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Climate Change, Human Impacts, and the Resilience of Coral Reefs

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The diversity, frequency, and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened globally. Projected increases in carbon dioxide and temperature over the next 50 years exceed the conditions under which coral reefs have flourished over the past half-million years. However, reefs will change rather than disappear entirely, with some species already showing far greater tolerance to climate change and coral bleaching than others. International integration of management strategies that support reef resilience need to be vigorously implemented, and complemented by strong policy decisions to reduce the rate of global warming.

Coral reefs are critically important for the ecosystem goods and services they provide to maritime tropical and subtropical nations (1). Yet reefs are in serious decline; an estimated 30% are already severely damaged, and close to 60% may be lost by 2030 (2). There are no pristine reefs left (3–4). Local successes at protecting coral reefs over the past 30 years have failed to reverse regional-scale declines, and global management of reefs must undergo a radical change in emphasis and implementation if it is to make a real difference. Here, we review current knowledge of the status of coral

reefs, the human threats to them now and in the near future, and new directions for research in support of management of these vital natural resources.

Until recently, the direct and indirect effects of overfishing and pollution from agriculture and land development have been the major drivers of massive and accelerating decreases in abundance of coral reef species, causing widespread changes in reef ecosystems over the past two centuries (3–5). With increased human populations and improved storage and transport systems, the scale of human impacts on reefs has grown exponentially. For example, markets for fishes and other natural resources have become global, supplying demand for reef resources far removed from their tropical

sources (6) (Fig. 1). On many reefs, reduced stocks of herbivorous fishes and added nutrients from land-based activities have caused ecological shifts, from the original dominance by corals to a preponderance of fleshy seaweed (5, 7). Importantly, these changes to reefs, which can often be managed successfully at a local scale, are compounded by the more recent, superimposed impacts of global climate change.

The link between increased greenhouse gases, climate change, and regional-scale bleaching of corals, considered dubious by many reef researchers only 10 to 20 years ago (8), is now incontrovertible (9, 10). Moreover, future changes in ocean chemistry due to higher atmospheric carbon dioxide may cause weakening of coral skeletons and reduce the accretion of reefs, especially at higher latitudes (11). The frequency and intensity of hurricanes (tropical cyclones, typhoons) may also increase in some regions, leading to a shorter time for recovery between recurrences (10). The most pressing impact of climate change, however, is episodes of coral bleaching and disease that have already increased greatly in frequency and magnitude over the past 30 years (9–14).

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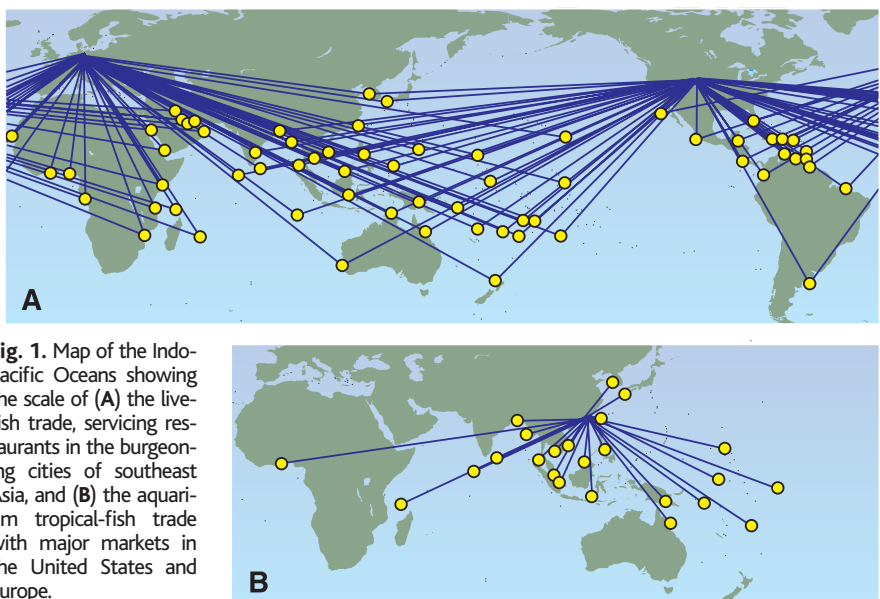


Fig. 1. Map of the Indo-Pacific Oceans showing the scale of (A) the live-fish trade, servicing restaurants in the burgeoning cities of southeast Asia, and (B) the aquarium tropical-fish trade with major markets in the United States and Europe.

