Colloquium

The future of coral reefs

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Coral reefs, with their millions of species, have changed profoundly because of the effects of people, and will continue to do so for the foreseeable future. Reefs are subject to many of the same processes that affect other human-dominated ecosystems, but some special features merit emphasis: (*i*) Many dominant reef builders spawn eggs and sperm into the water column, where fertilization occurs. They are thus particularly vulnerable to Allee effects, including potential extinction associated with chronic reproductive failure. (*ii*) The corals likely to be most resistant to the effects of habitat degradation are small, short-lived "weedy" corals that have limited dispersal capabilities at the larval stage. Habitat degradation, together with habitat fragmentation, will therefore lead to the establishment of genetically isolated clusters of inbreeding corals. (*iii*) Increases in average sea temperatures by as little as 1°C, a likely result of global climate change, can cause coral "bleaching" (the breakdown of coral–algal symbiosis), changes in symbiont communities, and coral death. (*iv*) The activities of people near reefs increase both fishing pressure and nutrient inputs. In general, these processes favor more rapidly growing competitors, often fleshy seaweeds, and may also result in explosions of predator populations. (*v*) Combinations of stress appear to be associated with threshold responses and ecological surprises, including devastating pathogen outbreaks. (*vi*) The fossil record suggests that corals as a group are more likely to suffer extinctions than some of the groups that associate with them, whose habitat requirements may be less stringent.

Coral reefs are often called the rainforests of the sea, although calling rainforests the coral reefs of the land might be even more appropriate (1). As with rainforests, the importance of coral reefs lies not so much in the diversity of the corals themselves, but rather in the millions of species that live primarily or exclusively in association with them. Veron (2), for example, gives a minimum estimate of 835 species of reef-building corals, and estimates for the biodiversity of reefs overall range from 1–9 million (3).

Unfortunately, modern human civilization and coral reefs make poor companions. Most activities of people (e.g., fishing, deforestation, nutrient enrichment, burning of fossil fuels, and use of toxic chemicals) either damage corals directly or damage them indirectly by adversely modifying interactions with their competitors, predators, pathogens, and mutualists. For example, Edinger and colleagues (4) document losses in coral species diversity ranging from 30–60% on reefs degraded by human activities, with a 25% loss in generic diversity on two of these reefs over just 15 years. Thus, although concerted efforts to protect reef habitats may slow their ongoing decline, it is difficult to be optimistic about the health of reefs globally over the short term in the context of increasing human populations and economic growth (5).

As the world changes with growing human domination, ecological and evolutionary changes on coral reefs similar to those outlined for terrestrial and other marine organisms and ecosystems (e.g., refs. 116–118 and other articles in this colloquium) are inevitable. A few factors do work in the favor of coral reefs. For example, the widely dispersing larvae and still large population sizes of many important reef builders probably provide some protection against extinction (6). The diversity of coral reef ecosystems may also make catastrophic invasions of exotic species less likely, although invasibility may increase with disturbance (7) and the degree to which diversity *per se* inhibits invasions remains unclear (8). The fossil record clearly shows, however, that marine species and ecosystems have their limits (refs. 119 and 120 and other articles in this colloquium), and the recent record indicates that these limits may be approached with little warning (9, 10). The broader ecological consequences of reducing biodiversity (11) remain essentially uninvestigated for coral reefs. Indeed, our understanding of even the basic physical parameters of global change of relevance to reefs is inadequate (12).

Below I focus on some of the peculiar features of corals and other reef dwellers that are likely to affect their ecological and evolutionary futures. Many of the examples are drawn from the Caribbean, because change (and thus a possible glimpse of the future) has been much greater there over the last several decades. Nevertheless, the major points have applicability to reefs worldwide.

Reproduction: Allee Effects, Inbreeding, and Hybridization

Sessile marine organisms, with very few exceptions, depend on water to bring their gametes together; either eggs and sperm are both released into the water column or eggs are fertilized internally by sperm picked up from the water column. One immediate consequence is that low gamete densities caused by low population densities, asynchronous reproduction, or low reproductive output per individual can lead to reproductive failure (13, 14), a classic example of an Allee effect (15).

