PERSPECTIVE

Warm-water coral reefs and climate change

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Coral reefs are highly dynamic ecosystems that are regularly exposed to natural perturbations. Human activities have increased the range, intensity, and frequency of disturbance to reefs. Threats such as overfishing and pollution are being compounded by climate change, notably warming and ocean acidification. Elevated temperatures are driving increasingly frequent bleaching events that can lead to the loss of both coral cover and reef structural complexity. There remains considerable variability in the distribution of threats and in the ability of reefs to survive or recover from such disturbances. Without significant emissions reductions, however, the future of coral reefs is increasingly bleak.

Warm-water coral reefs are celebrated for their spectacular diversity (estimates exceed 3 million species) and the critical ecosystem services they provide to many of the 275 million people living close by. Covering 0.07% of the ocean surface and living within 30° latitude of the equator, reef-building corals grow optimally between 23° and 29°C. They support over a quarter of the world's small-scale fishers, generate jobs and foreign exchange through tourism, and provide critical sea defenses against storms, flooding, and land erosion.

Coral reefs are biogenic carbonate structures that accrete over decadal time scales because of the active growth of a living veneer of corals and other calcifying organisms (*1*). Disturbance is a natural part of reef growth and development. Reefs are subject both to local impacts (such as waves, grazing, and bioerosion by coral-boring animals) and to large-scale temporally rare perturbations. The latter include physical impacts (such as storms, tsunamis, and seismic events), ecological imbalances (such as disease and predatory starfish outbreaks), and oceanographic influences (such as altered seawater temperature and pH as well as sediment, nutrient, and freshwater inputs).

Measures of reef state or health such as coral cover, diversity, biomass, surface complexity (rugosity), or key species need to be viewed with an appreciation of this natural dynamism. In healthy systems, losses of key ecosystem components, be they reef-building corals or herbivorous fish, are often transitional. Fish stocks recover, and the net decadal growth of biogenic structure may be maintained even if coral growth is reduced and erosion predominates for a few years. Despite this natural variability, reefs are highly vulnerable to human-induced degradation (*2*). Growing concern for their long-term future has led to urgent calls for action across many public-sector, governmental, and even faith communities.

Human pressures fall into the same broad classes as natural perturbations: physical, ecological, and oceanographic (table S1). The challenge they present is twofold. First, anthropogenic effects act in addition to natural disturbances. Thus, although coral bleaching can be a natural phenomenon, it now occurs more frequently and more severely. Second, many of these pressures are chronic: Although reversible, they are not being reversed. Thus overfishing has left large areas of reefs without key functional groups such as top predators, or with reduced herbivore biomass and diversity, for many years.

In a seminal study of a Caribbean reef, Hughes showed that coral reefs could be taken out of their naturally dynamic equilibrium and shifted toward an alternative state by a combination of natural and anthropogenic perturbations. The observed ecological shift from coral to algal domination (*3*) was later replicated on an Indo-Pacific reef (*4*), and the reality of such phase shifts has now become an established paradigm.

Climate change impacts

Most warm-water corals exhibit a symbiotic relationship with single-celled algae (zooxanthellae) from which they derive much of their nutrition. This relationship breaks down under stress. Algal densities decline and photosynthetic pigments may be reduced. As a result, corals become pale or "bleached" and in some cases die. Mass bleaching events around the world were first noted in 1983 and have been linked to elevated sea temperatures. These events usually last for a few weeks to a few months and are acute threats to the corals, whose presence and structure underpin the entire ecosystem. Severe seawater warming in 1998 affected most coral reef regions and caused widespread coral mortality, particularly in the Indian Ocean.

Most corals live close to their upper thermal maximum, and an increasing frequency of bleaching is projected with warming background temperatures. Even corals surviving bleaching may be affected, with impaired reproduction, susceptibility to disease, and reduced calcification. Within the Caribbean, increases in thermal minima have probably played a role in the spread of disease in acroporid corals (*5*).

