson 2006). While a temporary loss of the *A. palmata* zone via storm activity is a natural, and repetitive, occurrence (Blanchon and Jones 1997), the wholesale loss of this zone in many areas is a reason for concern (Fig. 4). It is believed that newly emergent diseases are the primary culprits of the spectacularly fast dieback of Caribbean *Acropora,* and beginning in the late 1990s similar phenomena affected *Montastraea* (Aronson *et al.* 1998; Bruckner and Bruckner 2006b; Edmunds and

Elahi 2007). While the Indo-Pacific has not experienced similar extensive ravages at the hands of coral diseases yet, severe outbreaks of corallivores, such as the crown-of-thorns starfish *Acanthaster planci* or the snail *Drupella cornus*, along with unprecedented levels of bleaching-related mortality (Baker *et al.* 2008) have taken their toll. It appears that also in the Indo-Pacific, well-established and apparently long-time stable zonation patterns might be at the tipping point.

For over >600 Ma of reef evolution the greatest threats to reefs were large-scale environmental perturbations. Obviously, when ocean basins disappeared, reefs disappeared with them, and nothing stands up against tectonic change. But climate change has always played an important role, with probably the greatest extinction of them all occurring at the Permo/Triassic boundary. Among other causes, it was due to cooling that made the tropics disappear (other factors, like increased volcanism that created huge epicontinental basalt flows and deleterious effects on atmosphere and water chemistry also contributed; Wood 1999). Almost every ice-house climate caused a severe reef, crisis. Climate rarely got too hot for reefs, and they persisted throughout the hot Cretaceous and PETM. However, changes in ocean chemistry may have triggered the evolution of the corallimorpharia—essentially naked corals without a skeleton (Medina *et al.* 2006). Every dramatic change in climate and/or ocean chemistry had some evolutionary consequence—and herein lies the true lesson. Since humans are manipulating these very factors (Karl and Trenberth 2003), we must expect major biotic upheaval. So what, if any, are the signs indicating that we might be steering toward a systemic modern reef crisis?

Modern Reef Crisis in the Anthropocene: Global Threats

The Anthropocene (Crutzen and Stoermer 2002, 2003) is the present time, dominated by the activities of *Homo sapiens* in all global aspects of ecology, geomorphology, and evolution. Humans are as efficient geomorphic change agents as riverine and glacial sediment transport (Haff 2003a,b). Evolutionary change in the Anthropocene is largely due to forcing extinctions (present extinction rates may exceed by 1000–10,000 times those before human intervention; Wilson 1988). There is general debate concerning exactly when the Anthropocene began (Crutzen and Steffen 2003; Ruddiman 2003), and for reefs we certainly do not know. Coral-reef science is relatively young, and therefore our documentation of ecological trends in the past is sketchy at best. While reefs were considered stable and well biologically accommodated ecosystems only three decades ago (Endean 1977; Connell 1978), the last two decades have revealed them to be very dynamic (Mumby and Steneck 2008). In the final decade of the 20th century it appeared that coral reefs had started to unravel ecologically on a worldwide scale, mostly due to large-scale changes in climate and environment brought on by human activities (Baker *et al.* 2008). While ultimately all threats caused distally (by changing climate) or proximally (by direct, local impact) from human activity can be considered man-made, we distinguish in the following between "global threats" by climatic or large-scale environmental phenomena that reef management has no or little control over, and "local threats" that refer to proximal, direct human impacts that can be regulated and avoided.

Atmospheric Warming and Bleaching

A major and apparently very recent threat to coral reefs, with the potential of negating success to all conservation efforts, is bleaching and associated coral mortality (Baker *et al.* 2008). Dinoflagellate symbionts of the genus *Symbiodinium*, referred to as "zooxanthellae," live within coral tissues. They exist in what is an obligatory association for the host coral, but not for the algae, which contribute photosynthates and aid calcification (Muscatine and

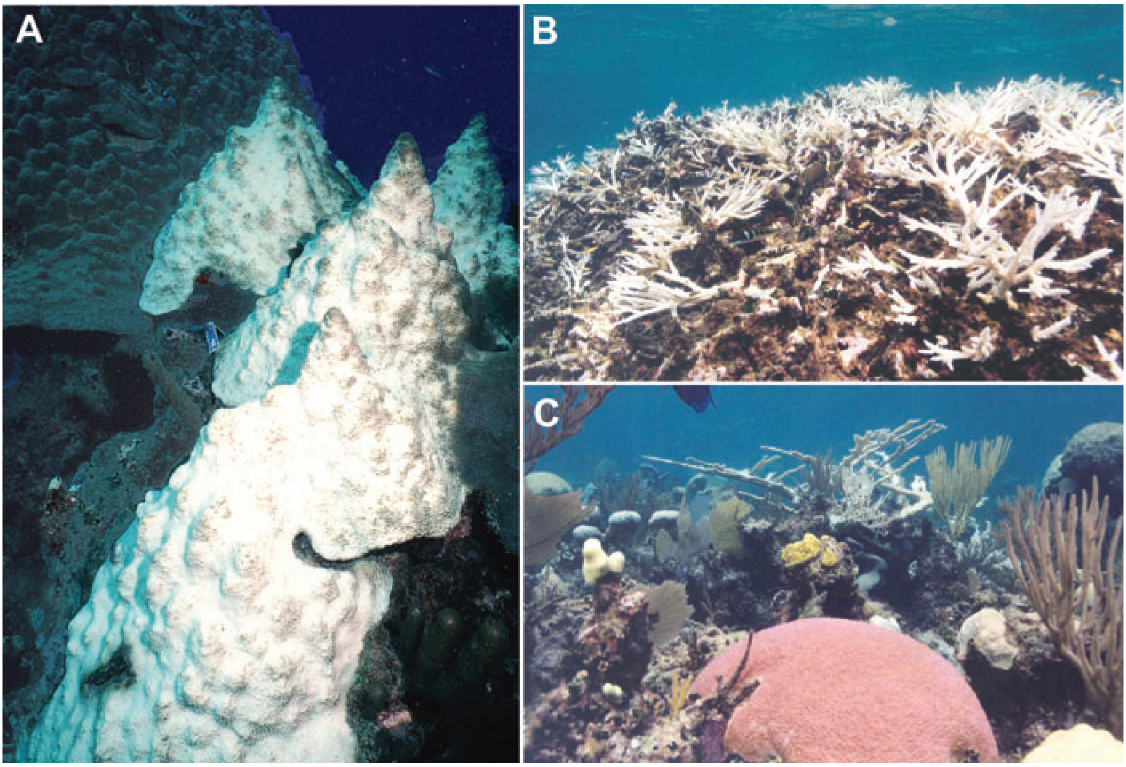

Figure 5. Bleaching is a discoloration of coral tissue due to loss of photosynthetic algae. (**A**) Partly bleached *Montastraea faveolata* from Puerto Rico. (Photo by A. Bruckner.) (**B**) Fully bleached *Acropora cervicornis*. (**C**) Nonphotosynthetic pigments give a bleached *Siderastrea siderea* an attractive pink color. The coral has, however, lost the photosynthetic pigments needed for survival. In the background, bleached *Montastraea annularis* and *Acropora palmate.* (B & C from Andros, Bahamas, 1998.)

Porter 1977). Stress caused by high temperature or irradiance damages the symbionts' photosynthetic system, leading to overproduction of oxygen radicals that damage the symbionts and their hosts (Goreau 1964). As a result, the symbionts can be expelled or die (Lesser 2006), turning the coral white since the yellow-brown pigmentation of the symbionts is lost—this phenomenon is referred to as bleaching. A variety of nonphotosynthetic pigments inside the corals may not be diminished during bleaching and corals can appear in a variety of attractive, mortality-masking pastel colors (Fig. 5). Bleaching events, when they occur, are usually not confined to corals alone, but can also affect numerous other organisms (gorgonians, soft corals, anemones, foraminifera; Hallock 2001; Hallock *et al.* 2006; Rodolfo-Metalpa *et al.* 2006).

Since at least one of the primary culprits of coral-reef bleaching appears to be elevated temperature, it comes as little surprise that in a rapidly warming world (IPCC 2007) the number of coral-reef bleaching events has risen dramatically since the early 1980s (Glynn 1993; Hoegh-Guldberg 1999; Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007; Baker *et al.* 2008). The frequency and scale of coral bleaching over the past few decades have been unprecedented, with hundreds of reef areas bleaching at some point, and occasionally even entire ocean basins affected (Fig. 6). Bleaching is often variable and patchy over micro (mm to cm) to meso (km) scales. This can be explained by fluctuations in environmental conditions, spatial heterogeneity of reef surfaces, genetic differences in hosts or symbionts, and differences in environmental history. Bleaching has been reported

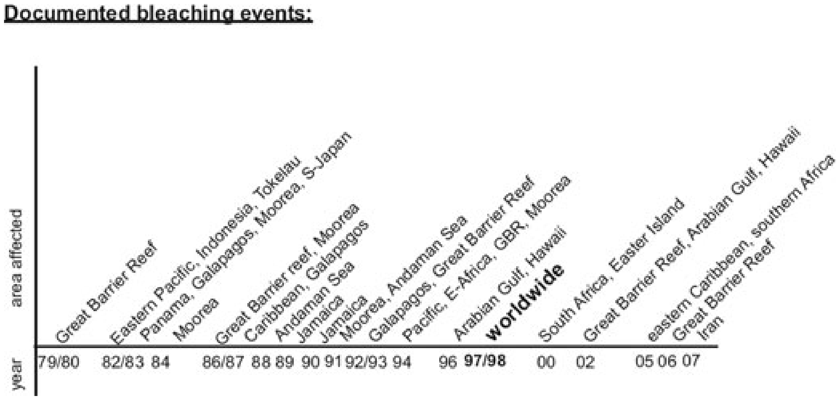

Figure 6. Documented bleaching events. ((**A**)from Baker *et al.* 2008) show that virtually all reefs around the world have been affected. The events here are only such with noticeable coral mortality. The frequency of bleaching events is predicted to increase (Sheppard 2003a).

from almost every coral-reef region and wherever corals occur (even if not reef building, like the Mediterranean; Cerrano *et al.* 2000; Rodolfo-Metalpa *et al.* 2006).

Corals and other reef organisms with zooxanthellae live very close to their upper thermal tolerance limits, which makes them susceptible to heat (~1.0 to 1.5°C above seasonal maximum mean temperatures). Interactions between temperature and light damage Photosystem II (Iglesias-Prieto *et al.* 1992; Fitt and Warner 1995; Lesser 1996; Warner *et al.* 1996, 1999; Jones *et al.* 1999; Brown *et al.* 2000). At high temperatures and light, the lipid composition of thylakoid membranes in the symbiont changes and degrades (Tchernov *et al.* 2004). Also increased nitric acid synthase accompanies bleaching (Trapido-Rosenthal *et al.* 2005). In general, bleaching results from accumulated oxidative stress on the thylakoid membranes of symbiont chloroplasts (Lesser 1996, 1997; Downs *et al.* 2002) as a result of damage to Photosystem II (see Lesser 2006 for review), which causes degradation and expulsion of the symbionts from host tissue. Protective mechanisms involve enzymatic antioxidants that degrade reactive oxygen species (Lesser *et al.* 1990), and also the xanthophyll cycle can dissipate excess absorbed energy (Brown *et al.* 1999). While other stressors, like low temperatures (Coles and Jokiel 1977; Glynn and D'Croz 1990; Coles and Fadlallah 1991; Hoegh-Guldberg *et al.* 2005), can also cause bleaching, light/heat interactions cause the majority of events on tropical reefs.

Coral bleaching is patchy both on the scale of reefs and individual corals. This is a result of interaction between environmental stressors and the patchy distribution and/or zonation of different *Symbiodinium* within and among coral species (Rowan and Knowlton 1995; Rowan *et al.* 1997). Within the coral, different types of zooxanthellae are found. Since these can respond differently to environmental stressors, the distribution of symbiont diversity within and among coral colonies and species can influence patterns of bleaching, and the proportion of the symbiont clades may change following a bleaching event. *Symbiodinium* in clade D (particularly D1a) are resistant to elevated temperature conditions (Rowan 2004) and can remain much longer in coral-host tissues than other clades (Baker 2001; Glynn *et al.* 2001; Baker *et al.* 2004; Berkelmans and van Oppen 2006; Jones 2008). Thus, the heat resistance of corals may indeed be linked to the type of zooxanthellae they harbor. Buddemeier and Fautin (1993) suggested in their "adaptive bleaching hypothesis" that changes in algal symbiont communities following bleaching might be a mechanism allowing coral adaptation to environmental change—a point still very much in debate. Goulet and Coffroth (2003) and Iglesias-Prieto *et al.* (2004) found no change in symbionts after bleaching or transplantation, while Baker (2001) recorded shifts in symbiont communities in several species of Caribbean coral following bleaching due to irradiance stress and showed that corals that changed their symbiont communities experienced less mortality. Glynn *et al.* (2001) showed that corals containing clade D did not bleach, while those with clade C bleached severely. Baker *et al.* (2004) and Berkelmans and van Oppen (2006) observed increases in clade D after bleaching or after transplantation to hotter sites. Clade D was found more commonly on reefs recently affected by bleaching (e.g., Kenya) and on reefs routinely exposed to high temperatures (e.g., Arabian Gulf), but rarely on reefs not exposed to high temperatures (e.g., Red Sea), or without a history of recent severe bleaching (e.g., Mauritius). Also, Jones (2008) showed that 71% of colonies changed their symbiont communities to more heat-tolerant types following bleaching, with many corals shuffling preexisting symbiont communities at the colony level. All this would suggest that some natural protection mechanisms to bleaching indeed exist.

Bleaching events are predicted to recur more rapidly due to global warming (Sheppard 2003a). Bleaching is episodic, with the most severe events typically accompanying coupled ocean–atmosphere phenomena, such as the ENSO, which result in sustained regional elevations of ocean temperature (Glynn 1993, 1996). Bleaching episodes have resulted in catastrophic loss of coral cover in some locations and have changed coral community structure in many others, with a potentially critical influence on the maintenance of biodiversity in the marine tropics (Fig. 7). This has led many to develop models of coral-reef dynamics in future accelerated bleaching dynamics, none of which are particularly optimistic (Done 1999, Hoegh-Guldberg 1999; Sheppard 2003a; McClanahan *et al.* 2007b). Bleaching has also facilitated or initiated increases in coral diseases, the breakdown of reef framework by bioeroders, and the loss of critical habitat for associated reef fish and other biota (Jones *et al.* 2004; Pratchett *et al.* 2008). Secondary ecological effects, such as the concentration of predators on remnant surviving coral populations, have also accelerated the pace of decline in some areas.

Baker *et al.* (2008) studied the regeneration of coral reefs after bleaching events in a meta-analysis of published data and found variable rates of recovery among sites. In some cases it was high enough to be detected within only 2 years (Maldives), while no recovery was observed in other locations, even over 20 years (Galapagos). The rate of recovery did not appear to be related to the severity of the bleaching disturbance, and the degree of recovery was not related to the amount of coral cover remaining after the disturbance. Many reefs with high coral cover also continued to decline after a bleaching event (Cook Islands, U.S. Virgin Islands). Other reefs with low cover regenerated rapidly (Arabian Gulf recovered from 0% to 42% in 9 years; American Samoa recovered from 6% to 40% in 4 years). Numerical experiments (Fong and Glynn 2000; Riegl and Purkis 2009) show that even with repeated and severe bleaching mortality, at least limited recovery is possible given enough asexual regeneration or connected populations. However, changes in community structure must be expected at high bleaching recurrence. In particular, *Acropora* dominance may be compromised—model predictions and empirical observations (McClanahan *et al.* 2007b) seem to conform.

