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Reefs in
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Coral Reefs Under Rapid Climate Change and Ocean Acidification

O. Hoegh-Guldberg,[1]* P. J. Mumby,[2] A. J. Hooten,[3] R. S. Steneck,[4] P. Greenfield,[5] E. Gomez,[6]
C. D. Harvell,[7] P. F. Sale,[8] A. J. Edwards,[9] K. Caldeira,[10] N. Knowlton,[11] C. M. Eakin,[12]
R. Iglesias-Prieto,[13] N. Muthiga,[14] R. H. Bradbury,[15] A. Dubi,[16] M. E. Hatziolos[17]

Atmospheric carbon dioxide concentration is expected to exceed 500 parts per million and global temperatures to rise by at least 2°C by 2050 to 2100, values that significantly exceed those of at least the past 420,000 years during which most extant marine organisms evolved. Under conditions expected in the 21st century, global warming and ocean acidification will compromise carbonate accretion, with corals becoming increasingly rare on reef systems. The result will be less diverse reef communities and carbonate reef structures that fail to be maintained. Climate change also exacerbates local stresses from declining water quality and overexploitation of key species, driving reefs increasingly toward the tipping point for functional collapse. This review presents future scenarios for coral reefs that predict increasingly serious consequences for reef-associated fisheries, tourism, coastal protection, and people. As the International Year of the Reef 2008 begins, scaled-up management intervention and decisive action on global emissions are required if the loss of coral-dominated ecosystems is to be avoided.

Coral reefs are among the most biologically diverse and economically important ecosystems on the planet, providing ecosystem services that are vital to human societies and industries through fisheries, coastal protection, building materials, new biochemical compounds, and tourism (1). Yet in the decade since the inaugural International Year of the Reef in 1997 (2), which called the world to action, coral reefs have continued to deteriorate as a result of human influences (3, 4). Rapid increases in the atmospheric carbon dioxide concentration ($[CO_2]_{atm}$), by driving global warming and ocean acidification, may be the final insult to these ecosystems. Here, we review the current understanding of how anthropogenic climate change and increasing ocean acidity are affecting coral reefs and offer scenarios for how coral reefs will change over this century. The scenarios are intended to provide a framework for proactive responses to the changes that have begun in coral reef ecosystems and to provoke thinking about future management and policy challenges for coral reef protection.

Warming and Acidifying Seas

The concentration of carbon dioxide in Earth's atmosphere now exceeds 380 ppm, which is more than 80 ppm above the maximum values of the past 740,000 years (5, 6), if not 20 million years (7). During the 20th century, increasing $[CO_2]_{atm}$ has driven an increase in the global oceans' average temperature by 0.74°C and sea level by 17 cm, and has depleted seawater carbonate concentrations by ~30 μmol kg^{-1} seawater and acidity by 0.1 pH unit (8). Approximately 25% (2.2 Pg C year^{-1}) of the CO_2 emitted from all anthropogenic sources (9.1 Pg C year^{-1}) currently enters the ocean (9), where it reacts with water to produce carbonic acid. Carbonic acid dissociates to form bicarbonate ions and protons, which in turn react with carbonate ions to produce more bicarbonate ions, reducing the availability of carbonate to biological systems (Fig. 1A). Decreasing carbonate-ion concentrations reduce the rate of calcification of marine organisms such as reef-building corals, ultimately favoring erosion at ~200 μmol kg^{-1} seawater (7, 10).

We used global $[CO_2]_{atm}$ and temperature data from the Vostok Ice Core study (5) to explore the ocean temperature and carbonate-ion concentration (10) seen today relative to the recent past for a typical low-latitude sea maintain-ing a mean temperature of 25°C during the past 420,000 years (Fig. 1B). The results show a tight cluster of points that oscillate (temperature ±3°C; carbonate-ion concentration ±35 μmol kg^{-1}) between warmer interglacial periods that had lower carbonate concentrations to cooler glacial periods with higher carbonate concentrations. The overall range of values calculated for seawater pH is ±0.1 units (10, 11). Critically, where coral reefs occur, carbonate-ion concentrations over the past 420,000 years have not fallen below 240 μmol kg^{-1}. The trends in the Vostok ice core data have been verified by the EPICA study (6), which involves a similar range of temperatures and $[CO_2]_{atm}$ values and hence extends the conclusions derived from the Vostok record to at least 740,000 years before the present (yr B.P.). Conditions today ($[CO_2]_{atm}$ ~380 ppm) are significantly shifted to the right of the cluster points representing the past 420,000 years. Sea temperatures are warmer (+0.7°C), and pH (−0.1 pH units) and carbonate-ion concentrations (~210 μmol kg^{-1}) lower than at any other time during the past 420,000 years (Fig. 1B). These conclusions match recent changes reported for measurements of ocean temperature, pH, and carbonate concentration (8). In addition to the absolute amount of change, the rate at which change occurs is critical to whether organisms and ecosystems will be able to adapt or accommodate to the new conditions (11). Notably, rates of change in global temperature and $[CO_2]_{atm}$ over the past century are 2 to 3 orders of magnitude higher than most of the changes seen in the past 420,000 years (Table 1). Rates of change under both low (B1) and high (A2) Intergovernmental Panel on Climate Change (IPCC) emission scenarios are even higher, as are recent measurements of the rate of change of $[CO_2]_{atm}$ (9). The only possible exceptions are rare, short-lived spikes in temperature seen during periods such as the Younger Dryas Event (12,900 to 11,500 yr B.P.) (12). Given that recent and future rates of change dwarf even those of the ice age transitions, when biology at specific locations changed dramatically, it is likely that these changes will exceed the capacity of most organisms to adapt.