REVIEW

Bleaching, Acclimation, and Adaptation

Regional-scale coral bleaching is strongly associated with elevated temperatures, particularly during recurrent ENSO (El Niño–Southern Oscillation) events (8). Stressed, overheated corals expel most of their pigmented microalgal endosymbionts, called zooxanthellae, and become pale or white. If thermal stress is severe and prolonged, most of the corals on a reef may bleach, and many may die. A popular model (9) shows an invariant bleaching “threshold” at $\sim 1^\circ\text{C}$ above mean summer maximum temperatures. This threshold will be chronically exceeded as temperatures rise over the next 50 years, leading to predictions of massive losses of all corals (Fig. 2A). This model is based on two simplifying assumptions: that all corals respond identically to thermal stress, and that corals and their symbionts have inadequate phenotypic or genetic capabilities for adapting rapidly to changes in temperature. Below, we challenge the conventional understanding of these key issues.

Bleaching is conspicuously patchy (15–17), providing clear empirical evidence of the absence of a single bleaching threshold for all locations, times, or species (contrary to the conventional model depicted in Fig. 2A). Consequently, bleached and unbleached corals are often encountered side by side (Figs. 3A and 4B). The sources of this variation are poorly understood and have been variously attributed to extrinsic environmental patchiness (e.g. temperature, light, turbulence), as well as intrinsic differences (phenotypic and genetic) among corals and their microalgal symbionts (15–19). Whatever the mechanisms, bleaching thresholds are more realistically visualized as a broad spectrum of responses (Fig. 2B). Furthermore, bleaching susceptibilities may also change over time as a result of phenotypic and genetic responses (Fig. 2C). In particular, substantial geographic variation in bleaching thresholds within coral species provides circumstantial evidence for ongoing evolution of temperature tolerance.

Average summer water temperatures differ enormously within the geographic boundaries of a typical coral species' range. Based on our current knowledge of taxonomy, the median latitudinal extent of coral species in the Indo-Pacific is 56° (20), with many species' ranges straddling the equator and extending to or beyond the limits of reef growth (at $\sim 30^\circ\text{N}$ and $\sim 30^\circ\text{S}$) where water temperatures are much cooler (Fig. 3B). Similarly, the geographic extent of 35% of coral species in the Arabian Gulf (where the mean summer maximum is 36°C) (21) also includes Lord Howe Island (24°C), the southernmost coral reef in the Pacific Ocean (Fig. 3C). Importantly, corals in the Arabian Gulf do not bleach until they experience temperatures that are extreme for that location, well

over 10°C higher than summer maxima in cooler regions elsewhere in the same species' ranges, providing circumstantial evidence of local adaptation. Furthermore, the lower bleaching threshold in cooler locations implies that there is strong selection for corals and their zooxanthellae to evolve thresholds that are near, but not too far beyond, the expected upper temperature at that location. This pattern points to a potential trade-off between the risk of mortality from extreme temperatures versus a

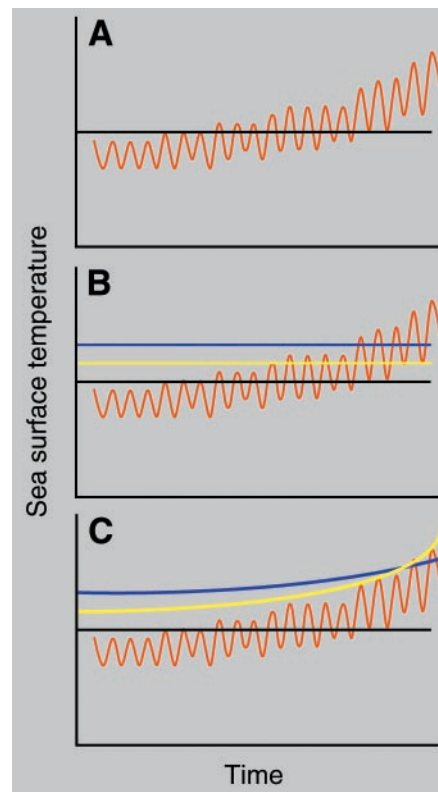


Fig. 2. (A) A model showing a constant coral bleaching threshold, which is likely to be chronically exceeded in the future as oceanic temperatures increase (9, 14). (B) An alternative model that incorporates differences in bleaching thresholds (e.g., among species, depth, and locations), indicated by parallel lines. (C) A more realistic scenario where changes in thresholds also occur over time, attributable to acclimation and evolution.

high cost of thermal protective mechanisms (e.g., antioxidant enzymes, heat shock, or photoprotective proteins and pigments).