The species documented by Baker *et al.* (2008) with most potential for successful regeneration were mostly broadcast spawners (Harrison and Wallace 1990). This may be due to a different life-history strategy, with larvae spending more time in the water column than those of brooders and dispersing further from the parent, thus reducing the extinction debt (see text under heading "Potential for Extinction"). While recruitment is important,

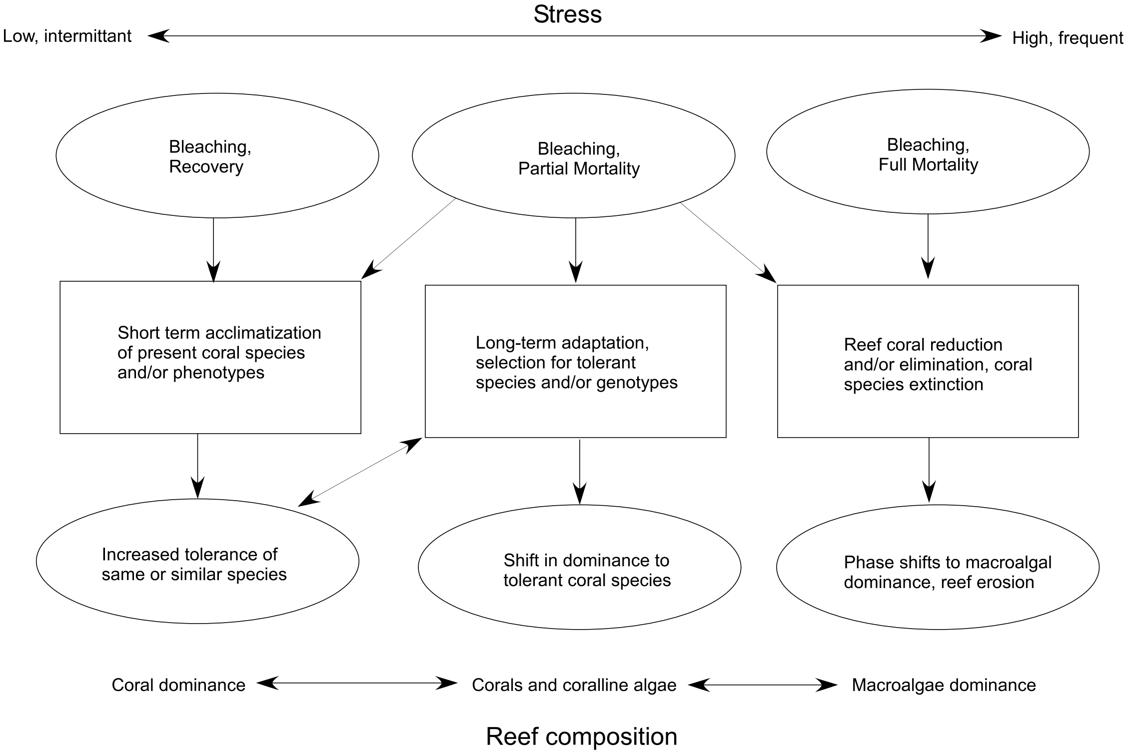

Figure 7. Conceptual model outlining the possible responses of coral communities to bleaching, in particular when events recur with increasing frequency, as predicted by global change scenarios (Coles and Brown 2003.)

the maintenance of reef framework is key for the conservation of biodiversity associated with corals. Loch *et al.* (2004) observed that collapsing *Acropora* tables, victims of the preceding bleaching, effectively negated the otherwise high recruitment success in the Maldives. The secondary effects of bioerosion continued to degrade potential settlement substrates, an observation also made by Sheppard *et al.* (2002) in the Chagos Archipelago. Thus, not only settlement substratum and coral recruits are lost, but also niche space for much associated fauna (Pratchett *et al.* 2009).

Clearly, coral bleaching, largely caused by global warming, is a major challenge for the conservation of coral reefs. It is unclear whether bleaching can be managed, but emphasis is put on attempting to minimize additional stressors, since bleaching is known to facilitate the outbreak of diseases and to weaken corals (Marshall and Schuttenberg 2006a, 2006b; Bruno *et al.* 2007). Most strategies to manage bleaching by restoring or maintaining ecosystem resilience search to identify areas less prone to bleaching, thus allowing conservation efforts to have the greatest opportunity for success. Proposed actions are to (1) identify local physical or environmental conditions that naturally protect reefs from bleaching, and (2) use climate models to identify coral-reef areas or regions most likely to escape the worst effects of warming (Baker *et al.* 2008). Coupled ocean–atmosphere climate models can help to forecast bleaching stress on reefs (Hoegh-Guldberg 1999; Donner *et al.* 2005), but other approaches to estimate bleaching susceptibility are also used (McClanahan *et al.* 2007a; Kleypas *et al.* 2008), including, for example, attempts to use the relative abundance of heat-tolerant *Symbiodinium* in corals to help identify relatively bleaching-resistant reefs. Other, more hands-on suggestions include shading corals, sprinkling reef surfaces with water to increase evaporative cooling and reflection of UV (Baker *et al.* 2008), or even feeding corals since increased heterotrophy seems to benefit bleached corals (Grottoli *et al.* 2006).

However, the most efficient possible management action would be a more responsible use of fossil fuels to slow the global greenhouse effect.

Seawater Chemistry and Reef Building

A major concern in all scenarios regarding the future of coral reefs are changes in seawater chemistry, most particularly acidification of ocean waters concomitant with rises in atmospheric CO_2 concentration. During Earth history, seawater chemistry has changed repeatedly and dramatically, and with it the ability of marine skeletal organisms to calcify. Hardie (1996) showed these large-scale, secular changes (Fig. 8) to be most strongly influenced by rates of seafloor spreading that change the Mg/Ca ratio in seawater, which strongly affects the type of calcium carbonate that can be precipitated by marine skeletal organisms (primarily aragonite at ratios >2, and calcite at ratios <1; Stanley 2006). Conflicting information exists about evolutionary consequences of changes in seawater chemistry for reef-builders. Some observed important consequences (Stanley and Hardie 1998) and claim that major extinctions were related to changes in ocean chemistry (Veron 2008a,b), while others find no correlation (Kiessling *et al.* 2008). In the modern ocean, the most important cause of seawater chemistry change is the anthropogenic enrichment of the atmosphere with CO_2, nitrogen, and sulfur (Doney *et al.* 2007). While mean atmospheric CO_2 ranged in the past 650.000 years between 200 and 300 parts per million (ppm), it now reached about 387 ppm and could reach 540–970 ppm by 2100—an increase about 100 times faster than over the past 650 ky (Fabricius 2008). Only half of the CO_2 that reaches the atmosphere remains there—$\sim$20% is absorbed by land and $\sim$30% by the sea—resulting in acidification and shifts in the production of bi/carbonate ions (Fig. 9). Increased availability of CO_2 lowers ocean pH and shifts the balance toward more formation of bicarbonate versus carbonate ions, making the precipitation of calcium carbonate more difficult (Kleypas and Langdon 2006; Kleypas 2007). The topic has received much recent review elsewhere (Stanley 2006; Guinotte and Fabry 2008), and we will be brief here. Present atmospheric CO_2 concentrations are the highest in the past 650,000 years and are expected to increase rapidly (Guinotte and Fabry 2008). This has the effect of reducing the present aragonite supersaturation (already down from 4.6 to 4.0 since preindustrial times; Kleypas *et al.* 1999; Hoegh-Guldberg *et al.* 2007) and thereby with the capability of many organisms to calcify efficiently (Kleypas 2007; Jokiel *et al.* 2008). The present decline in aragonite supersaturation and the ease of its precipitation in skeletons is being changed predominantly by pH in the modern ocean, via uptake of atmospheric CO_2 in contrast to shifts in the Mg/Ca balance in the fossil ocean. This illustrates the increasing disequilibrium in the ocean that is being created by atmospheric changes (Kleypas 2007). Unfortunately, among the organisms of concern are the major reef-builders and many of the important calcifiers in the plankton. Furthermore, increased levels of dissolved CO_2 seem to lead to synergisms with other damaging chemical factors such as nutrient enrichment, leading to increased coral mortality (Renegar and Riegl 2005). Some organisms can maintain, even increase, calcification in seawater; however, this can come at a cost of reduced muscle mass (Wood *et al.* 2008).

Corals do not necessarily die when subjected to conditions unfavorable to the production of aragonite skeletons. When subjected to seawater equivalent of calcite-ocean acidity (and Mg/Ca ratio; i.e., conditions simulating a Cretaceous ocean), coral growth decreased and they produced a calcite, instead

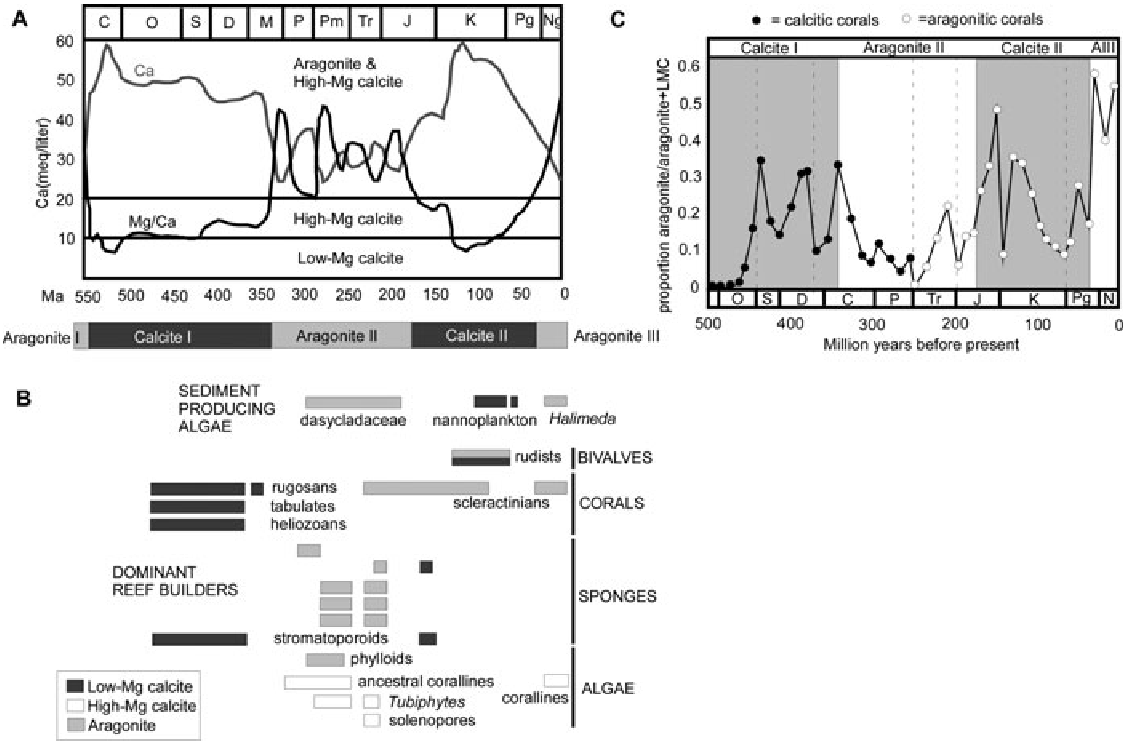

Figure 8. Aragonite and calcite seas with their faunas throughout earth history. (**A**) Temporal variability through geological time of the Mg/Ca molar ratio in seawater and the nucleation field for aragonite, high-Mg calcite, and low-Mg calcite. (**B**) Skeletal mineralogy of some dominant reef-builders through time. Aragonitic corals persist into the Cretaceous calcite sea, as do rudists, which have a part-aragonite skeleton. (From Stanley 2006.) (**C**) Proportional abundance of stony corals in macrofaunal assemblages (proportions are counts of genera with aragonite skeletons over the sum of aragonite and low-Mg calcite occurrences). This shows that coral was calcitic in the Paleozoic, but aragonitic in the Meso- and Cenozoic. The major evolutionary events do not coincide with changes in seawater chemistry, but with mass-extinction events (*vertical dotted lines*). (From Kiessling *et al.* 2008.)

of an aragonite, skeleton (Ries *et al.* 2006) or stopped making a skeleton altogether (Fine and Tchernov 2007). Skeletal growth resumed when acidity was again in an acceptable range. It is assumed that double preindustrial atmospheric CO_2 concentrations will lead to a 20–60% reduction in calcification (Langdon *et al.* 2006; Kleypas and Langdon 2007), which would then presumably lead to vastly increased bioerosion rates (Guinotte and Fabry 2008). Calcification by coralline red algae was found to decrease dramatically in acidification experiments (Jokiel *et al.* 2008). In short, it appears as if the most important modern reef-builders will precipitate much less skeleton in more acidic oceans. From the geologic record, it has been demonstrated that reef building apparently progressed slower in calcite seas (Stanley 2006); however reef-builder diversity was not affected by large-scale changes in ocean chemistry (Kiessling *et al.* 2008). In today's ocean and under the currently observed extremely rapid rate of acidification, not only shallow-water coral reefs are at risk. Since the aragonite saturation horizon is moving toward the surface at a rate of 1–2 m per year (Guinotte and Fabry 2008), it is believed that deepwater coral reefs, probably the most biodiverse system at greater ocean depths, may be sooner at risk than their brethren in the photic zone (Turley *et al.* 2007).

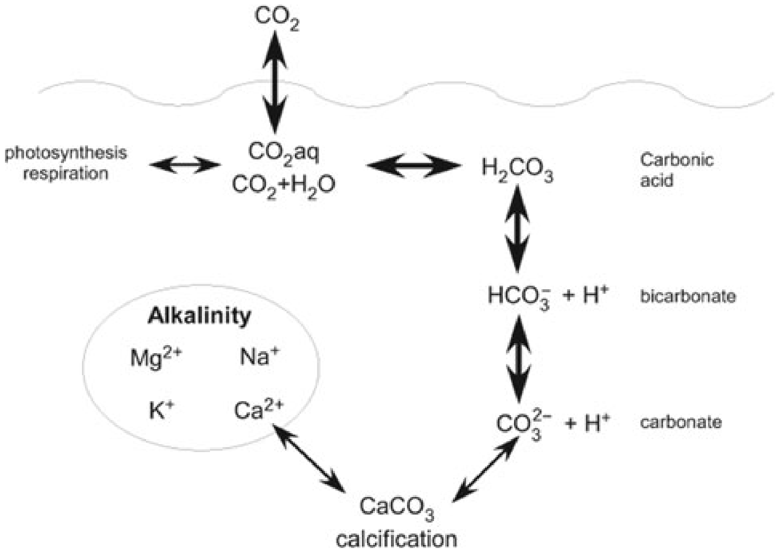

Figure 9. The carbonate system in seawater. (From Kleypas 2007) CO_2 entering the ocean forms (weak) carbonic acid, which rapidly dissociates to bicarbonate (HCO_3^-) or carbonate (CO_3^{2-}). Total CO_2 is the sum of HCO_3^-, CO_3^{2-}, and dissolved CO_2 in seawater. Total alkalinity is the excess positive charge in seawater that can be changed by shifts in the availability of Mg^{2+} and Ca^{2+}. The proportion of HCO_3^- and CO_3^{2-} adjusts to balance this positive charge. Throughout Earth history, the major secular changes in seawater chemistry were primarily via changes in the Ca^{2+}/Mg^{2+} ratio, which forced adjustment of the bicarbonate/carbonate component. In the modern ocean, unusually strong CO_2 input forces the bicarbonate/carbonate system by favoring bicarbonate over carbonate, which leads to decreases in calcification.