Ocean Acidification and Reef Accretion

Many experimental studies have shown that a doubling of pre-industrial $[CO_2]_{atm}$ to 560 ppm decreases coral calcification and growth by up to 40% through the inhibition of aragonite formation (the principal crystalline form of calcium carbonate deposited in coral skeletons) as carbonate-ion concentrations decrease (13). Field studies confirm that carbonate accretion on coral reefs approaches zero or becomes negative at aragonite saturation values of 3.3 in today's oceans (Fig. 4), which occurs when $[CO_2]_{atm}$ approaches 480 ppm and carbonate-ion concentrations drop below 200 μmol kg^{-1} in most of the global ocean (10, 13). These findings are supported by the observation that reefs with net carbonate accretion today (Fig. 4, 380 ppm) are restricted to waters where aragonite saturation

[1]Centre for Marine Studies, The University of Queensland, St. Lucia, 4072 Queensland, Australia. [2]Marine Spatial Ecology Laboratory, School of BioSciences, University of Exeter, Prince of Wales Road, Exeter EX4 4PS, UK. [3]AJH Environmental Services, 4900 Auburn Avenue, Suite 201, Bethesda, MD 20814, USA. [4]University of Maine, School of Marine Sciences, Darling Marine Center, Walpole, ME 04573, USA. [5]The Chancellery, University of Queensland, St. Lucia, 4072 Queensland, Australia. [6]Marine Science Institute, University of the Philippines, Diliman, Quezon City, Philippines. [7]Ecology and Evolutionary Biology, E321 Corson Hall, Cornell University, Ithaca, NY 14853, USA. [8]International Network on Water, Environment and Health, United Nations University, 50 Main Street East, Hamilton, Ontario L8N 1E9, Canada. [9]School of Biology, Ridley Building, University of Newcastle, Newcastle upon Tyne, NE1 7RU, UK. [10]Department of Global Ecology, Carnegie Institution of Washington, 260 Panama Street, Stanford, CA 94305, USA. [11]National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA. [12]National Oceanic and Atmospheric Administration, Coral Reef Watch, E/RA31, 1335 East West Highway, Silver Spring, MD 20910–3226, USA. [13]Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apdo. Postal 1152, Cancún 77500 QR, México. [14]Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, NY 10460, USA. [15]Resource Management in Asia-Pacific Program, Australian National University, Canberra, 0200 Australia. [16]Institute of Marine Sciences, University of Dar es Salaam, Tanzania. [17]Environment Department, MC5-523, The World Bank, 1818 H Street, NW, Washington, DC 20433, USA.

*To whom correspondence should be addressed. E-mail: oveh@uq.edu.au
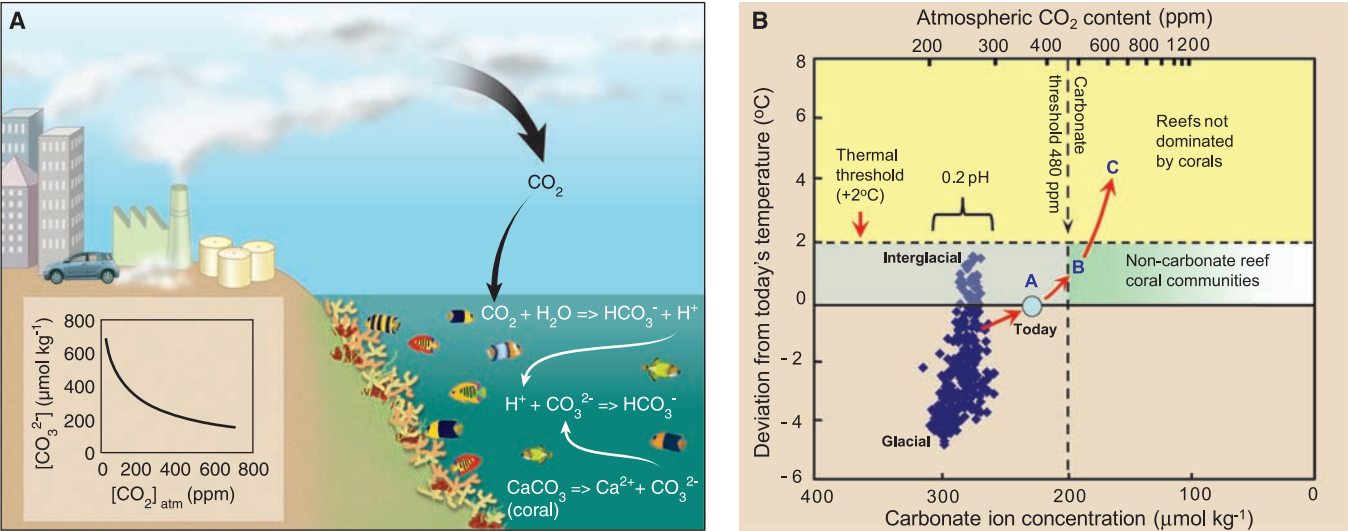
Fig. 1. (**A**) Linkages between the buildup of atmospheric CO_2 and the slowing of coral calcification due to ocean acidification. Approximately 25% of the CO_2 emitted by humans in the period 2000 to 2006 (9) was taken up by the ocean where it combined with water to produce carbonic acid, which releases a proton that combines with a carbonate ion. This decreases the concentration of carbonate, making it unavailable to marine calcifiers such as corals. (**B**) Temperature, $[CO_2]_{atm}$, and carbonate-ion concentrations reconstructed for the past 420,000 years. Carbonate concentrations were calculated (54) from CO_2 atm and temperature deviations from today's conditions with the Vostok Ice Core data set (5), assuming constant salinity (34 parts per trillion), mean sea temperature (25°C), and total alkalinity (2300 mmol kg^{-1}). Further details of these calculations are in the SOM. Acidity of the ocean varies by ± 0.1 pH units over the past 420,000 years (individual values not shown). The thresholds for major changes to coral communities are indicated for thermal stress (+2°C) and carbonate-ion concentrations ([carbonate] = 200 μmol kg^{-1}, approximate aragonite saturation $\sim\Omega_{aragonite}$ = 3.3; $[CO_2]_{atm}$ = 480 ppm). Coral Reef Scenarios CRS-A, CRS-B, and CRS-C are indicated as A, B, and C, respectively, with analogs from extant reefs depicted in Fig. 5. Red arrows pointing progressively toward the right-hand top square indicate the pathway that is being followed toward $[CO_2]_{atm}$ of more than 500 ppm.