An emerging area of research points to the importance of genetic variation as a determinant of bleaching responses in both corals and zooxanthellae. Corals exhibit high levels of genetic diversity, as expected for species with large population sizes and prodigious sexual reproduction (22). Similarly, zooxanthellae (*Symbiodinium* spp.) cluster into a number of groups (based on cladistic analysis

of DNA sequences), with seven clades being recognized so far, comprising many species (19). This recent finding raises the issue of current and future patterns in the distribution and relative abundance of zooxanthellae clades. A hypothesis that bleaching is “adaptive,” increasing coral fitness by facilitating expulsion of susceptible zooxanthellae species and uptake of more resistant ones (23), has not been supported by observations on the fate of bleached corals. Bleaching is more accurately described as a stress response, which is often followed by high mortality, reduced growth rates, and lower fecundity (16, 24). Although adult corals may acquire a previously undetected clade under experimental conditions (25, 26), a change in the relative proportions of zooxanthellae as a result of bleaching, like similar rearrangements of coral assemblages (Fig. 3B), does not necessarily indicate that any evolutionary response has occurred.

A major concern is that the accelerating rate of environmental change could exceed the evolutionary capacity of coral and zooxanthellae species to adapt. A common view is that corals are too long-lived to evolve quickly, and that geographic differences in temperature tolerances have evolved over much longer time frames than the decadal scale of current changes in climate. Although some corals are indeed very long-lived, sexual maturity is reached within 3 to 5 years and most species at all depths rarely live longer than 20 years (27). Nonetheless, highly skewed fecundity distributions (where a few very large, old individuals swamp the gene pool), strongly overlapping generations, and high levels of asexual reproduction are common traits that are likely to retard rapid evolution in many coral species. Although mortality rates from bleaching events are often very high, we know virtually nothing about how much selection this exerts or the heritability of physiological traits in corals. Furthermore, adaptive evolution could be limited if traits under selection are negatively genetically correlated (28) or if gene flow is high enough to preclude local adaptation. On the other hand, high gene flow or connectivity will promote resilience and recovery from recurrent bleaching. The available evidence indicates that rates of gene flow in corals vary substantially among species (22, 29), which implies that their differential ability to migrate in response to climate change and to adapt will result in further changes to community structure beyond the immediate effect of selective mortality caused by severe bleaching. In contrast, subpopulations on isolated islands or archipelagoes (e.g., Hawaii and Bermuda) may represent genetic outposts for virtually all coral reef species, with little input from other, distant

localities. If isolated reefs bleach, recovery is likely to be far slower than in more central, interconnected populations.

Lessons from the Past: The Geological Record

The geological record provides the only source of data on long-term effects of climate change on coral reef species and assemblages (30, 31). Many extant species of corals extend backwards in time to the Pliocene [1.8 to 5.3 million years ago (Ma)], and most scleractinian genera originated in the Eocene to Miocene (55.0 to 5.3 Ma) (32). Extant species have dominated modern reefs for the past half-million years, providing an invaluable baseline long before human impacts began (3, 4). New assessment of past climates has revealed unexpectedly rapid shifts over decades or less, especially at high latitudes, with ice-age transitions being linked to abrupt changes in the North Atlantic circulation (33). Further rapid climatic changes may have also occurred at lower latitudes in warmer periods since the last glacial maximum (34). Consequently, there is now some uncertainty about the speed of expected climate change relative to the past, although we can be certain nonetheless that the projected increases in carbon dioxide and temperature over the next 50 years will substantially and very rapidly exceed the conditions under which coral reefs have flourished over the past half-million years (10).