Projections from Orr *et al.* (2005) suggest that by the end of the century, 70% of deepwater reefs could be situated in a zone of aragonite undersaturation, while today more than 95% are situated in the supersaturated zone. This trend is disconcerting and might severely compromise the functioning of these ecosystems.

Clearly, acidification is as big a challenge for the conservation of coral reefs as any other factor. It appears that the only management action possible is a more responsible use of fossil fuels since we cannot otherwise regulate how much CO_2 enters the oceans. While the prospects of ocean acidification are certainly a potential threat to the future viability of corals, much remains to be learned about its exact mechanisms with regards to coral health and long-term effects on reef building (Kleypas and Langdon 2006; Kleypas 2007). Nonetheless, concern is big enough that some claim acidification could cause a mass extinction of coral reefs (Veron 2008b).

Diseases Old and New

Coral diseases are one of the biggest threats to the conservation of coral reefs and are predicted to become ever more prevalent with global change (Harvell *et al.* 2007). Diseases have primarily ravaged Caribbean reefs and led to an interruption of long-established ecological patterns yet they are beginning to invade the Indo-Pacific as well (Fig. 10). Occurring globally in most coral-reef habitats whether near human population centers or remotely offshore, their prevalence is generally low. Localized outbreaks have produced significant mortalities of scleractinian corals, gorgonians, sea urchins, reef fish, sponges, algae, and other coral reef organisms (Peters 1993;

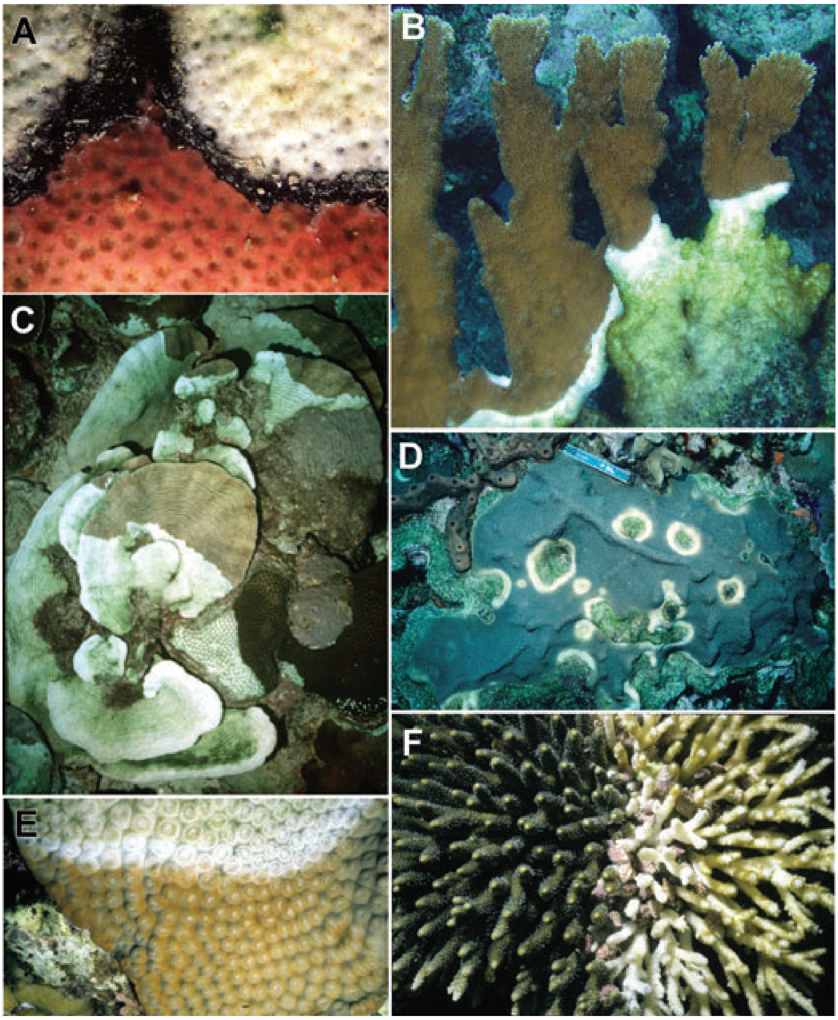

Figure 10. Coral diseases are apparently an emergent problem, since their frequency is seemingly increasing. (**A**) Black-band disease on the Caribbean *Siderastrea siderea*, is the oldest known coral disease. (**B**) White-band disease on *Acropora palmata* has ravaged *Acropora* populations throughout the Caribbean. (**C**) White plague on Caribbean *Agaricia lamarcki*. (**D**) Several yellow-band-disease infections on Caribbean *Montastraea faveolata*. (**E**) White syndrome on Indo-Pacific *Diploastrea heliopora*. (**F**) Corallivorous gastropod *Drupella cornus* destroying an Indian Ocean *Acropora* sp. Outbreaks of these voracious predators have reached plague proportions in Australia and the Red Sea. (All photos by A. Bruckner.)

Harvell *et al.* 1999; Williams and Bunkley-Williams 2000). In corals, additional to tissue-loss, diseases can cause significant changes in reproduction, growth, species diversity, abundance, and size structure.

Between 1972 and 2005 coral diseases were reported on 39 coral genera and 148 species worldwide, with observations in 63 countries. Although Pacific reefs have a higher diversity of reef-building corals than the Atlantic and harbor 92% of the world's coral reefs (Spalding and Greenfell 1997), only 14% of the global observations of coral disease were from the Indo-Pacific (Green and Bruckner 2000; Sutherland *et al.* 2004). The first Caribbean epizootics were reported in 1978 and led to die-offs of two dominant structure-forming corals, *A. palmata* and *A. cervicornis*. Between 1982 and 1984, a disease of unknown cause decimated populations of a keystone species, the herbivorous sea urchin *Diadema antillarum*. This mortality triggered increases in fleshy macroalgae and concurrent losses of coral cover, biodiversity, and habitat in many locations (Lessios *et al.* 1984; Hughes 1994; Aronson and Precht 2001). Since 1998 there has been an emergence of new and virulent diseases in the wider Caribbean, where over 30 named diseases affect 45 species of scleractinian corals, 3 hydrozoan corals, 10 octocorals, 2 zoanthids, 9 sponges, and 2 crustose coralline algae (Green and Bruckner 2000; Weil *et al.* 2006; Fig. 10). Thus the Caribbean has been referred to as a "hotspot" for disease, largely because of the rapid emergence, high prevalence, wide distribution, large number of host species, and virulence of diseases in this region—and, not least, the large body of research. Much less is known about the Indo-Pacific, but surveys there revealed new diseases, suggesting either a rapid emergence of diseases or a new realization of their presence.

While first described in the western Atlantic over 35 years ago (Antonius 1973), the realization of diseases as a significant factor accelerating the deterioration of coral reefs is relatively recent (Epstein *et al.* 1998; Harvell *et al.* 1999; Green and Bruckner 2000; Sutherland *et al.* 2004; Weil 2004). Over half of all published coral disease records up to the year 2005 were for black-band disease (BBD, Fig. 10A), white-band disease (WBD, Fig. 10B), and white plague (WP, Fig. 10C) (Antonius 1973; Dustan 1977; Gladfelter 1982). Since the mid-1990s new diseases have been reported with increasing frequency, including four [dark-spot disease (DSD), yellow-band disease (YBD), white pox disease (WPX), and aspergillosis (ASP, Table 1] that are widely distributed and four (YBD, WPX, WP-II, and ASP) that are causing substantial coral mortality (Porter *et al.* 2001; Kim and Harvell 2002; Williams and Miller 2005; Bruckner and Bruckner 2006a, 2006b). Close to 80% of all western Atlantic coral species are now affected (45 scleractinian corals, 8 gorgonians, 2 hydrozoan corals), with some corals (especially *Montastraea annularis* complex) susceptible to as many as eight diseases and individual colonies showing signs of two to three diseases at any one time (Weil 2004; Bruckner and Bruckner 2006a, 2006b; Fig. 10D). Indo-Pacific corals had been known to have tumors (growth anomalies, Squires 1965), and diseases similar to those in the Caribbean (BBD and WBD; Antonius 1985, 1987, 1988), but recently many new diseases were identified [Table 2; white syndrome, yellow band, skeletal eroding band (SEB), and *Porites* ulcerative white spots; Littler and Littler 1996; Korrubel and Riegl 1998; Riegl and Antonius 2003]. Currently, *Acropora*, *Pocillopora,* and *Porites* appear to be most susceptible.

The recent emergence of diseases in the wider Caribbean may be unprecedented over a millennial time scale (i.e., >3800 yr) (Aronson and Precht 2001). Unfortunately, characterization of the cause, prevalence, and consequences of most disease outbreaks is limited or nonexistent. While hundreds of studies have been published, the causative agent has been confirmed for only five diseases (Raymundo *et al.* 2008). Other infections may be caused by opportunistic, nonspecific pathogens that exploit compromised health state of corals when exposed to environmental stressors (Lesser 2006). Thermal anomalies and bleaching events seem to be followed by outbreaks of disease (Harvell *et al.* 2001; Bruno *et al.* 2007; Miller *et al.* 2006). Changing environmental conditions could affect corals and lower their ability to fight infection and increase the virulence of potential pathogens (Rosenberg and Ben-Haim 2002). Pollution, nutrient loading, sedimentation, and any other anthropogenic stressors could further reduce coral health, alter the composition and virulence of the microbial community found in the surface mucopolysaccharide layer of corals, and reduce their resistance to pathogenic organisms (Ritchie 2006).

Obviously, diseases pose a major challenge for the conservation of coral reefs. Traditional management tools for human and wildlife

TABLE 1. Major Diseases Observed in Western Atlantic Scleractinian Corals and Gorgonians

Syndrome	Synonym	Host range	Prevalence/impact	Rates of tissue loss
White-band disease (WBD)	White-line disease; white death; white plague, WBD type II	*Acropora palmata, A. cervicornis, A. prolifera*	1–80% or more; most common in dense populations; up to 98% mortality over two decades	5 mm/day in 1970s; up to 2 cm/day today
Plague Type I (WPX)	White plague	13 species	1–4% average; up to 73% of individual species; maximum of 20–30% mortality	3.1 mm/day
White-plague type II (WP II)	Plague type III, white-band disease, white-line disease	40 species of plating and massive corals	<1–58%; losses of up to 38% of corals from a single outbreak	2–10 cm/day
White-patch disease (WPD)	White pox; patchy necrosis	*A.. palmata*	<1–100%; caused 87% loss of *A. palmata* in Florida from 1996 to 2002	2.5 cm^2/day
Black-band disease (BBD)	Black-line disease	24 scleractinian corals, 1 hydrozoan, 6 gorgonians	Mean <0.2–3%; up to 50% in isolated areas; increase during summer; typically causes partial mortality	3 mm–1 cm/day; various, depending on species, depth, and season;
Yellow band disease (YBD)	Yellow-blotch disease; ring bleaching[1], yellow-pox disease[2]; yellow-band syndrome[3]	*Montastraea annularis* complex, *M. cavernosa;* possibly other faviids and; *A. agaricites*	1–86%; infections may last 5–10 years until coral dies; caused losses of 40–80% of *M. annularis* over 10 years in Puerto Rico	Mean = 0.5 cm/month in winter and 1 cm/month in summer; max = 3 cm/month
Dark-spots disease (DSD)	Dark-spot disease, dark-spot syndrome; ring disease, DSD type II; purple-band syndrome	11 species; mostly *M. annularis* (complex), *Siderastrea spp.; Stephanocoenia intersepta,* and *Agaricia agaricites*	Up to 94%; increases during summer.	0.5–1.33 cm^2/month
Caribbean ciliate infection (CCI)	Skeletal eroding band (SEB)	26 species, especially *Dichocoenia, Montastraea, Acropora*	Up to 25%, increases in summer	1.2 cm/month in winter; 2.6 cm/month in summer
Growth anomaly	Hyperplasia, calicoblastic epithelioma, tumors. Gigantism, area of accelerated growth, chaotic polyp development	*Acropora, Diploria, Colpophyllia, Montastraea, Agaricia, Porites, Dichocoenia, Madracis*	Generally rare; can affect all corals in restricted area	<1 cm/month
Aspergillosis (ASP)	Sea-fan disease	7 species, 5 genera of gorgonians	8–60%; 31% mean in Florida in 1997, declined to 6% by 2003: >50% loss of sea-fan tissue area over 6 years, due to loss of largest sea fans	Not reported

TABLE 2. Major Diseases of Indo-Pacific Scleractinian Corals

Syndrome	Location	Host species	Prevalence	Impact
Black-band disease	Australia, Egypt, Fiji, India, Jordan, Papua New Guinea, Philippines, Saudi Arabia, Tonga, South Africa, CNMI, Palau	19 genera, 49 species; *Pocillopora, Acropora,* and faviids most frequently affected	Generally <1%; outbreaks of up to 50% in restricted areas	Average spread of 3 mm/day; mostly causes partial mortality
White syndrome	Egypt, Australia, Solitary Islands	38 species 1 *Turbinaria, Acropora, Goniastrea, Pocillopora, Stylophora,* and *Porites*	Increased 20-fold in Australia between 1998 and 2003	Up to 2–4 cm/day with 3–20% coral mortality during outbreaks
Ulcerative white-spot disease	Philippines, East Africa, Indonesia, Guam, Palau,	*Porites: 7 species; Echinopora, Goniastrea, Heliopora, Favia, Montipora*	Up to 82% of susceptible corals; increases in summer	Slow spread, lesions 2–5 mm in diameter
Vibrionic bleaching	Mediterranean, Israel, Tanzania	*Oculina pategonica; Pocillopora*	All corals may have *Vibrios* that become pathogenic at high temperatures	Can cause bleaching and tissue sloughing if temperatures elevated for long periods
Atramentous necrosis	Florence Bay and Bright Point, Australia	*Montipora Acropora Echinopora, Turbinaria, Merulina*	Unknown	Unknown
Growth anomalies	CNMI, Australia, Hawaii, Guam, Palau, Enewetak, French Polynesia, New Caledonia, Maldives, Micronesia, Marshall Islands, Japan, Oman, China, Philippines	*Acropora, Pocillopora, Pavona, Fungia, Madrepora, Montipora, Platygyra*	Generally <1%, but lesions increase in number on affected corals	Unknown
Pink-line syndrome	Papua New Guinea, Sri Lanka, Kavaratti Island, Indian Ocean	*Porites*	Increased from 20% in 1996 to 80% in 1999 in one location	Unknown
Fungal syndrome	East African Coast	*Astreopora, Montipora, Echinopora, Acropora, Goniopora, Platygyra,* massive *Porites, Pocillopra, Goniastrea Hydnophora, Cyphastrea*	Unknown; single event in 2002 caused extensive colony mortality	Unknown
Plagiosporus trematode infection	Hawaii	*Porites compresssa, P. lobata*	Not reported to kill corals	Does not advance; colony may have multiple infections
Skeleton eroding band (SEB)	Australia 3 Egypt, Jordan 1 PNG, Mauritius 2, Australia 2	21 genera scleractinian corals, 1 hydrozoan	In Australia increased 20× in summer	1 mm/week to 1 mm/day
Yellow-band disease	United Arab Emirates; Arabian Gulf; Iran2	4 genera, 12 species	Unknown?	9.4 mm/week in winter; 19.7 mm/week in summer
Brown-band disease	Australia	*Acropora, Pocillopora, Echinopora,* 16 spp.	Generally rare; 0.3% in Australia	Unknown

diseases such as quarantine, culling, and vaccinating are not viable options. The oceans, as well as the corals themselves, support vast and diverse microbial communities, some of which may be pathogenic or potentially so, and we are just beginning to understand the complex relationships between the coral and its associated microflora. The coral holobiont is a complex consortium involving beneficial surface bacteria as well as potential pathogens, and indiscriminate use of antibiotics may harm this beneficial microbial community. Various treatments, like removing infectious agents by aspirator, covering the area with underwater putty that forms an impermeable barrier preventing spread of the disease, or even phage therapy (Efrony *et al.* 2007) have been tried. But these methods are costly and time-consuming and likely viable only to save certain high-value colonies, such as particularly large, long-lived corals (Raymundo *et al.* 2008).