Corals themselves are commonly hermaphroditic and exhibit two primary types of reproductive strategies: broadcasting and brooding (16, 17). Physically large and long-lived coral species, the primary reef builders, are typically broadcasters that reproduce once or twice a year during an event known as mass spawning. Buoyant bundles of eggs glued together with sperm are released in approximate synchrony on just a few nights of the year, when they float to the surface, break apart, and with luck achieve fertilization. The small larvae of broadcasting species typically disperse for at least 4 days (17).

As with other outbred marine invertebrates (18), species in this group do not generally self-fertilize successfully (17). Thus, eggs from one colony need to reach sperm from another for reproduction to succeed. For broadcasting corals, we know very little about critical gamete densities necessary for supporting successful fertilization. The best study is that of Oliver and Babcock (19), who showed that fertilization rates drop to low levels by 3 h after peak spawning and on nights other than the major night of spawning. This suggests that colonies spawning in

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temporal or spatial isolation (measured on the scale of a few hours and tens or at most hundreds of meters) will often experience nearly complete reproductive failure. Adverse environmental conditions can also reduce fertilization rates independent of gamete density (20, 21). Moreover, nearby colonies may release few gametes and thus be ineffective mating partners if they are recovering from stressful conditions or damage (21–24) or are small for whatever reason [size rather than age determines reproductive output (25, 26), so that fragments typically have reduced fecundity or are infertile (22, 27)]. Thus, reef degradation may lead to sharply reduced reproduction, not only because of lowered gamete production, but also because of reduced rates of fertilization for those gametes that are released.

However, eggs failing to encounter conspecific sperm will not necessarily remain unfertilized, even when self-fertilization is not feasible, because simultaneous or nearly simultaneous spawning provides potential opportunities for interspecific hybridization (2). The extent to which this happens is a matter of debate, because some species are clearly separated by either subtle temporal differences in spawning time or gametic incompatibilities (28). However, these barriers are likely to become less effective as opportunities for conspecific matings decrease. For example, mechanisms to prevent selfing often decline in efficacy after 4 h (29), and the same might happen with gametic barriers to interspecific fertilization. Similarly, subtle temporal differences in spawning times between species whose gametes are otherwise compatible (28) would be less effective if, for example, unfertilized eggs from an early spawning species remained near populations of later spawning species. Laboratory experiments do clearly suggest that many species are capable of hybridization, including species with very different morphologies (30, 31). However, the potential evolutionary impact of hybridization between morphologically and ecologically distinct taxa is difficult to evaluate empirically, because of long generation times and the difficulty of maintaining corals in captivity for determining long-term survival and fertility of hybrids.

Brooding corals exhibit a very different reproductive strategy. Only sperm are released, and fertilized eggs are retained within the colony and released as swimming planula larvae. These corals often reproduce on a lunar cycle for a number of months per year (25), and the large larvae that are released probably do not travel far, despite their physiological potential to do so without feeding, thanks to the zooxanthellae that brooded larvae contain (32). For example, Carlon and Olson (33) found that the average swimming time for the larvae of the brooding coral *Favia fragum* was only about 4 min. Such limited dispersal suggests that biparental inbreeding (mating between relatives) is not uncommon in brooding corals (17). Distances between potential mates are probably even shorter than they are for broadcasting species, perhaps as little as a few meters (34). However, brooding species are more likely to be able to self-fertilize (17, 35), probably as a consequence of regular biparental inbreeding (18). Thus, one likely consequence of habitat deterioration and destruction is an increase in selfing as distances between fertile colonies increase.