Although recovery from the 1998 bleaching has been documented on many reefs, elsewhere it has been linked to phase shifts toward macroalgal dominance (see the case study below). An El Niño–Southern Oscillation event currently beginning has been predicted to match that of 1998 in terms of intensity (*6*) and could drive further

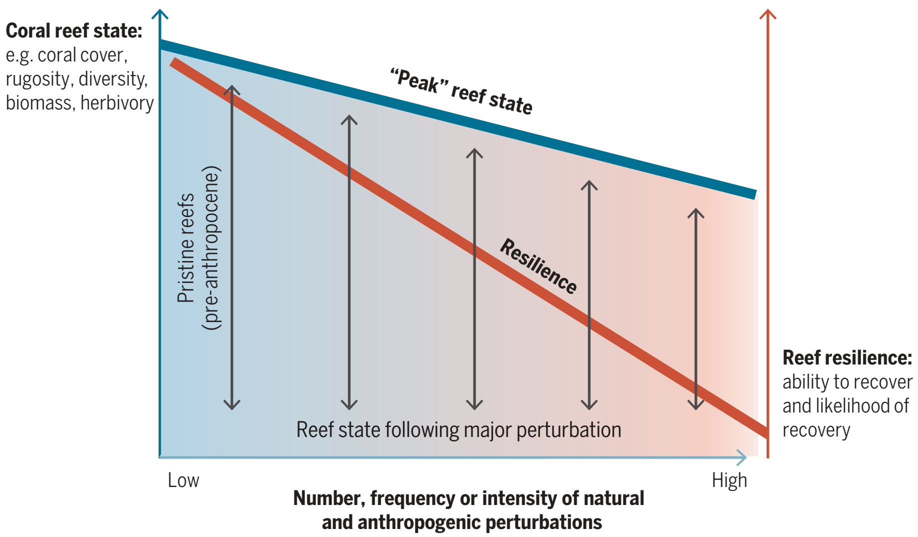

Fig. 1. Reef state varies across a broad spectrum, even in natural conditions, but increasing number, frequency, or intensity of perturbations (*x* axis) will typically affect both the peak state that a reef can attain (blue line) and the resilience of that reef (red line). Double-headed arrows indicate that at any given threat level, reefs may be observed across a broad range of states. For this reason, the large decrease in resilience with increasing threats may not be apparent from simple one-off measures of reef state.

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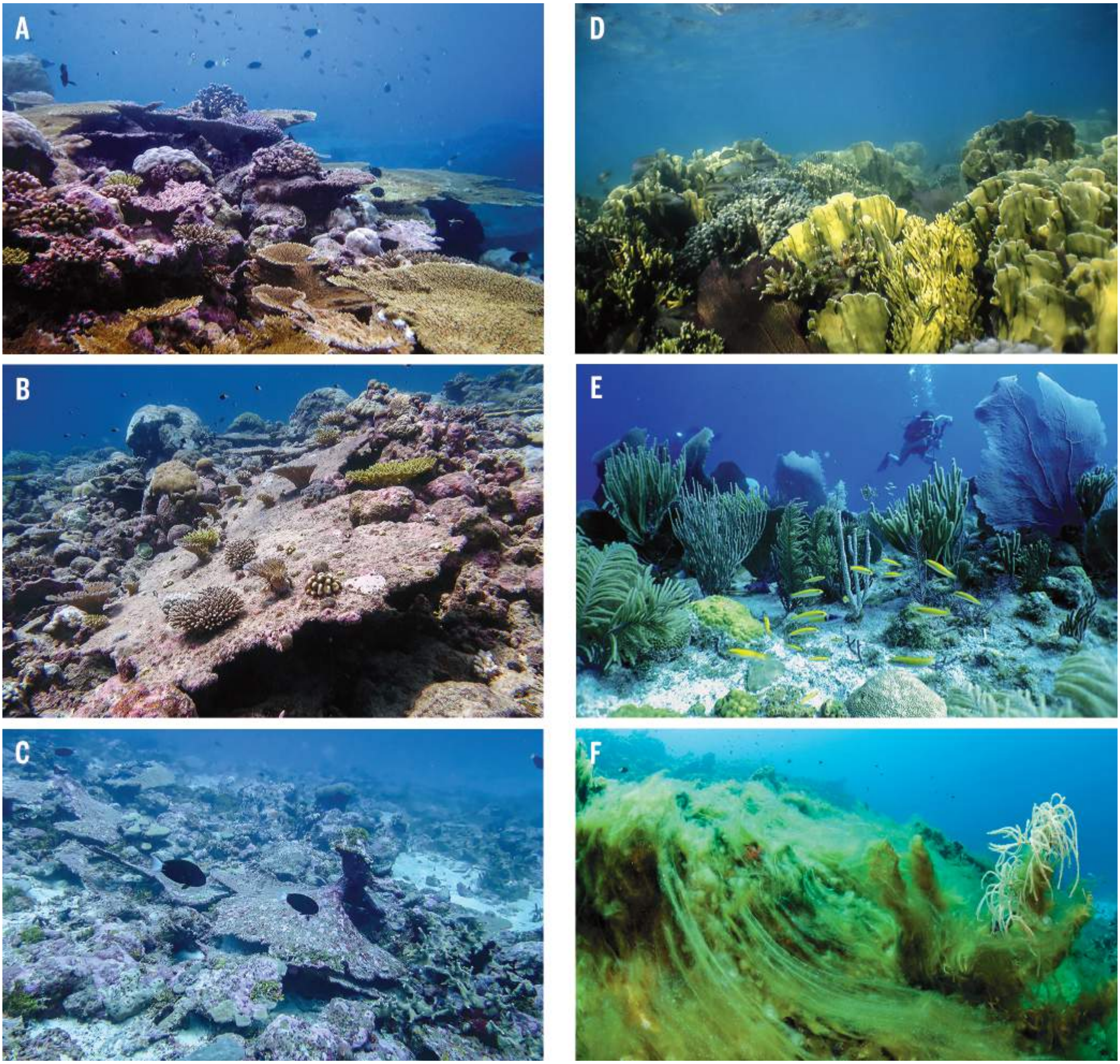