Since disease outbreaks may be facilitated by high nutrient levels and temperatures (Bruno *et al.* 2003; Lesser 2004; Marshall and Schuttenberg 2006a), remedial actions that reduce land-based pollution and other direct human impacts may improve the coral's chance of resisting or recovering from infections. Some mortality by diseases may have been facilitated by bleaching events that weakened the corals (Lesser 1997; Miller *et al.* 2006). Therefore, any reduction of stresses would be to the coral's advantage. Improved watershed management and better waste-water treatments have the potential to reduce nutrient levels, thereby reducing macroalgae, which stress a coral through direct contact and also may provide refuge for certain pathogens (Nugues *et al.* 2004). And again, a more rational and responsible way of using fossil fuels to slow temperature rise would be at the core of successful management, since it might alleviate global warming, which not only stresses corals with heat but also increases moisture content in the atmosphere, leading to more precipitation that can deliver nutrients and pathogens to the reefs.

Predator Outbreaks

Spectacular depredation has been visited onto coral reefs by outbreaks of organisms that prey on living coral. In the Indo-Pacific, the most notable of these are the crown-of-thorns starfish (COTS) *Acanthaster planci* and the coral-eating snails *Drupella cornus* (Turner 1992; Schuhmacher 1992; Fig. 10F). In the Caribbean, the primary predator is the coral-eating snail *Coralliophila abbreviata* (Bruckner *et al.* 1997; Baums *et al.* 2003), but other corallivores, such as the fireworm (*Hermodice carunculata*), stoplight parrotfish (*Sparisoma viride*), and three-spot damselfish (*Stegastes planifrons*), are of growing concern, especially as coral populations are reduced and corallivores experience reduced predation pressure due to overfishing of their predators. Interestingly, while Caribbean reefs have been racked by diseases, predator outbreaks have been relatively mild, with the opposite situation in the Indo-Pacific. The best-studied and most devastating organism is the COTS, the outbreaks of which have been widely studied in the literature. It is now believed that a certain level of infestation will always plague coral reefs, and it is assumed that the clearly pulsed population outbreaks may be natural. However, it is also possible that anthropogenic nutrification of coastal waters favors the phytoplankton on which both starfish and corallivorous snail larvae feed, thus enabling a higher survival rate that then leads to outbreaks of adult populations (Birkeland 1982; Ayukai *et al.* 1997). It has also been surmised that removal of other predators, like the triton shell *Charonia tritonis*, a voracious predator of starfish, allows coral predator populations to go unchecked.

Bradbury *et al.* (1985a,b) investigated COTS outbreaks on the Great Barrier Reef (GBR) from a theoretical ecological viewpoint with qualitative models harnessing graph theory and were able to make a case for the existence of metastable points, cycles, and chaos (Fig. 11). The observed dynamics conformed to the ecological theory (May 1973, 1975, 1976)

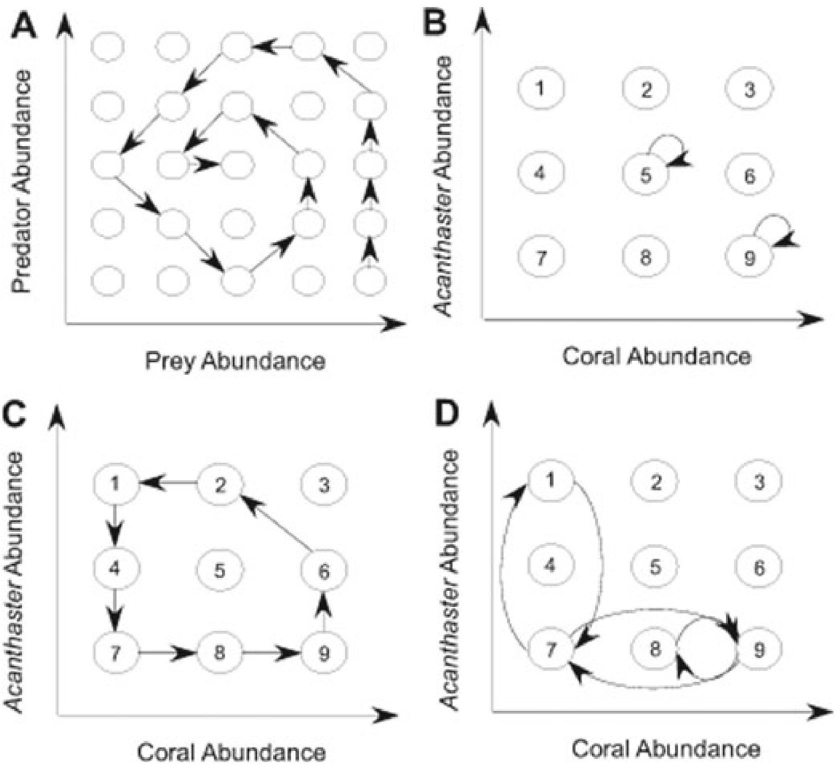

Figure 11. Phase-space approximation of predator–prey dynamics as envisaged by Bradbury *et al.* (1985a,b) for the crown-of-thorns (COTS)/coral system. (**A**) Shows the general phase-space representation of a stable equilibrium point. Wherever started on the phase lattice, the system will converge toward the stable point. Such a pattern would be exhibited by regular Lotka–Volterra type dynamics. (**B**) Metastable states observed in the Great Barrier Reef (GBR) coral system. The loop returning to the starting point indicates that the system "rests in itself" and will not transit into another state (in appreciable time). Some reefs seem to persist indefinitely with high coral/low COTS or medium coral/medium COTS. (**C**) Expression of a stable cycle, also as observed in the GBR. Some reefs go through cycles from high coral/high COTS (outbreak) to low coral/high COTS, to regeneration of high coral/low COTS. (**D**) Some reefs express chaotic "flip-flops" between high/low COTS and/or high/low coral.

of endogenously driven cyclicity. According to Bradbury *et al.* (1985a,b), the most likely asymmetries driving qualitatively stable cycles would be asymmetrical predator preferences or lags in the responses of predator and prey to each other due to the disparate nature of reefs in space. Recruitment, reproduction, and growth, would be other logical factors (Birkeland 1982; Ayukai *et al.* 1997). The distribution of these asymmetries over space would in itself be an interesting indicator of how uniform large reef-complexes are in their internal dynamics, that is, whether these reef systems consist of a multiplicity of separate bounded ecosystems or whether general models can hold over the entire system.

Whatever the causes, coral predator outbreaks have been intensely managed. From early on, volunteers and paid workers have responded to COTS outbreaks by gathering up the starfish and bringing them onshore for burial, or giving them lethal injections (Yamaguchi 1986). Similarly, divers have collected corallivorous snails in an effort to reduce their populations (Turner 1992). While some outbreaks could be controlled, others were simply too big to allow the divers' efforts to make any dents into the vast numbers of predators.

Again it appears that a more responsible management of our watersheds might be the best insurance for life in the sea. If nearshore nutrification is indeed a root cause for these outbreaks via increased phytoplankton availability for predator larvae, then better watershed management will be required. This will, however, require improved interagency cooperation, since frequently the land and the sea are managed by different government departments.

Alien Species and the Integrity of the Local Ecosystem

Invasions by introduced (alien) species have been ranked among the most potential perturbations of marine ecosystems (Carlton 1994), and alteration of habitats and food webs by invasive species has been proposed as a major factor in degradation of coral reefs (Birkeland 2004). Most information is available from harbors, the logical entry point for marine introductions, and much less from coral reefs (Coles *et al.* 1999a,b, 2004; Paulay *et al.* 2002; Hewitt 2002; Buddo *et al.* 2003; Ray 2005). However, in harbors most invasions originate and many species escape onto the reefs. Of the 85 introduced marine species on Guam, 23% occurred on reefs outside of Apra Harbor (Paulay *et al.* 2002), and from 28 introduced species in Pago Pago Harbor on Tutuila, American Samoa, six made their way onto coral reefs (Coles *et al.* 2003). Of ~100 introduced and cryptogenic (of uncertain origin) species in Hawaiian harbors and Kāneohe Bay, 54 were found on reefs in the main Hawaiian Islands (max. 23 at a single site; Coles *et al.* 2006). None of these species were considered invasive, that is, monopolizing habitat or excluding native species, at any reef site. Further afield from busy ports, only ten introduced or cryptogenic species were found at Johnston Atoll (Coles *et al.* 2001), two at French Frigate Shoals (DeFelice *et al.* 2002), and three at Midway in the northwestern Hawaiian Islands (DeFelice *et al.* 1998).

Introduced or invasive species can become a major threat and disrupt reef communities, especially when the latter are subject to other disturbances. A striking example is Kaneohe Bay (Oahu, Hawaii), where reefs in the south basin experience low circulation, have restricted exchange with open ocean water, receive urban storm runoff, and had received sewage for about 20 years that produced eutrophication and caused a shift from corals to sponges and ascidians. After removal of the sewage outfall in 1997, substantial coral recovery occurred, but subsequently invasive species began to dominate shallow reefs. The invasives are macroalgae (*Gracilaria salicornia, Kappaphycus alvarezii, Kappaphycus striatum,* and *Eucheuma denticulatum*) that were intentionally introduced into the bay for mariculture in the 1970s (Russell 1992; Rodgers and Cox 1999; Woo *et al.* 1999; Smith *et al.* 2002, 2004) and a sponge (*Mycale grandis,* first noted in the mid-1990s; Coles and Bolick 2007). Reef flats and back reef slopes are now overgrown by dense algae mats, providing habitat for other introduced invertebrates and excluding native fauna. The sponge now undermines and overgrows corals (Fig. 12C). And these are only the most invasive of 116 introduced or cryptogenic species (Coles *et al.* 2002b), comprising a whopping 19% of all species identified in Kāneohe Bay. *G. salicornia* also dominates reef flats along Waikīkī (Fig. 12B). Other problematical invaders are *Acanthophora spicifera*, the earliest introduced algae (first noted in 1950; Doty 1961) and now the most widespread in Hawaii (Smith *et al.* 2002) and *Hypnea musciformis* (Russell 1992), also intentionally introduced into Kāneohe Bay in 1974 for mariculture. It spread and now occupies up to 80% of available substrata on some reefs in Maui, where piles of rotting algae cause net losses of over $20 million per year due to declining beachfront property values (Cesar *et al.* 2002; Smith *et al.* 2004).

Other notable Hawaii invasives are an alga (*Avrainvillea amedelpha*), two invertebrates (*Gonodactylaceus falcatus* and *Carijoa* sp. aff. *riisei*), and two reef fishes (*Lutjanus kasmira* and *Cephalopholis argus*), all of which have proliferated and altered coral-reef ecology and habitats (Fig. 12D). *A.*

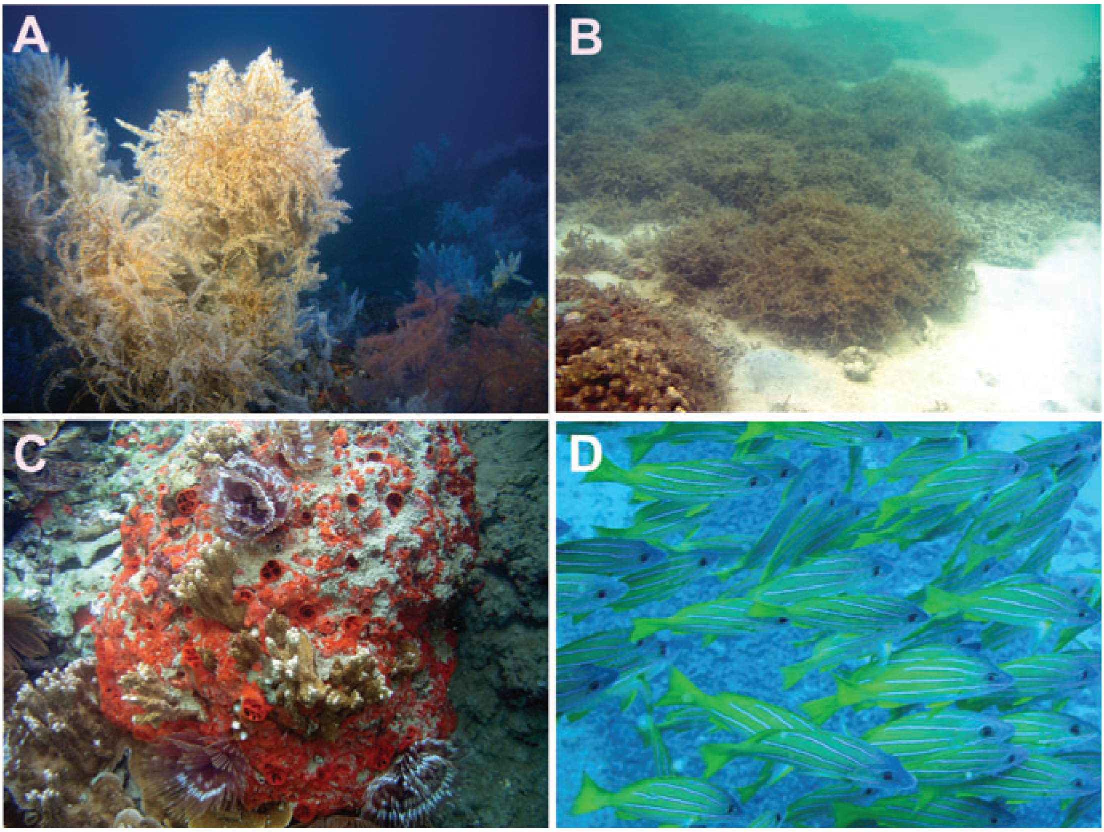

Figure 12. Alien invaders on coral Kaneohe Bay reefs. (**A**) *Carijoa sp. aff. reesei* overgrowing black corals in Hawaii. (**B**) A mass of *Gracilaria* covers what formerly was coral at Kaneohe Bay, Oahu. (**C**) The sponge *Mycale grandis* busy killing a *Montipora* at Kaneohe Bay, Oahu, Hawaii. (**D**) A school of the common introduced snapper *Lutjanus kasmira* on Oahu. (All images by S. Coles.)

amedelpha was first reported in 1981 and dominates soft or sandy bottom areas, displacing sea grasses on Oahu (Smith *et al.* 2002). *G. falcatus*, a stomatopod common in coral rubble that arrived from the Philippines at the end of World War II (Kinzie 1968), now outnumbers the native species by a factor of 100 (Coles and Eldredge 2002). The "snowflake" octocoral *Carijoa* sp. aff. *riisei* was first reported in 1972 in Pearl Harbor and has since spread to all the Hawaiian Islands (Grigg 2003, 2004; Kahng and Grigg 2005). It overgrows the deep black-coral trees (*Antipatharia* sp.) that are a probable major source of larval replenishment for the black corals that are harvested in shallow depths for jewelry production (Fig. 12A).