exceeds 3.3 (10). Geological studies report a notable gap in the fossil record of calcified organisms, including reef-building corals (14) and calcareous algae (15), during the early Triassic when $[CO_2]_{atm}$ increased dramatically and reached levels at least five times as high as today's (16). Phylogenetic studies suggest that corals as a group survived the Permian-Triassic extinction event (14) but may have done so through forms lacking calcified skeletons (17, 18). Although Scleractinian (modern) corals arose in the mid-Triassic and lived under much higher $[CO_2]_{atm}$, there is no evidence that they lived in waters with low-carbonate mineral saturation. Knoll et al. succinctly state that "it is the rapid, unbuffered increase in $[CO_2]_{atm}$ and not its absolute values that causes important associated changes such as reduced $[CO_3^{2-}]$, pH, and carbonate saturation of sea water" (19). The rate of $[CO_2]_{atm}$ change is critical given that modern genotypes and phenotypes of corals do not appear to have the capacity to adapt fast enough to sudden environmental change.

Reef-building corals may exhibit several responses to reduced calcification, all of which have deleterious consequences for reef ecosystems. First, the most direct response is a decreased linear extension rate and skeletal density of coral colonies. The massive coral *Porites* on the Great Barrier Reef has shown reductions in linear extension rate of 1.02% $year^{-1}$ and in skeletal density of 0.36% $year^{-1}$ during the past 16 years (20). This is equivalent to a reduction of 1.29% $year^{-1}$ or a 20.6% drop in growth rate (the product of linear extension rate and skeletal density) over the 16-year period. While at present it is not possible to confidently attribute the observed decrease in growth and calcification to ocean acidification, it is consistent with changes reported in oceanic pH and carbonate-ion concentrations.

Second, corals may maintain their physical extension or growth rate by reducing skeletal density. However, erosion could be promoted by the activities of grazing animals such as parrotfish, which prefer to remove carbonates from lower-density substrates. Increasingly brittle coral skeletons are also at greater risk of storm damage (21); thus, if rates of erosion outstrip calcification, then the structural complexity of coral reefs will diminish, reducing habitat quality and diversity. A loss of structural complexity will also affect the ability of reefs to absorb wave energy and thereby impairs coastal protection.

Third, corals may maintain both skeletal growth and density under reduced carbonate saturation by investing greater energy in calcification. A likely side effect of this strategy is the diversion of resources from other essential processes, such as reproduction, as seen in chronic stress (21), which could ultimately reduce the larval output from reefs and impair the potential for recolonization following disturbances.

Resilience and Tipping Points

Maintaining ecological resilience is the central plank of any strategy aiming to preserve coral reef

Table 1. Rates of change in atmospheric CO_2 concentration ($[CO_2]_{atm}$, ppm/100 years) and global temperature (°C/100 years) calculated for the past 420,000 yr B.P. using the Vostok Ice Core data (5) and compared to changes over the last century and those projected by IPCC for low-emission (B1) and high-emission (A2) scenarios (8). Rates were calculated for each successive pair of points in the Vostok Ice Core record by dividing the difference between two sequential values (ppm or °C) by the time interval between them. Rates were then standardized to the change seen over 100 years. Ratios of each rate relative to the mean rate seen over the past 420,000 years are also calculated.

Period	$[CO_2]_{atm}$ (ppm $century^{-1}$)	Ratio (relative to past 420,000 years)	Temperature (°C $century^{-1}$)	Ratio (relative to past 420,000 years)
Past 420,000 years (99% confidence interval; n = 282)	0.07 + 0.223	1	0.01 + 0.017	1
Past 136 years (1870–2006)	73.53	1050	0.7	70
IPCC B1 scenario: 550 ppm at 2100	170	2429	1.8	180
IPCC A2 scenario: 800 ppm at 2100	420	6000	3.4	420

ecosystems. Ecological resilience (*4*) is a measure of the rate at which an ecosystem returns to a particular state (e.g., coral-dominated communities) after a perturbation or disturbance (e.g., hurricane impacts). Recent changes to the frequency and scale of disturbances such as mass coral bleaching, disease outbreaks, and destructive fishing, coupled with a decreased ability of corals to grow and compete, are pushing reef ecosystems from coral- to algal-dominated states (*4*, *22*). If pushed far enough, the ecosystem may exceed a "tipping point" (*22*) and change rapidly into an alternative state with its own inherent resilience and stability, often making the possibility of returning to a coral-dominated state difficult.