During the Pleistocene and Holocene, many extant species of tropical and subtropical organisms underwent dramatic shifts in geographic range in response to periods of warming and cooling (35, 36). Some species migrated faster than others, producing rapid shifts in species composition, especially near faunal boundaries (35). For corals, range boundaries of extant coral species in the warm Late Pleistocene extended up to 500 km further south along the western Australia coastline (to 33°S) than they do today (37). Closer to the center of their geographic range, however, coral diversity and species presence or absence in eastern Papua New Guinea changed remarkably little during nine reef-building intervals from 125 to 30 ka (31). On a regional scale, these same species underwent dramatic changes in distribution and abundance as Quaternary glacial-interglacial cycles caused sea level to repeatedly flood and drain from continental shelves and oceanic islands (38). Many marine species exhibit a genetic legacy of these range shifts, local extinctions and expansions, and the marked population fluctuations caused by past climatic variation (29, 39, 40). Based on this past history, we can expect regional and global-scale disruption to coral reefs due to climate change to accelerate markedly in coming decades. Already, relative abundanc-

es of corals and of other organisms are changing rapidly in response to the filtering effect of differential mortality (from bleaching and other, more local human impacts) and differences in rates of recovery of species from recurrent mortality events (16, 17, 41, 42).

There are two major differences, however, between current climate-driven changes and the recent past. First, because the oceans today are already at a high sea-level stand, the projected rise [0.1 to 0.9 m in the next 100 years (10)] will be very small compared with sea-level changes during the Pleistocene. Second, unlike the past, the response of reef-dwelling species to projected climatic trends will be profoundly influenced by people. As outlined below, human impacts and the increased fragmentation of coral reef habitat have preconditioned reefs, undermining reef resilience and making them much more susceptible to future climate change.

Managing Coral Reef Resilience

Clearly, the capacity of coral reef ecosystems to continue to generate the valuable goods and services (on which human welfare depends) has

to be better understood and more actively managed. Sustaining this capacity requires improved protection of coral reef resilience (43). Marine protected areas (MPAs) are currently the best management tool for conserving coral reefs and many other marine systems (44, 45). MPAs range from ineffective “paper parks,” to multiple-use areas with varying degrees of protection, to marine reserves, or no-take areas (NTAs). NTAs provide the most effective protection for extractive activities such as fishing, affording a spatial refuge for a portion of the stock from which larvae and adults can disperse to adjoining exploited areas (44, 45).

NTAs, when properly supported and policed, are effective in preserving fish stocks because they change human behavior. They do not, however, prevent or hold back warm water, or stop bleaching. For example, in 1998, the biggest and most destructive bleaching event to date killed an estimated 16% of the world’s corals, including reefs in the western Pacific, Australia, and Indian Ocean that are widely regarded as the best managed and most “pristine” in the world (2).