In an attempt to increase the diversity and abundance of reef game fish, federal and state fisheries agencies imported 11 species of snappers and groupers from the Marquesas and Society Islands to Hawaii between 1951 and 1955 (Brock 1960; Randall 1987). Of these, three have established breeding populations, and two are considered invasive pests. The bluestripe snapper *Lutjanus kasmira* is now abundant on reefs. Its dispersal rate was 18–70 nm per year, and it now has reached Laysan, 820 nm from the introduction site (Grigg *et al.* 2008). It occurs in large schools, is not considered a desired target fish, and is believed to compete with more desired native reef fish for habitat and food. The peacock grouper *Cepholopholis argus* is also not a desired food fish because of reported Ciguatera poisoning. It is an effective predator considered to compete with native fishes for resources, although recent research has indicated that its impact to the reef ecosystem may indeed be relatively low. It dispersed only 490 miles from the introduction, suggesting a spread of 5–17 nm per year (Grigg *et al.* 2008).

Two of only three known scleractinian coral introductions are from the Caribbean (the third being the ahermatypic *Oculina patagonica* into the Mediterranean; Zibrowius 1974; Fine *et al.* 2001). The orange cup coral *Tubastrea coccinea* was first reported at Curaçao in 1943 (Cairns 2000) and has since spread to Brazil (Ferreira 2003; Creed 2006), Florida, and the Gulf of Mexico (Fenner and Banks 2004). It may have originated from the Cape Verde Islands or the Gulf of Guinea (Fenner and Banks 2004), since it would have been exposed to freshwater if transported as vessel fouling through the Panama Canal. Or its planula larvae might have been transported in ballast water. In Jamaica, T. F. Goreau introduced the solitary mushroom coral *Fungia scutaria* at Discovery Bay in 1966 for experimental purposes, and despite hurricanes, ecological degradation of the reef, and attempted eradication, they yet persist (Bush *et al.* 2004), indicating a surviving breeding population after more than 40 years. Off southeast Brazil, the introduced soft coral *Stereonepthya* aff. *curvata* competes with the native octocoral *Phyllogorgia dilatata* (Ferreira 2003).

An incredibly efficient invader, the Pacific lionfish *Pterois volitans* was apparently the first successful introduction of a marine fish from the western Pacific to the Atlantic (Whitfield *et al.* 2002; Ruiz-Carus *et al.* 2006). First noted off Palm Beach in October 1992 shortly after an accidental release of six fish from a marine aquarium during Hurricane Andrew in August 1992, it reached Long Island, New York, and Bermuda a decade later. By 2008 it had occupied west Florida, other east Atlantic states, the Bahamas, Cuba, the Cayman Islands, Jamaica, Turks and Caicos, the Dominican Republic, and Puerto Rico (Ray 2005). It is unknown if the entire population stems from the originally documented accidental release, since about 80,000 have been imported to Tampa and Miami in the past 40 years (Ruiz-Carus *et al.* 2006) and additional releases are probable. The lionfish is a highly effective predator and could become a keystone species substantially altering food webs and energy availability to native predators. It also carries a leach parasite that may infect native species with unknown consequences.

Other introduced or invasive species on Caribbean coral reefs are (1) the Mediterranean portunid crab *Charybdis hellerii*, first reported off Cuba in 1987 and now occurring from Florida to Brazil (Tavares and De Mendonca 1996); (2) the invasive Pacific green mussel *Perna viridis*, first seen in Trinidad in 1990 and now in Jamaica and Tampa Bay since 1998 (Buddo *et al.* 2003); (3) the "world's most common brittlestar" *Ophicatis savignyi,* which dispersed from the Pacific Ocean to the western Atlantic (Roy and Spooner 2002); (4) the Pacific batfish *Platax orbicularis* and many species of Pacific ornamental reef fish, all apparently from aquarium releases (Semmens *et al.* 2004).

Although introduced species are usually a minor component of the total biota of reef ecosystems, alien invasions can have serious negative impacts. Proliferation, competition with native species, and alteration of the invaded habitat appears to be greater in reef areas that are already disturbed by other negative environmental influences. Management implications are therefore relatively clear-cut and relate to avoidance and early detection. Although the vectors of introduction of alien species are often unknown, some of the worst impacts occurred from intentional introductions, for example, macroalgae for mariculture and marine fishes for "fisheries enhancement," with unplanned and unwanted results. Any such efforts must be viewed skeptically and if alien species are brought into proximity of any marine ecosystem, all effort and caution must be exerted to isolate them from the natural environment. There is often a lag time of about a decade between the time an alien species is introduced and when it shows invasive properties. Early detection and control are therefore important in preventing serious environmental impacts.

Once an invasive alien species has become established, it is difficult to impossible to eradicate it, and even reducing or controlling its population requires an intense and expensive effort. At a cost of over Australian $2.2 million (Bax *et al.* 2002) the black-stripe mussel *Mytilopsis (Congeria) sallei* was successfully removed from Darwin Harbor (Labowitch *et al.* 2005) and in Hawaii, a vacuumcleaner-like device (the "Supersucker"; Conklin *et al.* 2008) appears to be the only device able to reduce the densities of introduced algae. Manual removal (Smith *et al.* 2004) proved inefficient. To destroy *Carijoa riisei* in Port Allen Harbor, Kauai, 738 pier pilings were wrapped with plastic for 15 months and still did not manage to remove the entire population (A. Montgomery, personal communication).

Public awareness of the impacts of alien species should be increased, discouraging the release of imported maricultured or aquarium species and intercepting introduced species that may be transported by both commercial and private vessels as hull fouling or ballast water.

Connectivity and the Threat Posed by the Lack Thereof

While the propagation of nonnative fauna is highly problematic, that of native fauna is desired and absolutely necessary. The effectiveness and long-term success of a coral-reef marine reserve will be compromised if its propagules have no place to go, or even worse, if the reserve itself is never reached by propagules from other areas (Gaines *et al.* 2003). The concept of connectivity was early on recognized as crucially important for coral-reef conservation and is receiving much attention (Cowen *et al.* 2006, 2007). Connectivity refers to the linkage of populations in space through the exchange of offspring (Roberts *et al.* 2006). The existence of planktonic larval phases gives the impression of easy connectivity across large distances in the ocean. This would suggest that habitat fragmentation should be less severe than on land, where the loss of corridors between intact habitat patches rapidly leads to isolation and biodiversity loss (Turner 1996; Lens *et al.* 2002). However, coral reefs may not act all that much differently from terrestrial systems, and while most organisms have larvae with at least a short planktonic phase, within-reef retention of larvae emerges as apparently very important (Cowen *et al.* 2007). Even if that was not so, and long-range dispersal of species was always readily feasible, local declines of species in shrinking habitat patches reduce the amount of larvae available, and thus the chances of reaching a distant refuge dwindle.

Thus, to ensure survival, networks of protected reefs are needed that operate on all scales of the landscape and the populations. Protected reefs should link with unprotected reefs outside the boundaries. But how much reef should be protected? Theoretical considerations (Roberts *et al.* 2006) suggest that many small reserves may be as good as a few big reserves, since connectivity between many small and closely spaced reserves is higher than among few, widely spaced ones. Gaines *et al.* (2003) have shown the overriding importance that local current patterns can have. In the presence of strong currents, due to connectivity between reefs, several small reserves are more efficient than a single one of the equivalent size. And well-connected reserves can outperform effort-based management strategies in terms of fisheries yield.

Management action in this case is soundly based in good science prior to the declaration of reserves (Gaines *et al.* 2003). Explicit information regarding currents and larval transport in the areas targeted for new marine reserves will be required. Thus investments in ocean observation networks that give information on water movements have an important payoff for conservation planning. Salm *et al.* (2006) also suggest the introduction of wide buffer zones around existing reserves to account for any shifts in habitat utilization due to climate change and to avoid disruption of established connectivity patterns.

When coral-reef species become rare, knowledge of connectivity patterns can help generate valuable management-related information.

Population genetic work on the two Atlantic *A.* species, *A. palmata* and *A. cervicornis* has shown spatial structure in their connectivity (Baums *et al.* 2006; Vollmer and Palumbi 2007). *A. palmata* appears to have a largely open population structure and seems to fall into two major populations (an eastern and a western Caribbean population), with clear dispersal breaks caused by oceanic phenomena (Baums *et al.* 2005; 2006a,b). Also, sexual recruitment appeared more frequent in the species' eastern range than in the west. From this, one could deduce that the eastern populations would have higher gene flow with more likely adaptation to changed environment (Baums *et al.* 2006a,b), making them potentially more valuable for conservation. Zvuloni *et al.* (2008) showed in the Red Sea that relatively rapid adaptation is indeed possible, given frequent enough sexual recruitment. Both endangered species of Atlantic *Acropora* propagate only in relatively small regions (Pineda *et al.* 2007; Vollmer and Palumbi 2007), often within a few hundred meters of a spawning locus. This clearly shows that at least these species need local source populations for their recovery and that management must act on local, not just large connectivity scales. Ridgway *et al.* (2008) using a similar genetic approach found larger-scale connectivity patterns in southern Africa. Thus, population genetics offers much insight into connectivity patterns and can support the development of regional and local management plans. Palumbi (2003) showed how genetic patterns of isolation can be useful to help estimate connectivity between areas (e.g., reserve networks) where this may be difficult to do by observation of recruitment alone.

Potential for Extinction

Coral reefs are widely distributed, as are many of the constituent species. Extinction of widely distributed species is arguably less likely, due to broad distribution and large populations. However, it appears that many coral-reef organisms are indeed vulnerable and that, in fact, many coral-reef species may be headed for extinction (Carlton *et al.* 1999; Dulvy *et al.* 2003; Carpenter *et al.* 2008). Geologically speaking, extinction of coral-reef taxa is not unusual; however, the last faunal turnover took place over 2 million years ago (Budd and Johnson 1999; Budd 2000), and even the upheavals of the ice ages have not led to massive extinction (Pandolfi and Jackson 2006). Rather, many new species, in particular of the genera *Acropora* and *Montipora*, have arisen only in the Qaternary, and we are graced by several species *in statu nascendi* (Veron 1995; Willis *et al.* 1997). It is many of these young species that, according to Carpenter *et al.* (2008), are headed for extinction. Why would their tenure on Earth potentially be such an unusually short one?

Many species accrue extinction debt once their population numbers reach certain low levels. Besides extinction debt (Tilman *et al.* 1994), the Allee effect, too low numbers of reproductive units to allow successful fertilization, can come into play (Gascoigne and Lipcius 2004). Many Caribbean corals have become locally so rare that successful reproduction appears more and more questionable (Edmunds 2007; Edmunds and Elahi 2007). In the Caribbean coral *M. annularis* fertilization success drops dramatically when the number of spawning corals in an area becomes too low (Levitan *et al.* 2004). But Allee effects in the ocean are difficult to quantify and apparently do not always relegate species to extinction, as is well demonstrated by the case of the Caribbean sea urchin *Diadema antillarum* that is staging a slow comeback, despite near extinction in the 1980s (Miller *et al.* 2003). Extinction debt refers to species extinction due to habitat shrinkage. Despite remaining locally abundant, the extinction-prone species eventually are outcompeted by better dispersers. The present decline of two *Acropora* in the Caribbean carries hallmarks of two conflicting messages. It may well be the case of species committed to extinction. They are common where they exist but recruit rarely. Thus, population crashes are dramatic and do not reverse easily. However, also in this species some interesting, at least temporary recovery (Idjadi *et al.* 2006) and persistence (Keck *et al.* 2005; Riegl *et al.* 2009) have been observed. But, asexual reproduction through fragmentation may help ensure persistence of these branching corals, which occurs much less frequently in other endangered corals like *Montastraea* (Bruckner and Bruckner 2006b). Maybe we ought not be too pessimistic. After all, no extinctions of corals have yet been observed, although near extinction is on record (Glynn and de Weerdt 1991; Glynn and Feingold 1992). However, even if corals may not become fully extinct, ecological extinction, that is, them becoming so rare that they can no longer fulfill their role, would be worrying. Not only would it mean an end to reef-framework production, but a host of associated species that depend on the corals for their existence would probably suffer similar population restrictions, if not extirpation. Coral extinctions would only be the tip of the iceberg for a much greater number of extinctions of obligatorily associated species.

From a conservation standpoint the lessons are clear. A multitude of protected reefs helps keep extinction debt low, since sufficient habitat is available, even for the locally dominant but badly dispersing species. A large number of reserves can also reduce Allee effects by maintaining sufficiently strong populations to avoid Allee's dip in the early phases of population rebuilding. Also, many reserves provide a means of insurance in the face of large-scale disturbance (Halpern 2003; Palumbi 2003). The more representative types of environments are included in protected areas, and the more this protection is replicated within reserves, the less the likelihood that a single catastrophic event will cause extinction (Allison *et al.* 2003; Salm *et al.* 2006).

Alternative Stable or Quasi-stable States

What can be done to prevent a coral reef from flipping into a state where structure and function has deteriorated, goods and services are reduced, and that we humans consider as undesirable? The concept of phase shifts on coral reefs, namely that such a complex system can apparently come completely undone and fall into an alternative stable state, has received much attention since it has been demonstrated on Jamaican coral reefs (Hughes 1994). The idea is that, through a variety of natural and anthropogenic stressors, corals declined dramatically and then, after a population crash of the dominant herbivore *Diadema antillarum*, a formerly coral-dominated system became dominated by fleshy algae (Fig. 13) due to the absence of top-down control, that is, a lack of grazers since the reefs were overfished and the urchins had died. Absence of the natural predators, removed by overfishing, allowed this situation to persist in a stable state and the phase shift was accomplished (Hughes 1994; Mumby *et al.* 2007; Fig. 13). Others have argued that such phase shifts are only quasi-stable (Knowlton 2006), until one or the other organism returns to sufficient population density to effect the return shifting of the phase. However, convincing case studies of reversals are yet missing. While in some areas corals seem to be recovering or persisting (Vargas-Angel *et al.* 2003; Keck *et al.* 2005; Rowlands *et al.* 2008; Zubillaga *et al.* 2008; Riegl *et al.* 2009), in other areas gains are undone by new disturbances. A phase-shift reversal observed by Idjadi *et al.* (2006) and Precht and Aronson (2006) in which *A. cervicornis* appeared to regain dominance over macroalgae and coral cover was on the general increase, unfortunately collapsed again in 2005 when yet another bleaching event depressed coral cover even further than pre-reversal (Quinn and Kojis 2008). But there seems to be some hope that even the badly stressed Caribbean coral reefs still have some resilience left (Fig. 14). There is also the possibility that *Acropora* and *Montastraea* may never regain their dominance, but other branching and massive corals may replace them, serving similar ecological and geological functions. This trend appears to be underway in some remote locations in the Caribbean, such as Mona Island in Puerto Rico (Bruckner *et al.* 2009).