Compared with the mass spawning species, brooding corals have many of the attributes of weeds: they often grow to smaller sizes, reproduce earlier, have shorter life spans, and are competitively inferior to larger and more aggressive broadcasting species (25, 26, 36). Moreover, their ability to self-fertilize would make them less vulnerable to Allee effects and allow them to persist even at low densities. Brooding corals have come to dominate many Caribbean reefs following disturbances of the 1980s and 1990s (37), and they also succeeded disproportionately during the Oligocene–Miocene extinction event (38). Nevertheless, brooding corals are very vulnerable to some forms of disturbance, including high-temperature disruption of their symbiotic associations (39), to which I now turn.

Coral–Algal Symbiosis

One of the striking features of coral reefs is the intimate nutritional symbiosis between the coral animal and single celled dinoflagellates, typically known as zooxanthellae. Corals provide excretion products to their algal guests, which in turn provide photosynthetic products to their coral hosts (40). All reef-building corals are obligately dependent on their zooxanthellae, which are probably responsible for the characteristically high rates of calcification that reef-building corals achieve (41).

The ecological balance between corals and their algal partners, and hence the success of corals as reef builders, is potentially very sensitive to environmental conditions. This stems from the fact that although we tend to think of mutualisms as cooperative relationships, they are often better viewed as reciprocally selfish associations (42). That is, other things being equal, each partner tries to maximize its net gain from the association by minimizing costs and maximizing benefits. This selfishness has the potential to lead to ecological instability, because if stress makes it difficult for one partner to provide its normal complement of benefits, the other partner may respond in the short term by terminating the relationship, a strategy that is normally an appropriate response to the ever present threat of cheaters [partners that receive but do not return benefits (42)].

The implications of this are more than academic in the context of the environmental changes to which reefs are subject today. When corals are exposed to elevated temperatures or UV radiation, for example, they "bleach"—that is, photosynthetic pigments are drastically reduced, typically because of algal death or expulsion (43). Bleached corals can survive without their normal complement of zooxanthellae for weeks or sometimes months, but their growth and reproductive output are reduced and eventually they die. Global warming is of particular concern, because temperatures as little as 1°C over the normal seasonal maximum can provoke substantial bleaching (44). Coral bleaching has increased dramatically over the last several decades (44), and 1998 (with its unusually strong El Niño) was characterized by massive bleaching on a worldwide scale (45). In some areas, reefs were decimated to unprecedented extents, based on the fossil record (39), and climate models suggest that temperatures sufficient to induce bleaching could become annual events within a few decades (45).

Nevertheless, it remains unclear whether coral reefs as we know them will succumb to global warming, because coral–algal symbioses do have some capacity to increase their ability to withstand stresses such as high temperatures. For many years, physiological acclimatization was viewed as the primary mechanism (46), and recent studies have shown, for example, that acclimation to high light can provide some protection against high temperature (47). There is also renewed interest in evolutionary responses with the realization that zooxanthellae have far more genetic diversity than previously realized. Pioneering studies by Trench (48) and Rowan (49) have shown that what was once viewed as a single species living in association with multiple invertebrate phyla, is in fact a diverse assemblage, now shown to consist of at least four major clades (50, 51) whose genetic differences are comparable to those exhibited between different families or orders of free-living dinoflagellates (49). Some coral species host just one type of symbiont, whereas other corals host multiple types, sometimes within individual colonies (49–51).

This diversity is of particular significance with respect to global change, because different types of zooxanthellae exhibit striking differences in their susceptibility to bleaching (52) and their ability to recolonize bleached hosts (53). Thus, reefs may be able to survive predicted increases in sea temperature and other coming environmental changes by shifts in the kinds of zooxanthellae that are typically hosted by corals. Indeed, even

bleaching itself may be adaptive if it facilitates symbiont exchange (54).

Experimental bleaching does appear to result in novel associations (51, 53) but we know almost nothing about the long-term consequences of such shifts in symbiont associations. Symbionts that initially colonize bleached colonies are probably rapidly growing opportunistic genotypes (53) that may not be ideal partners from the coral's perspective. These may subsequently be replaced by stress-resistant mutualists (53), but again we do not know how these associations perform as mutualisms relative to those that were established before bleaching. Thus, although opportunistic or stress-resistant symbionts may provide protection against outright mortality (51), the consequences for growth rates or reproductive output are unclear.