Fig. 2. Indo-Pacific and Caribbean reefs may be observed across a broad spectrum of states. (Left) Reefs of the well-protected Chagos Archipelago (BIOT) were badly damaged by the bleaching event in 1998 (**C**), but most recovered with high recruitment (**B**) over several years to return to high coral cover (**A**). (Right) In the Caribbean, high coral cover (**D**) is now very rare indeed, and "peak" condition for many reefs is a mix of hard corals, soft corals, and macroalgae (**E**). In many places, phase shifts have led to highly altered, algal-dominated "reefs" (**F**), which might no longer meet the definition of a true coral reef.

reef loss. Future trajectories of warming ocean waters present a bleak picture.

Patterns of bleaching, and the responses of corals, are far from homogeneous. McClanahan and others have pointed to considerable variability in bleaching susceptibility between both taxa and locations (*7*, *8*). Bleaching susceptibility appears lower in areas of prior thermal stress and/or in regions subject to natural fluctuations in sea temperature. At finer scales, recent work by Palumbi *et al.* (*9*) in American Samoa showed that at least one widespread species had the ability to acclimatize over a time scale as short as 2 years. Other researchers have demonstrated decade-long memories of acquired tolerance (*10*) and the possibility of transferring thermal tolerance between generations (*11*). Nevertheless, there remains concern about the ability of any species, or indeed the ecosystem as a whole, to adjust sufficiently quickly to match projected rates of temperature rise.

Ocean acidification poses a further chronic threat for coral reefs through reductions in the saturation state of aragonite, which is required to build the coral skeleton. Projected impacts on corals and reef structures include reduced growth, weaker skeletons, increased bioerosion, and potentially dissolution of carbonate substrates and coral skeletons (*12*). As with sea-temperature increases, a rapidly growing research base has added many nuances to original concerns. For example, some coral species will cope better than others, at least in the early stages of rising CO_2 conditions, and the response among other fauna and flora is highly variable (*13*).

The current state of reefs and resilience

About 75% of the world's reefs are considered threatened by human activities (*2*). Long-term and multisource syntheses reveal dramatic changes to coral reefs in recent decades. The complete physical loss of reefs remains rare, but degradation is now almost ubiquitous. In the Indo-Pacific, coral cover has declined to only 22% of total reef surfaces, after an estimated 2% decline per year from 1997 to 2003 (*14*). On the relatively well-protected Great Barrier Reef, more recent declines are even steeper: An average of 3.4% loss of coral cover per year from 1985 to 2012 has led to a current mean coral cover of only 14% (*15*).

Other metrics for the state of reefs indicate similar patterns. For example, massive declines in rugosity have been reported from the Caribbean (*16*), where over one-third of reefs no longer have sufficient coral to maintain their structure and are now eroding (*17*). Overfishing has affected most of the world's coral reefs: Herbivore biomass is, on average, double on reefs that are not accessible to fishing (*18*), and the abundance of large reef fish species, including sharks, is often 10 times higher around unfished reefs (*19*).