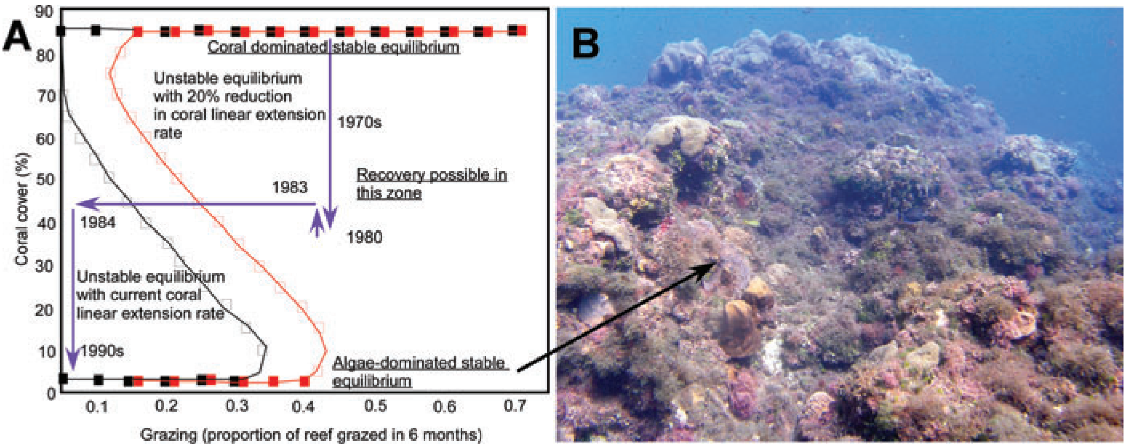

Figure 13. The existence of stable and unstable equilibria in (**A**) coral reefs suggests that vistas of (**B**) degraded coral reefs could remain permanent. Coral reefs, like many complex adaptive systems, exhibit hysteresis. This means that stresses effect changes, but the removal of the stresses does not assure that the system reverts to a stage it has previously been in. Stable (*solid squares*) and unstable (*open squares*) equilibria are situated along model trajectories by Mumby *et al.* (2007). Once the system is pushed over a threshold, it does not return to its previous state.

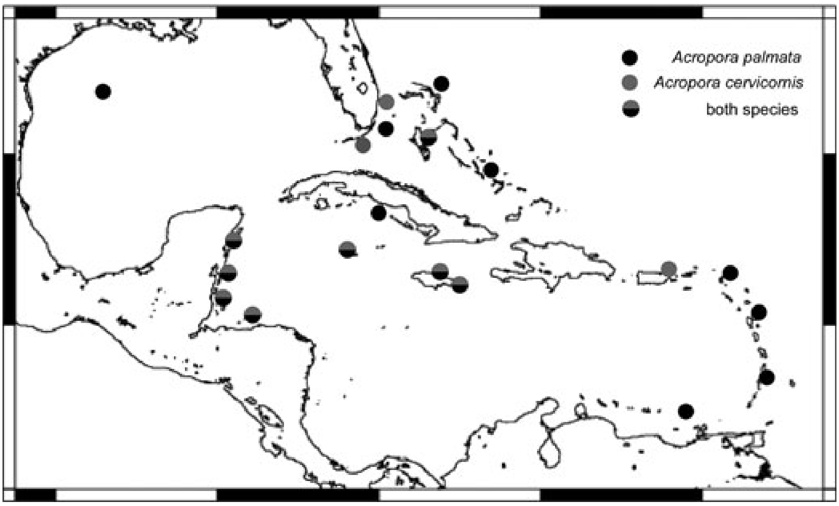

Figure 14. Areas in the Caribbean where the beleaguered *Acropora* species have been reported to hold their own, or increase. Not all such increases have persisted, but they are nevertheless a hopeful sign. (Modified from Precht and Aronson 2006; added points are based on data in Keck *et al.* 2005; Macintyre and Toscano 2007; Rowlands *et al.* 2008; Zubillaga *et al.* 2008; Riegl *et al.* 2009.)

Alternative stable states are not easily addressed in management action. With regard to algae-dominated reefs, the best action is to combat overfishing in order to maintain top-down control on proliferation of algae (Mumby *et al.* 2006). Bottom-up control (i.e., algal proliferation caused by nutrient input) can be managed via better watershed and wastewater management that hopefully reduce the import of nutrients into the system, a key factor in algal proliferation. When corals are simply scarce, but the habitat still suitable, coral nurseries and transplantation (Jaap *et al.* 2006) or reseeding reefs with mass-cultured larvae (Hayward *et al.* 2002) have proven successful in increasing coral numbers.

Some key factors for management as outlined by Mangel (2006) are the realization that thresholds exist, up to which ecosystems are fairly resilient and changes are relatively small. However, once these thresholds are exceeded, changes happen fast and can be irreversible. When radically altered, complex adaptive systems may never return to the original state, even if the stress is removed. This process, called *hysteresis*, has been demonstrated to exist in coral reefs (Mumby *et al.* 2007). Diversity is important, and even if productivity may not be decreased with the loss of some species or landscape components, the resilience of the system may be affected. Also, since multiple spatial and temporal scales interact in complicated ecosystems such as coral reefs, they cannot be understood from the perspective of a single time or spatial scale. The strong linkages among components within reefs and among reefs, even over wider geographical areas, need to be taken into account. The impacts of disrupting these linkages are variable and need to be better understood. Coral reefs, like all ecosystems, change with time, and the different components change with different speed. It has to be borne in mind that the human components change probably more rapidly than any of the reef's biological components (Mangel 2006), and the danger of outstripping the capacity of the ecosystem for accommodating this change is real and its results plainly visible in the degradation of many reefs around the world.

Local Threats

Many natural threats beleaguer coral-reef ecosystems. Although ultimately caused by human action and the way we interfere with climate and ecosystems, these are large-scale threats that cannot be addressed by individuals, but rather require a concerted effort by societies. However, there are many localized threats, caused ultimately by our behavior as individuals or small-scale economic units that cause just as much destruction. If we could learn to mitigate or eliminate those local disturbances, much could be won. To avoid phase shifts, reefs must be managed to ensure the integrity of all its components. Reef fisheries must be strictly controlled, since even the healthiest corals will eventually deteriorate once the fish, and other herbivores, are gone (Hughes 1994; Mumby *et al.* 2007). Key ecological processes, such as top-down control of algal growth by herbivory, must be maintained to avoid knock-on effects that will eventually disrupt all other ecological processes as well (Hughes 1994).

Runoff, Sedimentation, and Nutrient Enrichment

Runoff and associated siltation stress and pollutant loading frequently goes hand-in-hand with development of coastal lands. Poor land-use practices in the headwaters of river basins can have pronounced negative effects on coral reefs. Australia's Burdekin River, for example, has been putting ecological stress on the GBR lagoon since colonists began altering the land and raising cattle in the late 19th century (McCulloch *et al.* 2003). In general, significant increases in sediment yield to the GBR have been documented with 14.4 million tons reaching the GBR lagoon, a threefold increase since precolonial times (Furnas 2003; Hopley *et al.* 2007). The situation is similar in Kenya's Sabaki River, which has been transporting increasing amounts of sediment toward the sea ever since the uplands came under the plough or were used as pastures (Fleitmann *et al.* 2007). This situation is replicated thousandfold across the tropics, and steep tropical islands or coastlines are particularly vulnerable to the effects of devegetation that increases runoff and sedimentation. In much of the tropics, pulsed high-intensity precipitation associated with tropical weather systems (Rogers *et al.* 2008) exacerbates the problem. Freshwater plumes and runoff can travel dozens of kilometers into the sea (Andréfouët *et al.* 2002). During such events, coral mortality can be dramatic, especially when preceded by other stresses like bleaching (Riegl *et al.* 2009). Over geologic time, runoff can shape coral communities more than even temperature variability (Pandolfi 1999), clearly disadvantaging the exposed corals (Ballantine *et al.* 2008; Rogers *et al.* 2008). On Molokai, rainfall and waves generated by storms can generate more than 1000 times greater sediment deposition than normal (Jokiel 2008) due to resuspension and deposition of fine, terrigenous sediment. Not only is sedimentation in and of itself harmful to corals, the associated increase in nutrient import from agriculture or sewage poses a significant problem. Coral reefs mostly grow in nutrient-poor environments (0.2 to 0.5 μM ammonium, 0.1 to 0.5 μM nitrate, and <0.3 μM phosphate; Furnas 1991) and increases in nutrient loading not only favor algal proliferation, that can lead to the displacement of corals, but also directly interferes with the corals' calcification mechanism, and increases mortality rates either directly (Renegar and Riegl 2005) or by increasing susceptibility to diseases (Bruno *et al.* 2003). There appears to be interaction between nutrients and pCO_2 that increases mortality in some corals (Renegar and Riegl 2003). Global climate-change scenarios forecast more precipitation in a warmer tropical atmosphere, leading to more runoff, at least during storms (Riegl 2007), as well as increased pCO_2.

In efforts to reduce grazing pressure and concomitant runoff on the Hawaiian Island Kahoolawe, over 20,000 goats are currently being eliminated. This is demonstrating success, as sediments are more rapidly winnowed from the reefs than redeposited (Jokiel 2008). A classic case study of sewage pollution and remediation is that of Kaneohe Bay in Hawaii. From the early 1960s, raw sewage was discharged into the south basin of Kaneohe Bay, which led to proliferations of phytoplankton and benthic algae that overgrew and killed corals. Removal of the sewage outfall in 1979 led to dramatic increase in water quality, decreases in nutrient levels, and a dieback of algae. By 1983, coral cover had begun recovering, going from 12% to 26% (Maragos *et al.* 1985; Hunter and Evans 1993; Jokiel 2008).

Management actions to alleviate direct sewage input are relatively straightforward, like effectively managing watersheds so that soil and vegetation naturally filter storm and waste waters, thereby keeping rivers clean. However, what sounds quite straightforward is in reality often complicated, since different government agencies with nonoverlapping jurisdictions and aims must collaborate to succeed in this effort. In many countries that challenge has effectively negated efforts to relieve stress from up-catchment onto the coastal reefs. In many areas governance is so ineffective that only an offshore location, which equates to a removal from the stresses due to stronger dilution of pollutants, gives reefs a good chance of survival. However, nitrification of coastal ocean areas may lead to coral-predator outbreaks, therefore, indirect effects can be far-reaching.

Coastal Construction

A significant threat in many countries across the reef belt is the proliferation of coastal construction directly affecting coral reefs. More and more people live in the coastal zone, and more and more infrastructure is needed to accommodate expanding populations along with the increased trade that sustains their economic system. It is assumed that coastal development threatens 33% of the Caribbean region's reefs (Wilkinson 2006). In the Arabian Gulf, which is undergoing an unprecedented building boom, the entire coastline of some political entities has been moved several kilometers into the sea, burying coral reefs and other habitats under artificial islands. Virtually the entire southern shoreline of the Arabian Gulf is currently subject to major reshaping. The Red Sea is not much better off, with massive development projects taking priority over preserving coral reefs. Florida has developed densely along its southeastern continental reef tract (Banks *et al.* 2008) and in the Florida Keys but has at least avoided building on the reefs. Nonetheless, coastal erosion that requires frequent beach renourishment, pollutant runoff, sewage discharge and anchorage off major ports, and ship groundings strain the system (Banks *et al.* 2008). Honolulu, Hawaii, and Tutuila, American Samoa, are of course not the only Pacific islands with an airport built on a reef flat. Dredging for construction and maintenance of coastal infrastructure near reefs often can cause significant stress or mortality (Wolanski 1994).

Coastal construction is often a necessity for local economic development and can be accomplished in relative harmony with the environment, when properly designed. But in many countries the environmental impact assessment (EIA) process, meant to avoid unnecessary environmental insults, is flawed or summarily ignored. Often, environmentally sound construction techniques, even where available and affordable, are not employed (Sheppard 2003b). Thus, a strengthening of the EIA process is required, in particular in smaller nations, that should go hand-in-hand with feedback monitoring, a form of adaptive management that monitors impacts during the construction phase for rapid correction of environmental damage (Turner *et al.* 2006).

Management intervention would again appear to be straightforward in this case. If all development projects in the coastal zone, in particular in coral-reef areas were properly evaluated for their expected impacts, then those could be mitigated. This, however, assumes an efficient and functioning, noncorrupt EIA process, which may be surprisingly rare in countries with coral-reef resources. Unfortunately, well-meaning laws or EIAs that identify potential problems are often discounted. In many places, self-regulation of the construction industry is observed, which is often far more efficient than formal actions taken by the local trustee of the marine resources. A worldwide overhaul of the EIA process would be extremely beneficial to coral-reef conservation (Sheppard 2003b).

Overfishing and Destructive Fishing

Overfishing has been well documented as a root cause of coral-reef decline (Jackson 1997; Jackson *et al.* 2001). Hughes (1994) saw overfishing of grazing fish (primarily parrot fishes) as a reason for a phase shift away from corals and toward fleshy macroalgae when the other major grazer, *Diadema antillarum*, was wiped out by a disease. It is unfortunate that coral reefs are often by necessity a primary target for fisheries since they are in truth not very productive fisheries systems (Hatcher 1997; McClanahan 2006). While algae production can be as high as in agricultural systems, the high internal demand for this production reduces the amount available for human consumption via fisheries to a mere 1%. Oceanic upwelling systems produce more than 50 times the fish biomass per unit algae as coral reefs do (McClanahan 2006). Not surprisingly, coral reefs are rapidly overfished when a hungry populace depends on them as protein source.

Overfishing is a primary threat to about 60% of Caribbean coral reefs (Wilkinson 2006), but this is probably a conservative number. Almost all regions that are well studied report some degree of overfishing (Ballantine *et al.* 2008; Jokiel 2008; Rogers *et al.* 2008). The situation is similar in the Pacific, with significant overfishing reported from American Samoa (Birkeland *et al.* 2008) Guam and the Marianas (Richmond *et al.* 2008), the main Hawaiian islands, and in most other island and coastal nations. In U.S. jurisdiction, only the northwestern Hawaiian islands and the Pacific Remote Islands Area report near-pristine fish populations (Birkeland *et al.* 2008; Grigg *et al.* 2008). However, even there, some targeted species have collapsed and not regenerated yet, like the overharvest of pearl oysters on Pearl and Hermes Atoll in the early 1900s (Grigg *et al.* 2008). To combat overfishing, Australia declared 33% of its Great Barrier Reef Marine Park no-take areas (Day *et al.*

2003; Fernandez *et al.* 2005). This is the world's biggest no-take area, and it has already shown success by increasing fish populations.

Overfishing is nothing new, since human–coral reef interactions date back at least 35,000 years (Pollnac 2007). While some consider the effects of early, preindustrial human exploitation mostly benign (Johannes 1978, 1981), others believe impacts to have been deleterious (Kirch and Hunt 1997) and potentially even responsible for the long-term degradation that eventually led to the deteriorated state of many of today's coral reefs (Jackson 1997; Jackson *et al.* 2001; Diamond 2005). Fitzpatrick and Donaldson (2007) provide evidence that coral-reef exploitation in Palau has over the past few thousand years led to declines in the numbers of finfish and mollusks. In the Palauan Rock Islands, as a clear sign of fishing pressure over 1400 years, the proportion of snappers and emperors found in middens declined, as did the overall size of all consumed fish (Masse *et al.* 2006). Signs of overharvesting in prehistoric times exist for giant clams (*Tridacna* sp. and *Hippopus hippopus*) as well as the humped conch (*Strombus gibberulus*). The list of overexploited species in prehistoric times is long and very similar to those of today (Fitzpatrick and Donaldson 2007). Also in the Caribbean, clear evidence of overexpoitation of coral-reef fishes exists at several Ceramic Age sites (LeFebvre 2007). The archaeological signs are a decrease in the size of exploited coral-reef species and an increase in the use of inshore and pelagic species over time (Wing 2001). Once overfished, resources may take a long time to regenerate, particularly if fishing pressure is maintained. Overfishing in the Marianas dates back to the Japanese period (1914–1944) and may have been influential in molding the current nearshore coral-reef community structure (Richmond *et al.* 2008). To compound the problem, Guam witnessed a further 70% reduction in coastal fisheries catch from 1985 to 1996. In response, no-take areas were established, that originally met with strong local opposition, but when finally enforced rapidly led to increases in fish stocks inside the reserves (Richmond *et al.* 2008), demonstrating again the efficacy of protected areas for fisheries management (Fig. 15).