Global warming is not the only aspect of global change with which corals and their symbionts must contend. Many aspects of the oceans' biogeochemistry are changing in response to human activities (55). Rising levels of carbon dioxide that underlie much of global warming may be detrimental in their own right to corals. Coral reef growth depends on the net accumulation of calcium carbonate, which is affected by the saturation state of calcium carbonate in surface waters. Kleypas and colleagues (56) argue that by 2100, increased levels of carbon dioxide might cause calcification to decrease by 17–35% relative to preindustrial levels. Such a decrease could result in weaker coral skeletons, reduced growth rates, increased susceptibility to erosion, and perhaps even a reduction in the ability of higher latitudes (a potential refuge from higher temperatures) to sustain reef growth (57).

Increased nutrients of the types associated with changing land-use patterns (58) may also directly harm corals. High nutrient levels can result in reduced rates of growth and calcification (59), as well as decreases in reproduction (60), probably because of their impact on the symbiotic association between corals and zooxanthellae (40, 59). Nevertheless, experimental manipulations of nutrient levels on corals often yield slight and sometimes unexpected results, particularly when done in the field (61). Thus, it remains unclear whether current levels of eutrophication are having a major, direct effect on the health of corals. However, nutrients may also have a variety of indirect effects that are discussed in later sections.

Emergent Diseases

Dinoflagellates are not the only important microbes on reefs. Although poorly known, pathogens probably greatly outnumber mutualists, and they are capable of completely transforming reef communities through their effects on ecologically dominant organisms. The most spectacular example of disease in the oceans is the decimation of the once abundant sea urchin *Diadema antillarum* throughout the tropical western Atlantic. Between 1983 and 1984, more than 95% of these urchins died because of a still uncharacterized pathogen that swept through the entirety of the urchin's geographic range with the exception of the eastern Atlantic (62). Nearly two decades later, recovery is still limited (63), and in many places densities remain extremely low, despite the relatively short generation times and high fecundity of *Diadema* (64). Although reasons for the failure of *Diadema* to recover may be complex, the effect of low density on fertilization rates is probably a major contributor (64).

Reef-building corals themselves appear to be increasingly affected by disease (65). The ecological effects of coral pathogens are likely to be especially severe because rates of mortality can be very high [up to 2 cm of coral tissue daily (66)], whereas coral growth and recruitment rates are typically intrinsically low [e.g., annual growth rates of ~1 cm per year in many massive corals (67)]. The Caribbean, once again, provides particularly troubling examples (68). Before 1980, shallow-water reefs throughout the region were dominated by the genus *Acropora*. By 1990, most stands of *Acropora* were reduced to scattered small patches by an unknown pathogen. Recovery has been slight (65), despite the relatively high growth rates that characterize the genus. Recovery from diseases of massive corals is likely to be especially prolonged because growth rates in these corals are far slower (67). Diseases that attack *Montastraea* (69) are perhaps the most threatening to Caribbean reefs, because of the dominance of this coral as a reef builder throughout the region.

The direct evolutionary impact of disease on coral reefs remains unclear. Lessios (62) found no evidence for reduced genetic variation in *Diadema* following catastrophic mortality, perhaps because even 95% mortality does not result in small enough populations sizes in formerly abundant organisms. Alternatively, the bottleneck in population size may not have persisted long enough at the time of the study for genetic effects to accumulate. The ecological impacts of diseases on reefs are already substantial, however, via the direct effects of coral pathogens on coral abundance and the indirect effects of the demise of a dominant herbivore on seaweeds (discussed below). These ecological changes appear to be without precedent over at least the last several thousand years, based on examination of the extensive Caribbean fossil reef record (70–72).