To examine the ecological implications of the 20.6% reduction in coral growth rate that Cooper *et al.* measured in Great Barrier Reef *Porites* (*20*), we simulated a similar reduction in the growth of massive brooding and spawning corals on exposed Caribbean forereefs specifically to investigate what happens to the balance between corals and macroalgae in a system of high primary production (Fig. 2). The ecological model (*22*) simulated a 50-year time series for a wide range of initial coral cover and grazing rates by fish on benthic algae while holding all other factors (e.g., nutrient concentrations) constant. Each time series revealed the underlying trajectory of coral recovery, stasis, or degradation between major disturbances, and the final equilib-
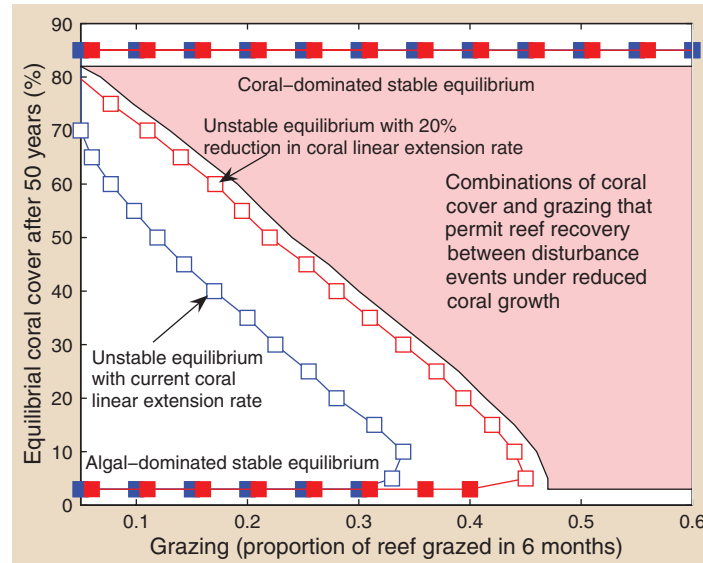

Fig. 2. Reduction in the resilience of Caribbean forereefs as coral growth rate declines by 20%. Reef recovery is only feasible above or to the right of the unstable equilibria (open squares). The "zone of reef recovery" (pink) is therefore more restricted under reduced coral growth rate and reefs require higher levels of grazing to exhibit recovery trajectories.

rium values of coral cover were plotted to illustrate potential resilience (Fig. 2). The unstable equilibria represent thresholds, and for recovery to outweigh mortality reefs must lie either above or to the right of the threshold. For example, if coral cover is low (<5%), the intensity of fish grazing on benthic algal competitors needed to shift the reef into a state where recovery is possible (i.e., to the right or above the unstable equilibrium) moves from 30% to almost a half of the reef having to be grazed. This implies that in the absence of invertebrate

grazers like the sea urchin, *Diadema antillarum*, which essentially disappeared from Caribbean reefs in the early 1980s after a massive disease outbreak, highly productive reefs would likely require the highest levels of parrotfish grazing (i.e., ~ 40% of the reef being grazed) for a reef to be able to recover from disturbance. The loss of ecological resilience occurs because coral cover increases more slowly after disturbance and competitive interactions with macroalgae become more frequent and longer in duration (Fig. 3) (*23*) (table S1). Although the ecological model only represents a single Caribbean reef habitat in a very productive physical environment and has not incorporated several other putative consequences of acidification such as a loss of rugosity, sensitivity analyses reveal that changes to coral growth rate have a relatively large impact on model predictions (*22*), and therefore the conclusions of a reduction in resilience appear to be robust.

Thermal Stress, Synergies, and Ecological Feedback Loops

The sensitivity of corals and their endosymbiotic dinoflagellates (*Symbiodinium* spp.) to rising ocean temperatures has been documented extensively (*24*). *Symbiodinium* trap solar energy and nutrients, providing more than 95% of the metabolic requirements of the coral host, which
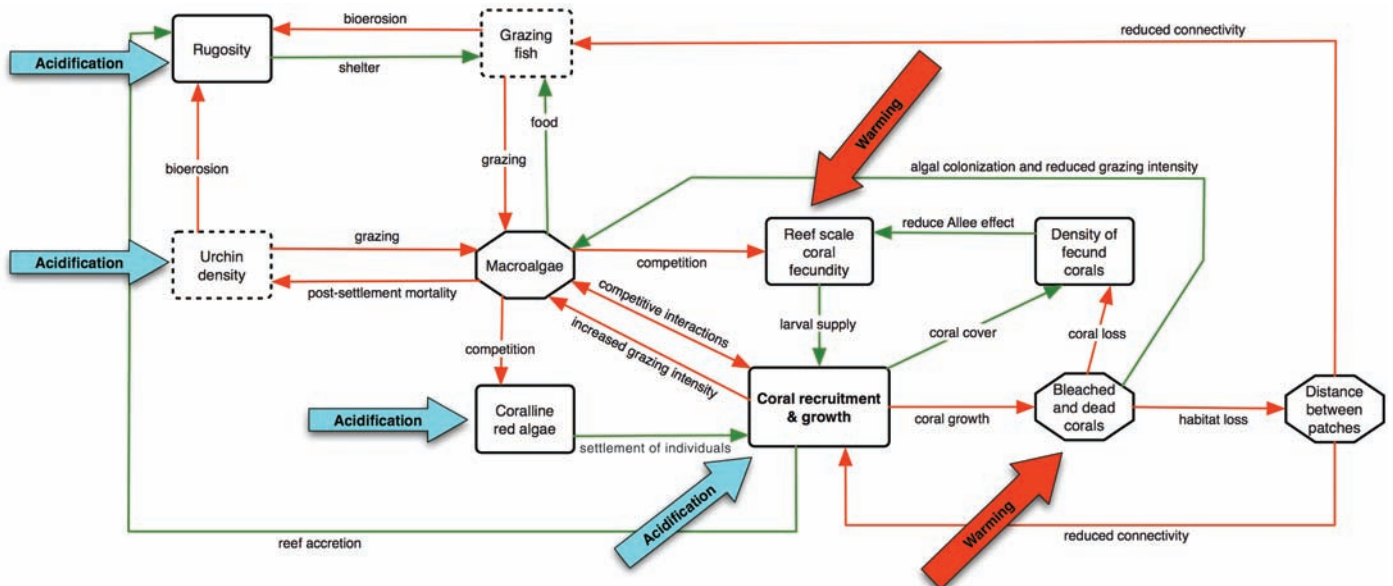