Destructive fisheries, like dynamiting, muro-ami, cyanide, and bleach fishing threaten many coral reefs. Dynamite fishing is particularly damaging and a major problem in parts of Asia and Africa (Riegl and Luke 1998; Fox and Caldwell 2006) and interesting cottage industries have developed around it. Sources of explosives are often discarded munitions or left-over land mines from past conflicts. Recovery of explosives is a specialized trade, and dynamiting teams consist of skilled bombers and fish retrievers. Dynamiting is well planned and in full knowledge of the damage that is done. Parts of reefs are dynamited repeatedly, since fish biomass (especially herbivores) can increase briefly after corals are destroyed and fleshy algae take over. Only after herbivore biomass declines is a new section of the reef dynamited (Riegl and Luke 1998). Many fishers are aware of the unsustainable nature of such practices. A frequent excuse was that the reefs were already lost to the fishermen, with the perspective that tourism development and/or protection in marine reserves would eventually make fishing impossible. Thus, no need to protect the resource for future livelihood was perceived. In the Caribbean, bleach fishing for lobster and other shellfish is a major problem, degrading primarily patch reefs and shallow reefs.

The successful management of reef fisheries has proven to be an elusive goal. Fisheries regulations are regularly ignored either for reasons of profit or because the reef fish are needed as protein sources or shellfish can be sold as curios (Fig. 16). Alcala *et al.* (2006) review the highly successful case of the voluntary reserves enacted by the local communities at Apo and Selinog Islands in the Philippines, where the reserve has indeed created a biomass source for surrounding areas (Fig. 15). Other successful community-based conservation efforts have been reported, for example, from Papua New Guinea (Aswani *et al.* 2007). Obura *et al.* (2006) report from Kenya that local community

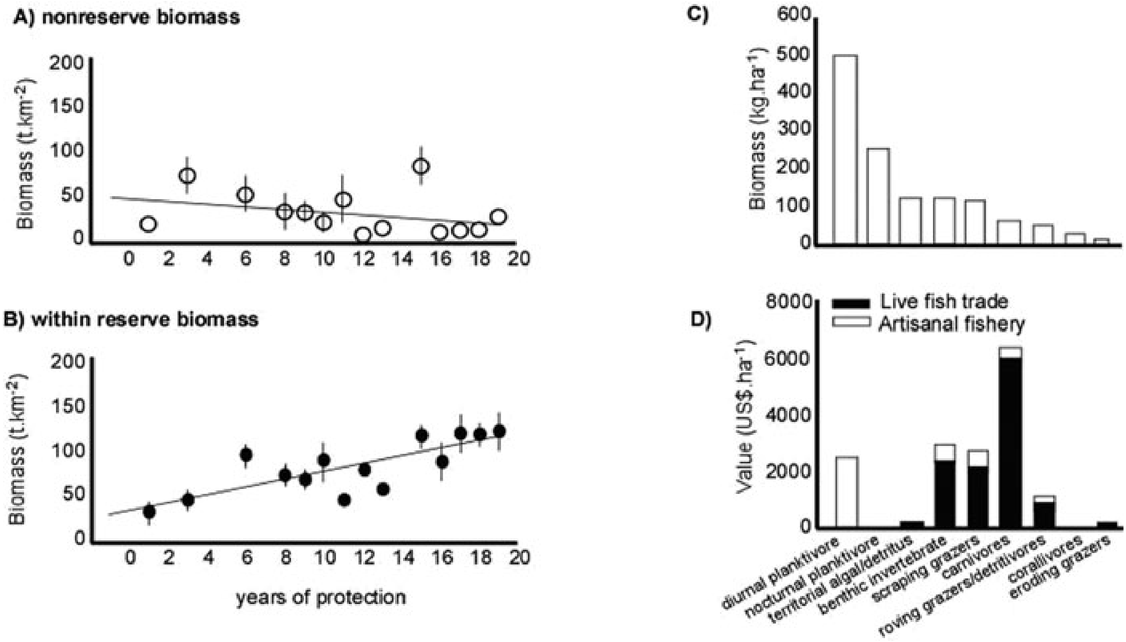

Figure 15. (**A** and **B**) The efficacy of marine reserves in increasing fish stocks, here acanthurids (sturgeons), carangids (jacks), lutjanids (snappers), and lethrinids (emperors) show how vulnerable reef fisheries are to overfishing. (From Alcala *et al.* 2006.) (**C** and **D**) Show the mismatch between economics of consumption and the ecological role of coral reef fishes. (**C**) Is the biomass of functional reef-fish groups in a Pacific ecosystem, and (**D**) contains their economic value. (From Bellwood *et al.* 2004.) It is little surprise that certain species are almost driven to annihilation.

Figure 16. Fisheries not only affects finfish but also corals and other components of coral reefs. Is this really the best use for these organisms? (**A**) These corals could have built a reef and been home to fish, and (**B**) this trumpet triton *Charonia tritonis* could have preyed on the corallivorous cown-of-thorns starfish *Acanthaster planci* and helped control its populations.

efforts at coral farming to make up losses from bleaching events also led to voluntary restrictions on fisheries, to avoid damaging the coral farm with fishing gear. These examples clearly show that, provided the local community has enough sense of ownership in the resource, successful fisheries management is indeed possible.

Attempting the Balance: Managed and Protected Coral Reefs

Ours is an increasingly crowded world with vast numbers of people living in the coastal zone. Some of the highest population densities in the world are in tropical coastlines close to coral reefs (Shi and Singh 2003). In the United States, the 17% of land that defines the coastal zone holds 53% of the nation's total population (Bowen *et al.* 2006). Many coral reefs occur in the world's economically disadvantaged regions and thus have a special importance as a source of scarce proteins, often the only one affordable, to a vast local populace. This dubious privilege has led to widespread degradation, and some claim that hardly any reef exists today that is not overfished (Jackson *et al.* 2001). Thus, many perceive some sort of protection from human exploitation as the only possibility to maintain even a semblance of healthy reef ecosystems. Enter the marine reserve or marine protected area (MPA). The world is dotted with small to large marine reserves, a great many of which attempt to preserve coral reefs (Fig. 17). The only ingredient that is needed for coral-reef survival is efficient management based on good science.

Theoretical approaches to MPAs have been elaborated in many publications (e.g., Lubchenco *et al.* 2003) and are outlined in Mangel (2006), who also gives a good review and pointers to pertinent literature. Both in theory and practice, it has been shown that MPAs can work. When managed properly, they have been shown to increase biomass and diversity both within the reserve and the adjacent areas via larval export and spillover of adults, which reduces the extinction probability of resident species. These beneficial effects are even observed in small reserves (Halpern 2003). Well-connected networks of MPAs ensure against catastrophes and provide for long-term persistence of marine communities (Lubchenco *et al.* 2003). Yet recent analyses of coral-reef MPAs show that most are not very efficiently managed and many achieve little to no protection of their entrusted resources (Alcala *et al.* 2006; Wells 2006).

Very clearly, science has a strong case in supporting management decisions. Unfortunately, too often the science is available, but implementation lags, and although the theory is well known, the practical "how-to, where, and when" of coral-reef conservation is hotly debated. Many traditional societies have quite capably conserved their reefs, but it is easier to conserve a reef when only a few hundred villagers depend on it than if thousands or even millions of people are the reef's neighbors. Thus, even though unquestionably successful (Johannes 1978, 1981; Aswani *et al.* 2007; Richmond *et al.* 2007), traditional values and village-based approaches work only where societal and political systems still accommodate them–and these traditional values can also erode very quickly (Oles 2007). In many coral reef areas, "Western-style" centralization of governance and decision making results in a top-down approach by legal fiat that frequently does justice to the word of the law, but as often does preciously little to conserve the resource (Latin 1993). Thus, a place exists for a theory of conservation that results in development of rational conservation principles upon which legislative action can be designed. The scientific literature is replete with such studies (Mumby and Steneck 2008).

MPAs (Fig. 17) are considered to be essential tools for conservation, perhaps most importantly for the conservation of biodiversity. However, the declaration of a protected area, and effective protection of the resources within, are two quite separate issues, and probably

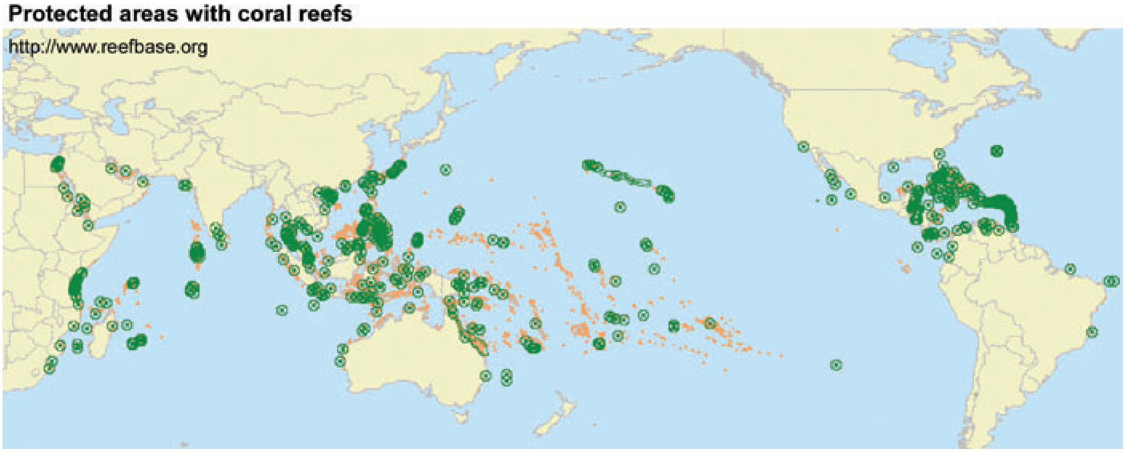

Figure 17. Many coral reefs are protected, at least on paper. Efficient marine reserves, however, appear to be few and far between. The biggest marine reserves with coral reefs are the Phoenix Islands Protected Area (PIPA, Kiribati), Papahanaumokuakea (northern Hawaiian Islands) National Marine Monument, the Pacific Remote Islands Areas Wildlife Reserves, and the Great Barrier Reef Marine Park.

the majority of coral-reef reserves are at best only marginally effective (Alcala *et al.* 2006; Ricciardi *et al.* 2006; Wells 2006). To aid in the development and assessment of protected areas, and to encourage standards for assessment and reporting and use of appropriate indicators that focus on outputs and outcomes, clear guidelines have been developed (Hockings *et al.* 2000; Pomeroy *et al.* 2004).

Conservation is traditionally considered to be within the realm of governmental custodians or nongovernmental organizations (NGOs), and much has been written about the effectiveness of government- or community-based efforts (Wells 2006). There also exist undeclared but de facto marine reserves. Since the biggest threat to coral-reef ecosystem integrity appears to be unfettered access by man, any activity restricting access can end up benefiting the reefs. For example, military use of coral reefs can in instances create remarkably efficient nature reserves. About two thirds of the Caribbean island of Vieques was used for practice bombing and amphibious assault from the 1940s until 2004 (Hernandez-Cruz *et al.* 2006). When the Navy left, unexploded ordinance made the land difficult to use and enabled transfer into the biggest National Wildlife Refuge in the Caribbean, making Vieques one of the most undisturbed Caribbean islands. Despite bombing, the health of the reefs was better than in nearby St. Croix, where reefs had been protected for decades (Riegl *et al.* 2008).

The major impacts on reefs had been due to hurricanes and coral diseases, and the absence of stressors from land-based sources helped Vieques reefs stay healthy. In the Pacific, Johnston Atoll, one of the world's most isolated atolls, was a military site for the storage and destruction of chemical weapons as well as some nuclear testing (Lobel and Lobel 2008). Wake atoll had been used as a Navy airfield since 1934. Military governance as "forbidden areas" isolated these reefs and despite modification of the islands, the reefs maintained excellent health (Lobel and Lobel 2008), and were largely unfished. Johnston atoll is an important stepping stone for larvae from the tropical Pacific to reach the Hawaiian Islands (Kobayashi 2006). Also the British Indian Ocean Territory (BIOT) benefited from remoteness due to military activity, with Diego Garcia being a major U.S. Naval base. The entire BIOT was depopulated in the 1950s to free the way for military installations that remained concentrated on Diego Garcia. With the atolls being under British Naval surveillance, the BIOT had effectively become one of the world's largest conservation areas, and one of the few uninhabited island chains. While the U.S. Navy modified Diego Garcia island and lagoon, conservation measures on half of the atoll allowed spectacular coral reefs to coexist with a major military installation. The northern atolls are home to spectacular and healthy coral reefs. These reefs suffered like many others in the 1998 mass bleaching event but, possibly due to the absence of any human stressors, but have recovered well, which supports the concept of resilience in areas subject to little direct anthropogenic stress (Sheppard *et al.* 2008). Nonformal and unintentional coral-reef conservation occurred at Bikini Atoll. Site of the test explosion of two hydrogen bombs, the island had been depopulated when chosen as a test site and due to continued radiation risk, had been kept population free. Early investigations showed the extent of the damage when nuclear bombs explode on a reef, but recent studies reveal impressive regeneration of the corals and how apparently resilient the corals were (Richards *et al.* 2008). An equivalent situation exists at France's Mururoa Atoll (Guille *et al.* 1996; Planes *et al.* 2005).

MPAs appear to work best and contain the healthiest reefs when distant from human habitation, like Hawaii's Papahanaumokuakea (northewestern Hawaiian Island) National Marine Monument (Rooney *et al.* 2008; Grigg *et al.* 2008), the U.S. Pacific Remote Islands Area National Wildlife Refuges (Maragos *et al.* 2008a,b), parts of Australia's GBR (Kelleher 1993) or Kiribati's Phoenix Islands Protected Area (PIPA). In these areas, management plans can be—and are—primarily science-based. Frequently, however, MPAs are sited within areas traditionally used by local communities and can therefore directly impact their livelihoods or social identity. The success or failure of many, if not most MPAs in coral-reef areas (Wells 2006; Christie and White 2007) is, among a multitude of capacity-related factors, linked to design, declaration process, and the involvement of the local communities. Studies in the Bahamas have shown that if an MPA is perceived as interfering with traditional activities regarded as key social components, strong local opposition can have deleterious impacts on the declaration process (Stoffle and Minnis 2007) or relegate an MPA to the already impressive heap of dysfunctional paper parks (Ricciardi *et al.* 2006; Wells 2006).