As with any recent change, evaluating the role of anthropogenic effects is a challenge. This is particularly true for marine diseases, because there is almost no baseline information on earlier disease prevalence and even the pathogens responsible are largely unknown (65, 68). Harvell and colleagues (68) suggest that apparent increases in the incidence of disease in marine ecosystems generally could be at least in part the consequence of global climate change, and they note that terrestrial activities of man appear to have introduced at least one pathogenic agent to coral reefs via run-off. It has long been recognized that stress can make corals vulnerable even to normally benign microbial associates (73), and thus, disease seems likely to be a major player on reefs of the future. The ability of corals to respond evolutionarily to the threat of pathogens is probably fairly limited, given the enormous difference in generation times between corals and their microbial enemies.

Shifting Ecological Balances: Competitors and Predators of Corals

Pathogens are not the only biological enemies of corals; substantial mortality is also associated with overgrowth by competitors and the feeding of predators. Evidence for increases in these sources of mortality in recent decades is accumulating, thereby suggesting that corals are currently waging a losing battle on this front as well.

The most important competitors of corals today on most reefs are seaweeds (74). There is general agreement that the competitive balance between corals and macroalgae is shaped primarily by the magnitude of herbivory and nutrient availability, but their relative importance and how they interact continues to be the subject of debate (75–77). Small-scale experiments suggest, however, that herbivory is often likely to be much more important than nutrients in limiting algal growth (78).

The histories of Kaneohe Bay, Hawaii (79) and Discovery Bay, Jamaica (37) illustrate many of the relevant issues on a broader scale. Concerns about eutrophication related to the explosion of the green bubble alga *Dictyosphaeria cavernosa* led to the diversion of sewage from Kaneohe Bay beginning in 1977, and the opportunity to monitor the response of the reef community to this major, albeit uncontrolled, experiment (79). By 1983, algal abundance had dropped to 25% of peak levels and coral abundance had increased. Since then, however, algal cover has again increased and coral recovery has slowed or even been reversed. In the case of Discovery Bay (37), the uncontrolled experiment was the Caribbean-wide die-off of the herbivorous

sea urchin *D. antillarum* described above, which at any one site occurred over the course of only a few days (62). In Discovery Bay (which was in the process of recovering from a major hurricane several years earlier) dead substrates were quickly colonized by small ephemeral algae, but these were replaced over several years by larger, long-lived species capable of overgrowing living coral. The result has been the decline of coral cover from 52% to 3%, and the increase in algal cover from 4% to 92% (37). Similar changes, albeit somewhat different in timing and extent, have occurred elsewhere (62). The general consensus is that the die-off of such an important herbivore, particularly in the context of low abundance of herbivorous fishes due to overfishing, was the primary cause of the shift from a coral-dominated to an algal-dominated reef (37, 75, 77).

These events suggest that herbivory is often the more important regulator of competition between algae and corals, although eutrophication can also shift the balance toward algal overgrowth, particularly when it is extreme (as in Kaneohe Bay). Algae are not the only competitors of corals that could be affected by eutrophication, however; nutrient enrichment and consequent increases in bacterial populations might also facilitate the success of filter-feeders that have few natural predators and are capable of overgrowing corals. The ascidian *Trididemnum solidum*, which increased on reefs of Curaçao by 900% between 1978 and 1993 (80), may be a case in point, although no data showing the cause of the increase exist. In any case, because the effects of both decreased herbivory and increased eutrophication are likely to be augmented in the future, the future of corals will almost certainly include increases in mortality from competitors.

The same anthropogenic factors that can affect the competitors of corals—*eutrophication and overfishing*—have also been implicated in some of the spectacular explosions in predators of corals (corallivores) witnessed over the last few decades. The crown-of-thorns starfish, *Acanthaster planci*, is the most infamous of these (81, 82), but explosions of predatory snails, particularly in the genus *Drupella*, have also been noted (83). At least in the case of *Acanthaster*, the extent of outbreaks appears to be unprecedented, because the size structure of corals preceding the earliest documented outbreaks could not have existed if current magnitudes and frequencies of outbreaks were a long-term feature of reefs (84). Outbreaks also appear to be shifting in nature from episodic to chronic (82). As with the competitors of corals, fishing out of predators on corallivores (top-down control) may play a larger role than the enhancement of survivorship of corallivores in the larval stage by eutrophication (bottom-up control; ref. 82). However, not all studies support the importance of the former (85) or the lack of importance of the latter (86). The factors contributing to *Drupella* outbreaks are even less well understood (83).