Fig. 3. Ecological feedback processes on a coral reef showing pathways of disturbance caused by climate change. Impact points associated with ocean acidification (e.g., reduced reef rugosity, coralline algae) are indicated by the blue arrows, and impact points from global warming (e.g., bleached and dead corals) by the red arrows. Boxes joined by red arrows denote that the first factor has a negative (decreasing) influence on the box indicated. Green arrows denote positive (increasing) relationships. Over time, the levels of factors in hexagonal boxes will increase, whereas those in rectangular boxes will decline. Boxes with dashed lines are amenable to local management intervention.

is consequently able to maintain high calcification rates. When temperatures exceed summer maxima by 1° to 2°C for 3 to 4 weeks, this obligatory endosymbiosis disintegrates with ejection of the symbionts and coral bleaching (24). Bleaching and mortality become progressively worse as thermal anomalies intensify and lengthen (24). Indeed, mass coral bleaching has increased in intensity and frequency in recent decades (24–27). At the end of the International Year of the Reef in 1997, mass bleaching spread from the Eastern Pacific to most coral reefs worldwide, accompanied by increasing coral mortality during the following 12 months (24). Corals may survive and recover their dinoflagellate symbionts after mild thermal stress, but typically show reduced growth, calcification, and fecundity (24) and may experience greater incidences of coral disease (28, 29).

To illustrate the combined effects of acidification and bleaching on reefs, we simplified the coral ecosystem into the nine features required to model feedback mechanisms (Fig. 3). Although it is not comprehensive, the model provides a theoretical framework indicating that acidification and bleaching enhance all deleterious feedbacks, driving the coral ecosystems toward domination by macroalgae and noncoral communities (Fig. 3) (table S1).

Trajectories in Response to Climate Change

Global temperatures are projected to increase rapidly to 1.8°C above today's average temperature under the low-emission B1 scenario of the IPCC, or by 4.0°C (2.4° to 6.4°C) under the higher-emission A1F1 scenario (Table 1) (8). Increases in the temperature of tropical and subtropical waters over the past 50 years (24) have already pushed reef-building corals close to their thermal limits. Projections for ocean acidification include reductions in oceanic pH by as much as 0.4 pH units by the end of this century, with ocean carbonate saturation levels potentially dropping below those required to sustain coral reef accretion by 2050 (Fig. 4) (7, 10, 13). Changes in ocean acidity will vary from region to region, with some regions, such as the Great Barrier Reef and Coral Sea, and the Caribbean Sea, attaining risky levels of aragonite saturation more rapidly than others (Fig. 4). Just as carbonate coral reefs do not exist in waters with carbonate-ion concentrations < 200 μmol kg^{-1} (10), they are likely to contract rapidly if future [CO_2]$_{atm}$ levels exceed 500 ppm. Similarly, unless thermal thresholds change, coral reefs will experience an increasing frequency and severity of mass coral bleaching, disease, and mortality as [CO_2]$_{atm}$ and temperatures increase (24–27).

We have projected three scenarios for coral reefs over the coming decades and century. In doing so, we recognize that important local threats to coral reefs, such as deterioration of water quality arising from sediment and nutrient inputs associated with coastal development and deforestation, and the overexploitation of marine fishery stocks, may produce synergies and feedbacks in concert with climate change (30) (Fig. 3) [supporting on-line material (SOM)]. How quickly we arrive at or

how long we stay within each of the three scenarios will depend on the CO_2 emission rate, with each scenario highlighting the context against which management and policy actions must be devised.

If conditions were stabilized at the present [CO_2]$_{atm}$ of 380 ppm, that is, Coral Reef Scenario CRS-A (Figs. 1B and 5A), coral reefs will continue to change but will remain coral dominated and carbonate accreting in most areas of their current distribution. Local factors—i.e., those not directly related to global climate change, such as changes to water quality—affecting levels of sediment, nutrients, toxins, and pathogens, as well as fishing pressure, will be important determinants of reef state and should demand priority attention in reef-management programs. However, as we move toward higher [CO_2]$_{atm}$, coral-community compositions will change with some areas becoming dominated by more thermally tolerant corals like the massive *Porites* (31) and others potentially dominated by thermally sensitive but rapidly colonizing genera, such as the tabulate *Acropora*. Under the current rate of increase in [CO_2]$_{atm}$ (>1 ppm year^{-1}), carbonate-ion concentrations will drop below 200 μmol kg^{-1} and reef erosion will exceed calcification at [CO_2]$_{atm}$ = 450 to 500 ppm, i.e., Scenario CRS-B (Figs. 1 and 5B). The density and

diversity of corals on reefs are likely to decline, leading to vastly reduced habitat complexity and loss of biodiversity (31), including losses of coral-associated fish and invertebrates (32).