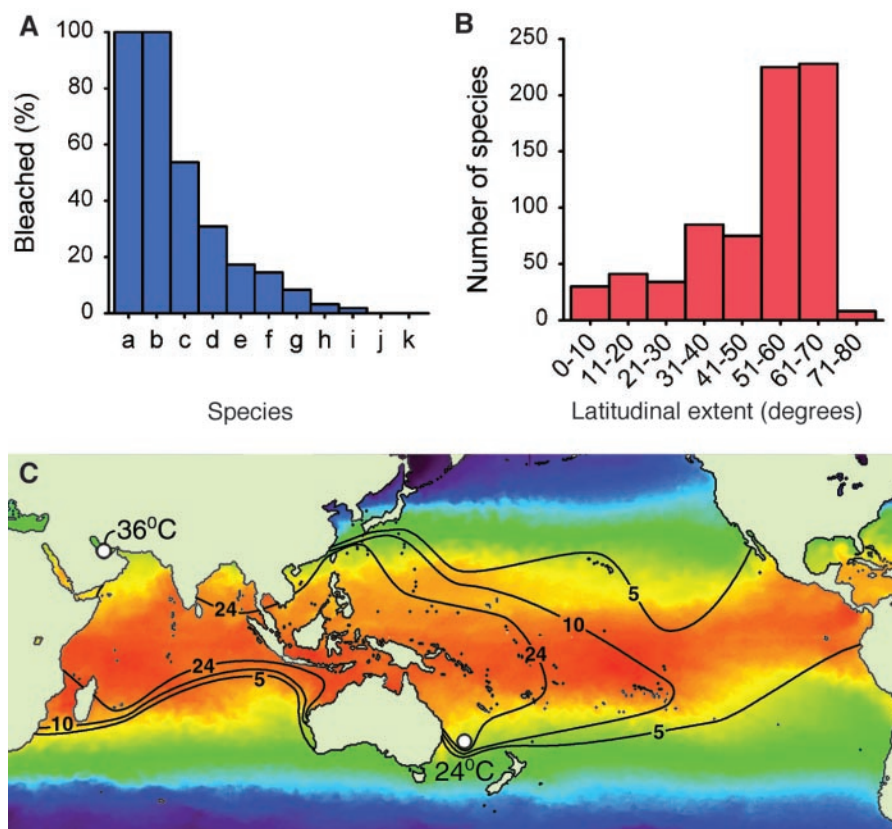


Fig. 3. (A) Differential bleaching responses of nine species of corals in Raiatea, French Polynesia, during May 2002. (a, *Acropora anthocercis*; b, *A. retusa*; c, *Montipora tuberculosa*; d, *Pocillopora verrucosa*; e, *M. caliculata*; f, *Leptastrea transversa*; g, *P. eydouxi*; h, *P. meandrina*; i, *L. bewickensis*; j, *Porites lobata*; k, *L. purpurea*. (B) Latitudinal extents of Indo-Pacific reef corals, measured from the northern- and southernmost point in their range. (C) Geographic range boundaries of 24 species of Indo-Pacific corals found in the Persian Gulf and at Lord Howe Island off Australia, where average maximum summer temperatures differ by 12°C. The coloring shows temperatures in the Southern Hemisphere summer of 1997/1998, when unprecedented mass bleaching occurred (2).

REVIEW

If NTAs do not provide a refuge from bleaching, then how can they help protect coral reefs from climate change? Overfishing, particularly of herbivorous parrotfish and surgeonfish, affects more than just the size of harvestable stocks—it alters the entire dynamics of a reef (3–5, 46). Reduced herbivory from overfishing, increased levels of disease, and excess nutrients can impair the resilience of corals and prevent their recovery following acute-disturbance events like cyclones or bleaching, leading instead to a phase shift to algal-dominated reefs (Fig. 4, D to F). Resilience is also eroded by chronic human impacts that cause persistently elevated rates of mortality and reduced recruitment of larvae (7, 12, 41, 43).

Although climate change is by definition a global issue, local conservation efforts can greatly help in maintaining and enhancing resilience and in limiting the longer-term

damage from bleaching and related human impacts. Managing coral reef resilience through a network of NTAs, integrated with management of surrounding areas, is clearly essential to any workable solution. This requires a strong focus on reducing pollution, protecting food webs, and managing key functional groups (such as reef constructors, herbivores, and bioeroders) as insurance for sustainability (7, 46).

NTAs also act to spread risk, whereby areas that escape damage can act as sources of larvae to aid recovery of nearby affected areas (47). This highly desirable property of NTAs raises the issue of how close they need to be to promote connectivity—the migration of larvae and/or adults—between them (44, 45). Critically, coral reef organisms, including different species of corals, vary greatly in their larval biology and potential for dispersal (22, 29). The clear implication is that NTAs

must be substantially more numerous and closer together than they are currently to protect species with limited dispersal capabilities. Furthermore, isolated reefs that are largely self-seeding are unlikely to be protected by distant NTAs, and therefore will be much less resilient to climate change.

Research and Management Challenges

Coral reefs are highly productive hotspots of biodiversity that support social and economic development. Their protection, therefore, is a socioeconomic imperative, as well as an environmental one. Global warming, coupled with preexisting human impacts, is a grave threat that has already caused substantial damage. However, the available evidence indicates that, at a global scale, reefs will undergo major changes in response to climate change rather than disappear entirely.

There is, nonetheless, great uncertainty whether the present economic and social capacity of coral reefs can be maintained. To limit the damage, emerging management strategies based on greatly expanded networks of NTAs, coupled with stronger protection of adjacent habitats, need to be vigorously implemented. NTAs are unlikely to prevent mortality of corals from bleaching, but they will facilitate a partial recovery of reefs that are reconfigured and populated by a subset of resistant species and genotypes. NTAs are not a panacea; their implementation needs to be complemented by heightened protection of adjacent areas and by strong international policy decisions to reduce the rate of global warming.

Research in support of reef management urgently needs to increase the scale of experiments, sampling, and modeling to match the scale of impacts and key biological processes (e.g., dispersal, bleaching, and overfishing) and go beyond the current emphasis on routine monitoring and mapping. Indeed, most coral reef research is parochial and short-term, and provides little insight into global or longer-term changes. For example, current knowledge of biogeographic-scale patterns on reefs is based on species presence or absence at local sites and pays scant attention to temporal, regional, or global patterns of relative abundance or functional attributes of species (48) that could be exploited for management of resilience. Similarly, studies of intergenerational (genetic) responses to climate change (28) are urgently needed for reef organisms, particularly corals and zooxanthellae. Another crucial area for future work is genetic dissection of population structure and modeling of connectivity, which could incorporate many of the unusual life-history traits of clonal organisms, selection coefficients based on mortality from bleaching, and experimental measurements of heritabilities. Emerging research on marine reserves and how they work to protect harvested stocks and