Sea Level, Storms, and Bioerosion

One of the most frequently discussed consequences of global climate change is rising sea level. Past rises in sea level have often been associated with global increases in reef development (87), but rapid sea level rise can also result in the drowning of reefs if it is too rapid, because of the light dependency of coral–algal symbiosis and declining light levels with increasing depth. Reef drowning is of potential concern because projected rates of future sea level rise come close to estimates of past sustained rates of reef accretion before the onset of anthropogenic effects (12). Although recruitment of newly submerged areas could keep many species from going extinct, the three-dimensional complexity of a true reef, on which other organisms depend, would be lost.

Net vertical reef accretion is a balance between growth and destruction (88), so that any of the features discussed previously that slow coral growth have the potential to contribute to reef drowning. However future global change is also likely to affect processes on the other side of the equation—*in particular, reef* destruction via storms and the activities of organisms that bore into or scrape the surfaces of calcium carbonate skeletons (bioeroders). Both bioerosion and storminess have been projected to increase in response to anthropogenic global change, the former because of the association between eutrophication and the nutrition of bioeroders (88), and the latter because of the association between high temperatures and cyclonic storms (12). The likely extent of these changes remains subject to debate, but either could result in a slowdown of reef accretion (88). Such a slowdown increases the probability that reefs will not be able to keep up with rising sea levels.

Increased bioerosion and storminess will probably have specific evolutionary consequences in addition to their general effects on reef growth. Fragmentation can facilitate production and spread of asexual propagules, but it is often costly for the organisms involved because many fragments die and survivors have lowered fecundity (22, 27). Thus, increased bioerosion and storminess should favor strong skeletons or the ability to propagate effectively by fragmentation. On the other hand, rising sea level should lead to selection for rapid vertical growth. Some of these selective effects may operate within species, but most will probably favor some species at the expense of others. However, because coral species with very dense skeletons are often slowly growing, and fragmentation results in lowered three-dimensionality, reefs of the future may find themselves caught evolutionarily between the proverbial rock and a hard place.

Threshold Effects, Multiple Stable States, and Metapopulations

Reef biologists who have watched coral cover decline from 50% to 5% over the course of their careers are understandably distressed by the state of reefs today and their prospects for the future. But even more alarming than the magnitude of the decline has been its speed and the fact that few scientists saw it coming. For example, by 1980 the reefs of Discovery Bay, Jamaica had been studied for decades and overfished for centuries (89). Nevertheless, the implications of extreme overfishing for resiliency of these reefs to subsequent disturbances was not appreciated until recovery failed.

Several common attributes of biological systems make prediction difficult. The first are threshold effects or breakpoints (90). These quintessentially nonlinear relationships are common, but nevertheless often surprising: when the thermostat is turned up one notch, people tend to expect one notch's worth of additional heat, not a house in flames. Responses to single variables can behave in this fashion; for example, calcification may remain constant over a range of saturation states, but then drop abruptly below some threshold value (56). Allee effects are classic threshold phenomena, because populations increase above a minimum population size but decrease below it (15).

When two variables interact synergistically, threshold responses and ecological surprises are probably even more likely (91, 92). For example, neither sedimentation nor high nutrient levels are good for corals, but their combined effect is far worse, because fine muds then aggregate into a smothering marine "snow" (93). Similarly, the collapse of reef ecosystems along the north coast of Jamaica seems to have resulted from the synergistic interaction of overfishing and disease (37). Unfortunately, our understanding of how multiple stressors interact remains limited (94, 95).