Coralline algae are a key settlement substrate for corals, but they have metabolically expensive high-magnesium calcite skeletons that are very sensitive to pH (33). Hence, coral recruitment may be compromised if coralline algal abundance declines. Coral loss may also be compounded by an increase in disease incidence (34). Ultimately, the loss of corals liberates space for the settlement of macroalgae, which in turn tends to inhibit coral recruitment, fecundity, and growth because they compete for space and light, and also produce anti-fouling compounds that deter settlement by potential competitors. Together these factors allow macroalgae to form stable communities that are relatively resistant to a return to coral domination (Figs. 2 and 3) (22, 23, 35). As a result of weakening of coral growth and competitive ability, reefs within the CRS-B scenario will be more sensitive to the damaging influence of other local factors, such as declining water quality and the removal of key herbivore fish species.

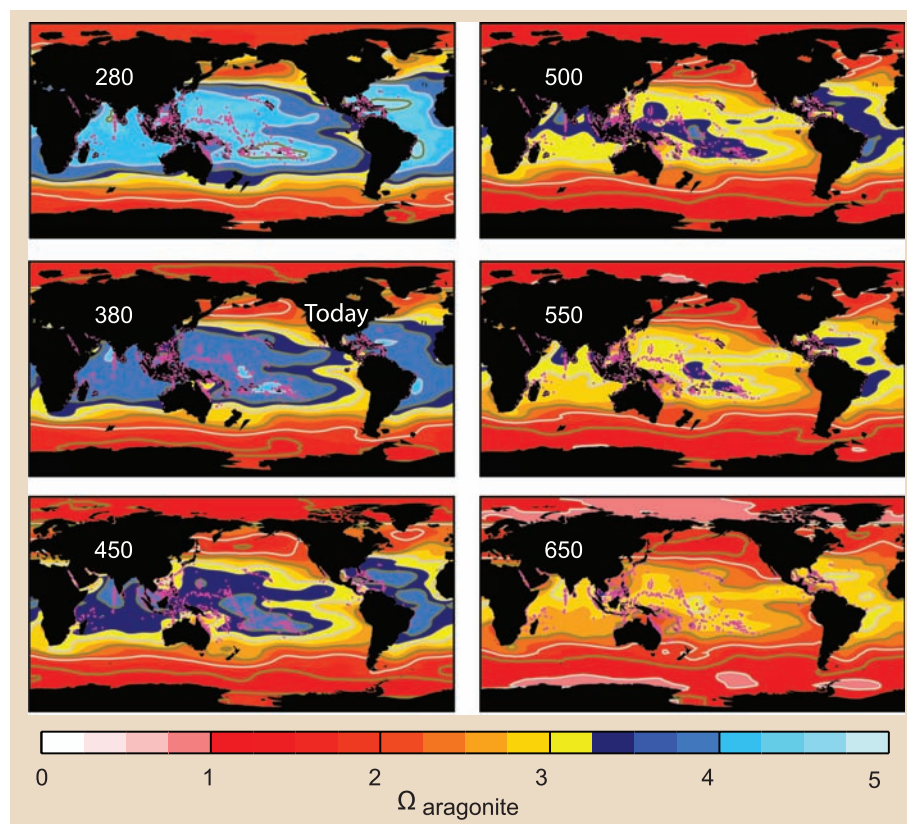Increases in [CO_2]$_{atm}$ > 500 ppm (11) will push carbonate-ion concentrations well below