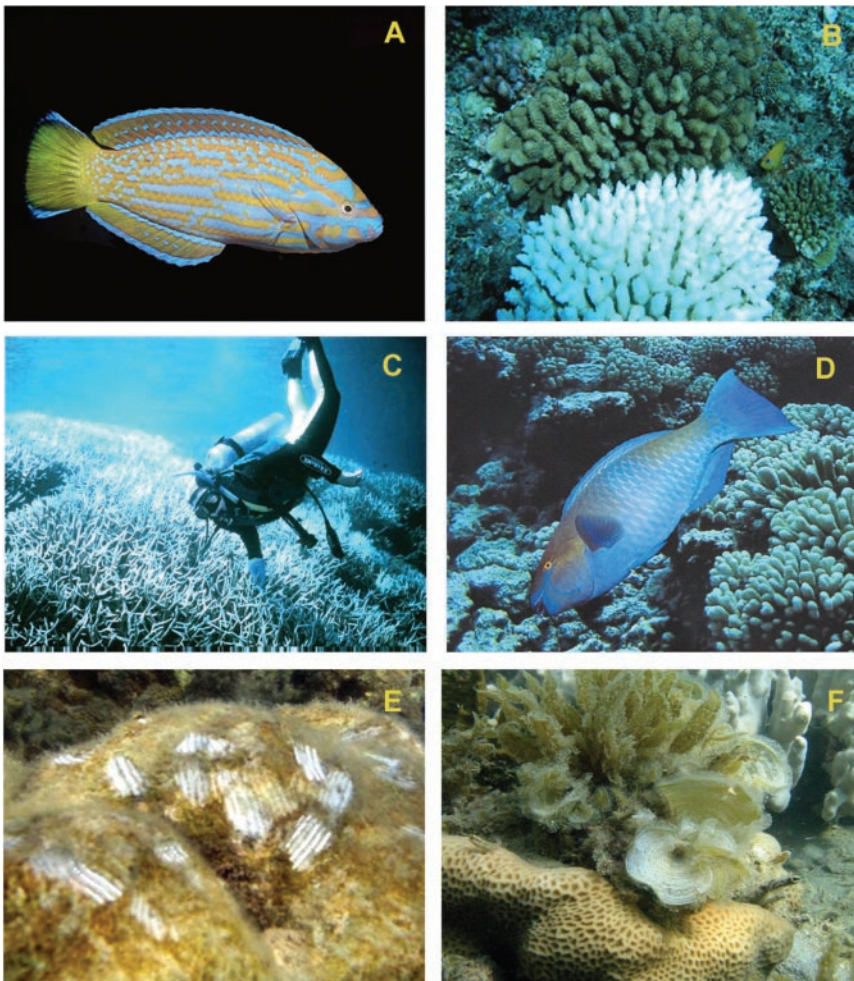


Fig. 4. (A) Aquarium fish, such as *Anampses lennardi* from northwest Australia, are often endemic species and susceptible to overharvesting. (B) A bleached colony of *Acropora nasuta* (bottom), and unbleached *Pocillopora meandrina* (top), showing contrasting responses to thermal stress. (C) A bleached monospecific stand of the staghorn coral *Acropora formosa*. (D) Parrotfishes, such as *Scarus ferrugineus*, are important herbivores. (E) Parrotfish grazing scars. (F) Macroalgae (top) and overgrowth of corals (bottom) are promoted by overfishing of herbivores and degraded water quality.

spread risk (44, 45) also needs to be expanded and applied specifically to the tropics. These approaches must be integrated with socio-economic aspects of coral reef resilience, incorporating adaptive management systems that operate locally, regionally, and globally.

International integration and scaling-up of reef management is an urgent priority (2). Ecological modeling studies indicate that, depending on the level of exploitation outside NTAs, at least 30% of the world's coral reefs should be NTAs to ensure long-term protection and maximum sustainable yield of exploited stocks (49, 50). Yet, even in affluent countries, such as the United States and Australia, less than 5% of reefs today are NTAs. Wealthy countries have an obligation to take the lead in increasing the proportion of reefs that are NTAs, while simultaneously controlling greenhouse-gas emissions.

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