Such changes are influencing the appearance and functional ecology of reefs. The flattening of reef morphology (*16*) is reducing the overall surface area for benthic species and reducing surface complexity associated with niche space for mobile fauna (*20*). The particularly strong declines and phase shifts observed on Caribbean reefs may be regarded as a harbinger for other regions, and indeed some recovery failure has also been noted on Indo-Pacific reefs (case study) (*21*).

Many reefs do, however, have a high capacity for recovery, and after a perturbation they typically return to previous levels of coral cover, rugosity, and biomass. One-off metrics of reef state such as coral cover are therefore of limited use for understanding where a particular reef lies on the threat spectrum (Fig. 1). After severe bleaching, coral cover can return within a decade, although return to the original ecological assembly may take longer and may not occur at all (*22*). The challenge comes when severe perturbations become too frequent to allow full recovery or when multiple perturbations occur at the same time (Fig. 2).

Case study: Coral bleaching impacts in the Indian Ocean

The reefs of the central and western Indian Ocean suffered some of the most extreme impacts from the 1998 bleaching event, with coral mortality often in excess of 90%. Since that event, and despite sublethal bleaching events in some subsequent years, many reefs, such as those in the British Indian Ocean Territory (BIOT; also known as the Chagos Archipelago), have moved toward recovery (*23*). These reefs are protected by the world's largest no-take marine reserve and have few direct anthropogenic pressures. Reefs around the granitic Seychelles islands showed more diverse response trajectories, with some reefs, including most deeper reefs, displaying strong recovery while others moved toward macroalgal–dominated communities with low coral cover (*24*). These were some of the first reefs to show phase shifts outside of the Caribbean. At least two of the five factors associated with these shifts can be linked to anthropogenic disturbance: low herbivore biomass and high nutrient concentrations. Efforts are now under way to improve reef management and undertake restoration in some of these reefs. Such efforts will help, but they may not be sufficient in the face of accelerating climate change. Despite their protection from local threats, some BIOT reefs have shown low recovery and also increasing disease occurrence.

Managing for the future

It is perhaps naïve to try and hold any ecosystem in a pre-Anthropocene state, but equally it is too early to proclaim the end of coral reefs. Reefs are declining in condition globally but not evenly. Furthermore, in many areas, other impacts such as overfishing and pollution are so severe that climate change impacts are at present of secondary importance (*15*). The threat array varies between reefs, but there are also natural differences in resilience, a fact that has led to the concept of building such resilience into reef management. The initial focus has been on identifying and focusing management interventions such as pollution mitigation and overfishing reduction around areas where resilience may already be high (*25*).

Alongside these management approaches are more active interventions such as reef restoration through the use of coral transplants and coral nurseries (*26*). Assisted colonization has been suggested as a strategy, whereby heat-tolerant corals from one region are transferred to another location within their natural range to enhance thermal tolerance in that location (*27*). However, there can be problems with the survival of transplants and risks with possible genetic alteration of subpopulations. There are even calls from some academics within the coral reef research community to consider more radical solutions, ranging from the genetic manipulations of corals or associated symbionts (*28*) to geoengineering through aerosol-based solar radiation management (*29*). Such approaches carry huge risks, from the unintended ecological consequences of genetic modifications to impacts on global hydrological cycles and stratospheric ozone from geoengineering. The fact that they are even being mooted indicates the levels of concern.

Without the stabilization of greenhouse gas concentrations, it seems inevitable that many of the world's coral reefs will become nonaccreting habitats—they will, based on most common definitions, cease to be coral reefs. This will happen more or less rapidly in different locations and will have concomitant and profound impacts on both biodiversity and people. As reefs decline, many of the millions of people who live near reefs will lose critical sources of food, as well as coastal protection and tourism revenues. Ironically, however, the main drivers of current reef decline—pollution, overfishing, sedimentation, and direct destruction—may be just as influential in the near term as climate drivers in the long term. Concerted efforts by governments with jurisdiction over coral reefs may be able to manage these direct threats. This could win critical time both for adaptation and, crucially, for the global community to act on stabilizing and reducing emissions.

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