Also coupled with threshold dynamics is the concept of multiple stable states (9, 90). The existence of multiple stable states implies that two different ecological communities can be stable under the same conditions, with history determining which community is present at any particular point in time. Multiple stable points are linked with threshold effects because it is often the case that the position of the breakpoint depends

on the direction in which the community is moving. For example, a switch from coral dominance to algal dominance might occur at specific levels of eutrophication and herbivory, but much lower nutrient levels or higher levels of herbivory might be required to shift the system back to its original coral-dominated state. This pattern of response is well known for lakes (96), and there is no reason in principle that it might not apply to coral reefs (9).

Switches from coral dominance to algal dominance are dramatic, but they are not the only cause for concern. As on land, potential coral reef habitat is being eliminated and fragmented with the spread of destructive processes both in the sea and on the shore. Models considering this aspect of changing spatial structure provide disturbing insights. For example, in a simple two-species model, habitat destruction (removal of suitable patches) can result in the extinction of a competitive dominant that disperses poorly at the expense of a competitively inferior species that disperses well, even when remaining patches undergo no intrinsic changes themselves (97). More elaborate versions of this idea predict a certain percentage of inevitable extinctions over time associated with a certain fraction of habitat loss—a so-called "extinction debt"—again affecting competitively dominant species first and rising sharply as habitat loss increases (98). Estimates of 40% reef habitat loss through irreparable damage over the next several decades (5) are sobering in this context, because the models imply that competitively dominant corals, which are often major reef builders, may not be able to persist even in areas not strongly impacted by the activities of people.

Applications of these models to specific coral reef situations are limited and require careful consideration of how model concepts and terms relate to the biology of reef organisms. Stone (99, 100) analyzed a Red Sea reef flat and concluded that numbers of species extinctions associated with habitat reduction would be especially catastrophic because competitively dominant corals were already rare. However, this result reflects the fact that reef flats are regularly disturbed and, thus, always dominated by weedy corals. In contrast, the major reef builders on Caribbean reefs are (or were until recently) competitively dominant species, either via aggressive interactions or their ability to overtop their neighbors, whereas weedy corals are typically small understory forms. Here, the number of species extinctions might be smaller, but the ecological impact larger. Records of sea level changes in the fossil record are particularly interesting in this context. Pandolfi (101) has shown that habitat loss of 90% associated with a marked drop in sea level about 18,000 years ago resulted in the rapid extinction of two coral species (which were, as predicted by the models, competitive dominants).

The models (97, 98), as they have been applied to reefs to date (99, 100), assume that each patch is occupied by a single species. In this sense, the analyses describe the dynamics on single reefs, with patches being de facto the spaces occupied by individual colonies. Metapopulation models in the strict sense describe patches surrounded by uninhabitable area, with rates of colonization between populations being slower than the dynamics within populations (ref. 102, and papers in this colloquium). This structure is more appropriate for describing regional dynamics—for example, the many reefs of Caribbean islands and banks separated by uninhabitable deep water that is only occasionally crossed by propagules (103). Marine organisms with limited dispersal abilities that occasionally disperse long distances by rafting (104) almost certainly meet these assumptions, but even organisms once assumed to be too widely dispersing to conform to metapopulation models have recently been shown to recruit to parental populations to a surprising extent (105–107). We do not currently have nearly enough information to parameterize a regional metapopulation model for coral reefs in a quantitatively useful way (103). It is worth noting, however, that at this spatial scale the true weeds might not be corals at all, because broadcasting corals can potentially travel but rarely successfully recruit, whereas brooders regularly recruit, but not at long distances. The weeds would instead be the rapidly colonizing ephemeral algae seen on reefs after hurricanes and other major disturbances.

Broader Consequences for Biodiversity

The extent to which degraded reefs and other habitats can support the associated diversity of healthy coral reef habitats—the current homes for the myriad crustaceans, worms, mollusks, bryozoans, and other groups that are found on reefs—is unknown. Given that reef associates have many times the diversity of the corals themselves, several issues are relevant: (*i*) Are reefs as ecosystems especially vulnerable to environmental change or slow to recover? (*ii*) Are reef dwellers less vulnerable than corals themselves? The fossil record of past extinctions provides the only real data for evaluating these questions.