Market forces tied to emigration, transmigration, the free flow of goods and capital, and a strengthening of cultural and material imports lead to changes in the social fabric of communities (Oles 2007), with implications for conservation attitudes toward coral reefs. Traditional values linked to coral reefs as well as ecological traditions and knowledge erode rapidly. Fortunately, coral reefs provide economic opportunities firmly rooted in the wage labor system, freeing people from the pressures of subsistence and providing access to more money and the spoils of the free-market economy. The potentially biggest opportunity arises through tourism (Spurgeon 2006; Diedrich 2007). Coral reefs are believed to have a worldwide income potential through tourism of at least US$ 9.6 billion per year (Jobbins 2006). But despite offering potentially huge economic gain, coral-reef-based tourism can also lead to conflict and degradation. Tourism, if well planned and managed, should result in social, economic, and environmental benefits to the host community. However, if benefits are not distributed equitably, significant conflict can be created and local communities can quickly begin to resent conservation measures. The feeling of loss of control and access to natural resources that are considered property will be aggravated if material gain from tourism activities cannot be realized. In Belize, touristic use of reefs contributes ~30% of the gross domestic product via extractive and nonextractive ecosystem services and a positive correlation between tourism development, and coral-reef conservation awareness and support was observed (Diedrich 2007). Support for conservation was largely linked to realized or expected financial gain, indicating that local communities expect protected areas to attract business. Financial gain from marketing coral reefs is certainly realized in four South Florida counties (Palm Beach, Broward, and Miami-Dade) adjacent to the Continental Florida Reef Tract (Banks *et al.* 2008). Reef use creates an annual contribution to the local economy of US$8 billion in sales and almost US$4 billion in income with 70,400 jobs (Johns *et al.* 2001). This number factors in direct and indirect spending in connection with the tourism, marine, infrastructure, and transport industries in order to gain access to the reefs. Many other countries also effectively market their reefs to build their coastal tourism. Tourism overall generated receipts of US$856 billion in 2007 (World Tourism Organization, http:/www.world-toursim.org). Such numbers should convince that losing coral reefs equates to losing money and that many people can benefit from reef conservation, directly and indirectly.

Which Reefs to Protect? Do Refuges Exist?

Conservation strategies for coral reefs vary from strengthening existing protection by better training (Wells 2006) and devising specific management responses to crises such as bleaching (Marshall and Schuttenberg 2006a,b; Obura *et al.* 2006), to searching specific attributes of reefs (such as expected resilience in the face of global change) for declaration of specially protected areas; and to scientifically tailor-making management approaches that promise to maintain the highest possible ecological and biodiversity integrity (Salm *et al.* 2006). In their efforts, coral-reef managers are aided by increasingly sophisticated monitoring and warning systems, such as the National Oceanic and Atmospheric Administration's (NOAA)'s Coral Reef Watch program (Strong *et al.* 2006).

Objectives for coral-reef conservation could be defined as efforts (1) to maintain or rebuild the biological and structural integrity of coral reefs, and (2) to secure the sustained delivery of ecosystem services to people (Roberts *et al.* 2006). Obviously, point 2 follows if, and only if, point 1 is achieved or achievable. Debate continues regarding which reefs should be selected for protection, that is, where best to invest sparse resources for maximum benefit. Since bleaching will likely continue to be a major issue for coral conservation, characteristics of areas have been sought that would lower the incidence of bleaching. These factors include low light [due to depth, shading, turbidity, or cloud cover (Mumby *et al.* 2001)], high flow (Craig *et al.* 2001; Nakamura and van Woesik 2001; Nakamura *et al.* 2003; Nakamura *et al.* 2005), lower temperatures (Riegl 2003; McClanahan 2008), and natural higher nutrient settings (Grottoli *et al.* 2006—higher nutrient availability can aid bleached corals, but increased nutrient levels by pollution can also damage—see the preceding sections; Fig. 18). Often specific environments correlate with these factors: deeper reefs (often near to shallow thermoclines), reefs in upwelling areas (although too much cold can kill corals; Glynn and D'Croz 1990; Hoegh-Guldberg *et al.* 2005), coastal areas with high levels of suspended terrigenous sediment, areas with strong currents, and shoreline and lagoonal reefs that are shaded by high islands (Glynn 1996; Riegl and Piller 2003; Salm *et al.* 2006; West and Salm 2003). Such potential "refuge" habitats have been singled out as preferred target sites for conservation (Salm *et al.* 2006). Some argument of course exists whether refugia are the same everywhere. McClanahan *et al.* (2005a,b) argued, for example, that high flow does not necessarily protect corals. Rather, low-flow areas with dramatic temperature fluctuations as a result of restricted circulation would help corals acclimatize, and those "spoilt" by the more uniform temperature regime in high-flow areas would bleach more easily during temperature anomalies. Thus, the role of the environment in helping corals acclimatize to temperature stress may be more important than its role in alleviating the metabolic effects of the stress itself. Such findings complicate identification of resilient areas and refugia

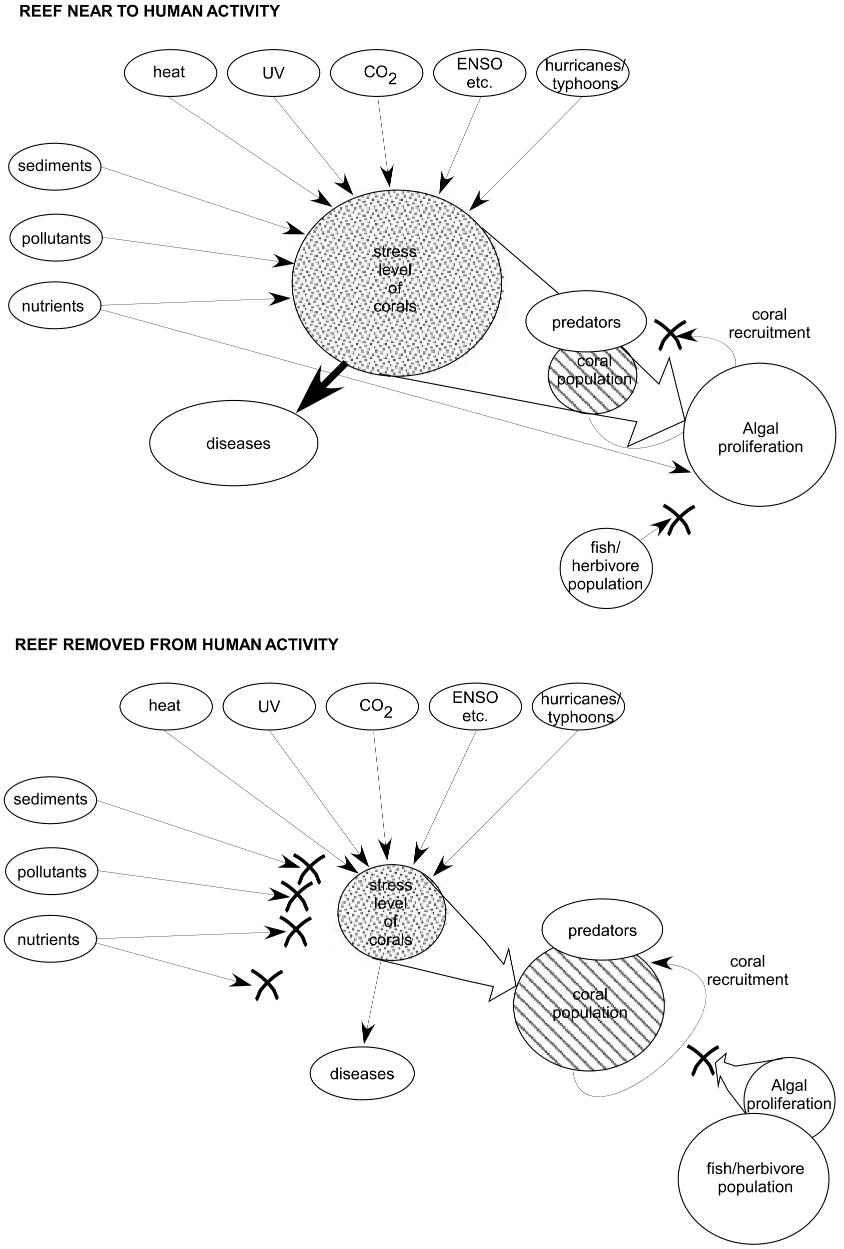

Figure 18. Conceptual diagram, based on information from or quantitative findings in other studies (Marshall and Schuttenberg 2006a,b; Salm *et al.* 2006; Riegl *et al.* 2009) on how the setting of coral reefs relates to the stress state of corals, likely degradation, and conservation value.

by using physical habitat characteristics alone, because previous "experience" (not necessarily predictable from simple habitat characteristics) is likely to play a critical role in determining whether or not corals actually bleach (Brown *et al.* 2000, 2002). This makes a strong case for monitoring both environment and corals over large scales and extended periods in order to obtain more clarity.

Where the environment does not naturally protect, legal protection may offer a solution. Recently, the corals *Acropora cervicornis* and

A. palmata, which have suffered spectacular population restrictions (Bruckner 2003), were listed as threatened under the U.S. Endangered Species Act. It remains to be seen whether this level of protection actually helps or hinders the conservation of the species. The strict protection of stony corals and black corals under Appendix II of the Convention on International Trade in Endangered Species (CITES) that only allows the export and import of corals under permits issued by the exporting country seems to be more a hindrance to research than to actually preserve the corals (Green and Hendry 1999), although it has raised international awareness about the impacts of the curio and aquarium trades (Bruckner 2001; Fig. 16).

Whatever their size, both small and large reserves have positive effects (Halpern 2003). In analogy to terrestrial-conservation science, which has been able to produce exact-size prescriptions based on theories of biogeography and biodiversity (McArthur and Wilson 1963; Diamond and May 1976; Wilson 1988; Hubbell 2001), it is certainly not wrong to also suggest the bigger, the better for coral-reef reserves. Theoretic relationships between reef sizes and contained biodiversity are less well established than in terrestrial systems. Coral reefs and habitats that contain corals follow a power law in their frequency (Purkis *et al.* 2007). This means that many more small reefs exist than big ones. Also, with regards to disturbances, there usually exist more small and localized than severe and widespread disturbances (Riegl *et al.* 2009). The conservation message is clear: If many small, localized disturbances recur randomly, any one of the many small reefs is in danger of being compromised by such a disturbance sooner or later. While nothing can ensure against the few, widespread disturbances, an MPA should be big enough to contain many small reefs, so that enough can escape the many small perturbances. Ideally, the biggest coherent reef structures, and many of the small, should be contained, in order to give the system a reasonable chance to contain refugia when the few large, widespread disturbances strike. This is the principle of insurance against unforeseen events suggested by Wilson and Willis (1975), Allison *et al.* (2003), and Mangel (2006). Of the many coral-reef MPAs, few fulfill such a size requirement (obvious examples being the Great Barrier Reef Marine Park, the Papahanaumokuakea National Marine Monument in the northwestern Hawaiian Islands, the Florida Keys National Marine Sanctuary, among others). Small reserves lose species due to ecological truncation (Wilson and Willis 1975), and ecological drift (Hubbell 2001) can lead to different species dominating in different small patches, requiring more patches to maintain high biodiversity in a refuge. If coral communities are neither niche-accommodated nor neutral (Dornelas *et al.* 2006), but shaped by high-frequency stochastic events, then the diversity of patterns and species compositions on coral reefs is even higher and less reproducible in small reserves. All this suggests that large and well-connected reserves are desirable to avoid losses of coral-reef biodiversity, especially at a time where stress events, like bleaching, will recur more frequently (Hoegh-Guldberg 1999; Sheppard 2003a).

If reefs cannot be protected, or if something goes wrong, there is a place for restoration and a ripe literature exists. Also artificial reefs can be useful and are becoming very popular in many parts of the world as a means to mitigate for damaged or destroyed reef habitat (Clark and Edwards 1994), to improve fisheries yields (Pickering and Whitmarsh 1997), or to reduce recreational dive pressure on natural reefs. Both restoration and artificial reefs are often met with skepticism since it appears better not to damage an ecosystem in the first place. However, large-scale natural impacts as well as the increasingly common insults visited upon reefs by ship groundings, other industrial accidents, and natural disasters make restoration capabilities desirable. Yet restoration remains a viable alternative only if the original threats leading to reef degradation in the first place are mitigated and appropriate strategies based on the type of species and environmental conditions are applied (Bruckner *et al.* 2009). Larval culturing techniques (Omori 2005; Miller and Szmant 2006; Omori *et al.* 2008), enhanced and directed recruitment (Hayward *et al.* 2002), asexual propagation (Epstein and Rinkevich 2001; Soong and Chen 2003), coral transplantation methods and coral gardening (Edwards and Clark 1998; Rinkevich 2006) hold much hope to artificially improve regeneration. It is in particular in the realm of reef rehabilitation and the creation of artificial reef ecosystems that basic and applied conservation research can generate synergy. It is a field where ecological theory can fruitfully be translated into informed and directed efforts to recreate lost biodiversity. If natural coral reefs remain on the currently observed downward trajectory, we may too soon require all the knowledge and techniques we can muster to giver nature a helping hand. Before we come to that stage, however, efficient conservation of what currently exists is the preferable option.

Conclusion

Coral reefs, in one taxonomic and evolutionary guise or the other, have graced the Earth for about 500 million years. Modern, scleractinian corals evolved about 215 Ma and have survived several major extinction events. While frequently of tectonic origins or caused by collision with extraterrestrial objects, most of these mass extinctions had a climatic component. The lesson is that rapid climatic changes have always caused major extinctions. Thus, given the currently observed rates of climatic change, there is reason to worry about the future of coral reefs.

The greatest global-scale threats currently faced by coral reefs appear to be all linked to man-made or man-mediated changes of climate:

- Bleaching, a heat- and light-mediated loss of symbiotic algae within the corals, has increased markedly in impact and severity over the past decades and affects virtually every reef worldwide.
- Diseases have increased in incidence and diversity and caused severe population declines of corals in the Caribbean and, to a lesser extent, the Indian and Pacific oceans.
- Predator outbreaks have recurred repeatedly, most particularly in the Indo-Pacific and have caused severe degradation on affected reefs. These outbreaks seem to follow natural dynamics, enhanced by man-made changes in the coastal zone, and they can be particularly severe when the host population is diminished or weakened by other threats.
- Losses in keystone predators and herbivores have created phase shifts away from corals and to the establishment of stable states dominated by algae. This phenomenon is typical of the Caribbean.
- Ocean acidification is an emergent problem that may threaten deep as well as shallow coral reefs.

Smaller-scale, localized, and entirely man-made threats include:

- runoff, sedimentation, and nutrient enrichment;
- coastal construction leading to smothering of habitat and creation of high turbidity around coasts;
- overfishing and destructive fishing techniques.

Conservation is attempted in marine reserves and by legal regulation of activities on coral reefs. Conservation science has provided a rich theoretical body with regard to the required ingredients, size, and connectivity of coral-reef reserves to be efficient. In general, larger protected areas with little extractive interference (ideally no-take) have a higher likelihood of conserving coral reefs long term.

It is estimated that costs due to lost economic opportunities from destroyed coral reefs will reach US$350–870 million per year by 2015 of the annualUS$3.1–4.6 billion of annual benefits from coral-reef fisheries, dive tourism, and shoreline protection services (Wilkinson 2006). These numbers are conservatively low and relate only to direct benefits lost. Bearing in mind that three counties in Florida alone benefit from annual revenues of circa US$4 billion (Johns *et al.* 2001), the direct and indirect financial losses associated with worldwide coral-reef degradation will have undesirable consequences to our global economy. Economic impacts aside, we have a moral, ethical, and cultural responsibility to prevent one of our world's most biodiverse and esthetically beautiful ecosystems from being wantonly destroyed.

A study of Earth's history teaches us that coral reefs have periodically survived destructive natural perturbations. What presently unfolds is a consonance of coral-reef disturbances imposed by both man and nature. If the current trajectory of coral-reef degradation continues unabated, we will remain on the path of a mass coral extinction event on the scale of an asteroid impact (after which corals took over a million years to recover). Corals will not likely go completely extinct, but the coral-reef ecosystems that currently harbor immense biodiversity, provide the necessities of life for millions of people, and produce valuable global economic services will disappear. We have demonstrated capabilities to exert great changes on our planet with negative consequences; now it is our obligation to harness our capabilities to arrest and reverse the trajectory of coral-reef decline.

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Conflicts of Interest

The authors declare no conflicts of interest.

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