Fig. 4. Changes in aragonite saturation {$\Omega_{aragonite}$ = ([Ca^{2+}].[CO_3^{2-}])/$K_{sp\ aragonite}$} predicted to occur as atmospheric CO_2 concentrations (ppm) increase (number at top left of each panel) plotted over shallow-water coral reef locations shown as pink dots (for details of calculations, see the SOM). Before the Industrial Revolution (280 ppm), nearly all shallow-water coral reefs had $\Omega_{aragonite}$ > 3.25 (blue regions in the figure), which is the minimum $\Omega_{aragonite}$ that coral reefs are associated with today; the number of existing coral reefs with this minimum aragonite saturation decreases rapidly as [CO_2]$_{atm}$ increases. Noticeably, some regions (such as the Great Barrier Reef) attain low and risky levels of $\Omega_{aragonite}$ much more rapidly than others (e.g., Central Pacific).
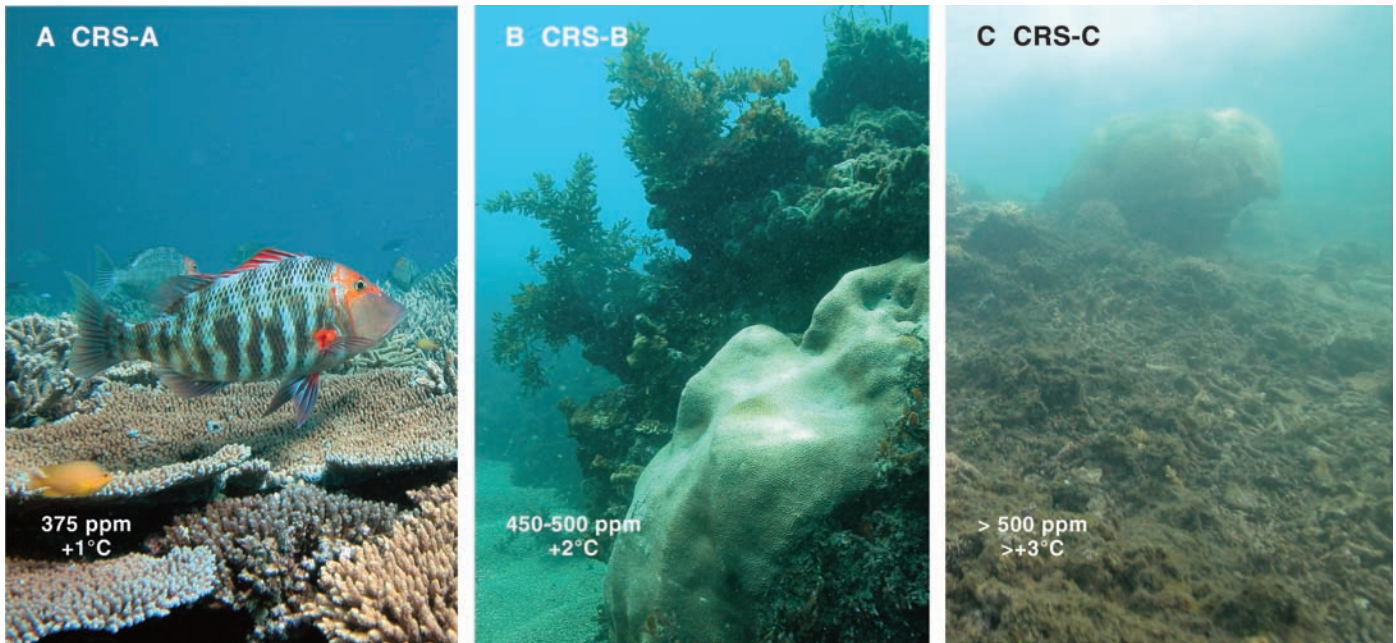
Fig. 5. Extant examples of reefs from the Great Barrier Reef that are used as analogs for the ecological structures we anticipate for Coral Reef Scenarios CRS-A, CRS-B, and CRS-C (see text). The $[CO_2]_{atm}$ and temperature increases shown are those for the scenarios and do not refer to the locations photographed. (**A**) Reef slope communities at Heron Island. (**B**) Mixed algal and coral communities associated with inshore reefs around St. Bees Island near Mackay. (**C**) Inshore reef slope around the Low Isles near Port Douglas. [Photos by O. Hoegh-Guldberg]

200 µmol kg^{-1} (aragonite saturation < 3.3) and sea temperatures above +2°C relative to today's values (Scenario CRS-C, Fig. 1). These changes will reduce coral reef ecosystems to crumbling frameworks with few calcareous corals (Fig. 5C). The continuously changing climate, which may not stabilize for hundreds of years, is also likely to impede migration and successful proliferation of alleles from tolerant populations owing to continuously shifting adaptive pressure. Under these conditions, reefs will become rapidly eroding rubble banks such as those seen in some inshore regions of the Great Barrier Reef, where dense populations of corals have vanished over the past 50 to 100 years. Rapid changes in sea level (+23 to 51 cm by 2100, scenario A2) (8), coupled with slow or nonexistent reef growth, may also lead to "drowned" reefs (36) in which corals and the reefs they build fail to keep up with rising sea levels.

The types of synergistic impacts on coral and reef-dependent organisms defined for Scenario CRS-B (Fig. 5B) will be magnified substantially for CRS-C (Fig. 5C), with probably half, and possibly more, of coral-associated fauna becoming rare or extinct given their dependence on living corals and reef rugosity (37). Macroalgae may dominate in some areas and phytoplankton blooms may become more frequent in others, as water quality declines owing to the collateral impact of climate change on associated coastal areas, drying catchments and causing episodic heavy rainfall that transports nutrients and sediments into coastal areas. Whether or not one defines the transition from CRS-B to CRS-C and $[CO_2]_{atm}$ of 450 to 500 ppm as the tipping point for coral reefs, it is clear that

coral reefs as we know them today would be extremely rare at higher $[CO_2]_{atm}$.

We recognize that physiological acclimation or evolutionary mechanisms could delay the arrival of some scenarios. However, evidence that corals and their symbionts can adapt rapidly to coral bleaching is equivocal or nonexistent. Reef-building corals have relatively long generation times and low genetic diversity, making for slow rates of adaptation. Changes in species composition are also possible but will have limited impact, as even the most thermally tolerant corals will only sustain temperature increases of 2° to 3°C above their long-term solar maxima for short periods (24, 31). However, such changes come at a loss of biodiversity and the removal of important redundancies from these complex ecosystems. Some studies have shown that corals may promote one variety of dinoflagellate symbiont over another in the relatively small number of symbioses that have significant proportions of multiple dinoflagellate types (38). These phenotypic changes extend the plasticity of a symbiosis (e.g., by 1° to 2°C) (21) but are unlikely to lead to novel, long-lived associations that would result in higher thermal tolerances (39). The potential for acclimation even to current levels of ocean acidification is also low given that, in the many studies done to date, coral calcification has consistently been shown to decrease with decreasing pH and does not recover as long as conditions of higher acidity persist (13).