It is often stated that reef ecosystems are both more vulnerable to extinction and slower to recover, but rigorous analyses are surprisingly limited (87). Past extinction events appear to have had a diverse suite of causes, not surprisingly, because global change in any direction from the status quo is likely to accelerate extinction; this probably explains why there is no strong bias against tropical ecosystems overall. Within the tropics, however, it does appear that shallow-water, low-nutrient carbonate platforms have been more vulnerable than other tropical environments, although there is no strong evidence that such ecosystems recover more slowly (87). There is also a limited amount of evidence suggesting that photosymbiotic organisms might have been more vulnerable to extinction than nonphotosymbiotic organisms, both at the end of the Cretaceous (87) and during the more minor Oligocene–Miocene extinction (108). Corals were also more vulnerable to the changes associated with the rise of the Isthmus of Panama; there are no living examples of closely related sister species among the zooxanthellate scleractinian corals on the two sides of the Isthmus, whereas such sister taxa are common in other groups (109).

One possible explanation for this pattern relates to differences in distributions between the groups. Many organisms characteristic of coral reefs are not restricted to reefs (87). This is true of corals themselves, of course, which can be found growing as scattered colonies without creating the three-dimensional structure and complexity that the term reef implies. However, extrareef distributions are likely to be even more characteristic of other groups of reef-dwellers, at a variety of taxonomic levels. In fishes, for example, all families considered typical of reefs have ranges that extend outside the boundaries of reefs (110, 111). Similarly in bryozoans, more than 75% of reef-associated species of the Caribbean are also found in nonreefal settings (112). Should this be a general pattern, which seems likely, then even elimination of most coral reef habitats would probably not result in the extinction of a comparable proportion of coral reef builders and dwellers (87). No taxonomically comprehensive analysis of obligate versus facultative reef associates exists, but the above suggests that even the loss of all true reefs would leave many facultative reef associates as survivors, and thus many of the deeper branches of the tree of life intact (113).

The most relevant guides to the future are, of course, past extinctions associated with changes similar to those projected for the coming century. Unfortunately, we have little to guide us in this regard. Mass extinctions have been intensively studied, but they are remote in time and, hence, involve organisms whose phylogenetic affinities are distant from the organisms whose responses we wish to predict. Moreover, despite the alarming nature of the ongoing anthropogenic extinctions, they do not begin to approach the severity of these cataclysmic events (ref. 119 and other articles in this colloquium); if they do, *Homo sapiens* will have a lot more to worry about than the future of

coral reefs. The most relevant comparisons are with the Oligocene–Miocene and Pliocene–Pleistocene extinctions (38, 108, 114), but both of these events involved cooling episodes rather than global warming. The combination of nutrification, global warming, and loss of top members of the food chain (not to speak of novel, introduced chemicals) is unprecedented over the last 65 million years. Thus, it is perhaps not surprising that many of the reef organisms that persisted and thrived during the most recent biological upheavals are those that are suffering the most now (114). Who the winners will be this time around is impossible to predict, but we may not be that happy with the outcome.

The Camel's Last Straw?

In the face of so many unknowns, qualitative analogies can provide an important complement to quantitative analyses. For this reason I close with the concept of the straw that broke the camel's back. No single straw "causes" ecological collapse; collapse is difficult to predict based on the response of the camel to earlier straws, but once collapse occurs, the camel does not return to its feet when the last straw is removed. The recent history of coral reefs suggests that collapse is not impossible, and indeed, that we may be closer to worldwide collapse than we realize. Moreover, the weight of the straws is likely to be multiplicative rather than additive because of negative synergistic effects between different types of stressors. Crippled coral reefs, like crippled camels, provide many fewer services, and they can be prohibitively expensive to repair (115). Although reefs are more likely than camels to recover unaided, having come and gone and come again throughout the history of life, it is likely to be a very slow process, and we may not be around to see true reefs when they do return.

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