Socioeconomic Impacts of Coral Reef Decline

The scenarios presented here are likely to have serious consequences for subsistence-dependent societies, as well as on wider regional economies

through their impact on coastal protection, fisheries, and tourism. These consequences become successively worse as $[CO_2]_{atm}$ increases, and unmanageable for $[CO_2]_{atm}$ above 500 ppm. Although reefs with large communities of coral reef-related organisms persist under CRS-A and CRS-B, they become nonfunctional under CRS-C, as will the reef services that currently underpin human welfare. Climate change is likely to fundamentally alter the attractiveness of coral reefs to tourists (compare Fig. 5, A and C), which is an important consideration for the many low-income coastal countries and developing small island states lying within coral reef regions. Under-resourced and developing countries have the lowest capacity to respond to climate change, but many have tourism as their sole income earner and thus are at risk economically if their coral reefs deteriorate (40). For instance, tourism is a major foreign exchange earner in the Caribbean basin and in some countries accounts for up to half of the gross domestic product (40). Coral reefs in the United States and Australia may supply smaller components of the total economy, but still generate considerable income (many billions of U.S. $ per year) from reef visitors that are increasingly responsive to the quality of reefs (41).

Reef rugosity is an important element for the productivity of all reef-based fisheries, whether subsistence, industrial, or to supply the aquarium trade. The density of reef fish (32) is likely to decrease as a result of increasing postsettlement mortality arising from a lack of hiding places and appropriate food for newly settled juveniles (42). Regardless of future climate-change influences, the total landing of coral reef fisheries is already 64% higher than

can be sustained, with an extra 156,000 km^2 of coral reef estimated as being needed to support anticipated population growth by 2050 (*43*). For example, in Asia alone coral reefs provide about one-quarter of the annual total fish catch and food to about 1 billion people (*43*). Climate-change impacts on available habitat will only exacerbate already overstretched fisheries resources.

The role of reefs in coastal protection against storms (*44*) has been highlighted in analyses of exposed and reef-protected coastlines (*45, 46*). We do not yet have estimates for how fast reef barriers will disappear (*47*), but we can anticipate that decreasing rates of reef accretion, increasing rates of bioerosion, rising sea levels, and intensifying storms may combine to jeopardize a wide range of coastal barriers. People, infrastructure, and lagoon and estuarine ecosystems, including mangroves, seagrass meadows, and salt marshes, will become increasingly vulnerable to growing wave and storm impacts. Observations of increasingly intense tropical hurricanes and cyclones in all oceans (*48*) suggest that losses of beach sand from coastal zones are likely to increase (*49*). Further losses may occur from reduced sand production, formed in many cases by coral reefs, as a consequence of ocean acidification and thermal stress on calcareous algae and other sand producers. Beaches are also under threat of erosion from rising sea levels. The combination of these factors will lead to less stable beaches and impacts on other organisms, such as turtles and sea birds that depend on beach habitats for reproduction, as well as leading to economic impacts on tourism and coastal fishing communities.

Opportunities for Management Intervention

The inherent inertia of the atmosphere and of our attempts to mitigate CO_2 emissions suggest that reef managers and coastal resource policies must first reduce the influence of local stressors such as declining water quality, coastal pollution, and overexploitation of key functional groups such as herbivores (*4*). These types of action are most likely to assist coral reefs through the decades of stress that inevitably face them. There may be opportunities for using coral restoration to reduce the risk that reefs will shift into a non–coral-dominated state (Fig. 3); however, the efficacy of coral restoration methods to increase rugosity and coral cover remains unclear, and further evaluation of methods is badly needed. With respect to the latter, there is a mismatch between the feasible scale of restoration (hectares) and that of the extent of degradation (many thousands of km^2). Nevertheless, new techniques for the mass culture of corals from fragments and spat may assist local restoration or the culture of resistant varieties of key organisms (*44*).

At the 100- to 1000-km scale of coral reefs, one of the most practical interventions is to facilitate grazing by fish and invertebrate herbivores. This is likely to play an important role in situations like that of the Caribbean where densities of one important herbivore, the sea urchin *Diadema antillarum*, were decimated by disease in the early 1980s (*50*). Clearly, the improved management of

reef fish, especially grazers such as parrotfish, would be expected to result in an improved ability of coral reefs to bounce back from disturbances (*51*), as long as other factors such as water quality are not limiting. Unfortunately, with the exception of marine reserves, there is negligible explicit management of herbivores in most countries, but this could be improved by setting catch limits (*52*). Diversification of the herbivore guild to include modest densities of invertebrates like sea urchins will also enhance the resilience of coral reef ecosystems.

Conclusion

It is sobering to think that we have used the lower range of IPCC scenarios in our analysis yet still envisage serious if not devastating ramifications for coral reefs. Emission pathways that include higher [CO_2]$_{atm}$ (600 to 1000 ppm) and global temperatures of 3° to 6°C defy consideration as credible alternatives. Equally important is the fact that IPCC scenarios are likely to be cautious given scientific reticence and the inherently conservative nature of consensus seeking within the IPCC process (*53*). Consequently, contemplating policies that result in [CO_2]$_{atm}$ above 500 ppm appears extremely risky for coral reefs and the tens of millions of people who depend on them directly, even under the most optimistic circumstances.

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Supporting Online Material for

Coral Reefs Under Rapid Climate Change and Ocean Acidification

O. Hoegh-Guldberg,[*] P. J.Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez,
C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin,
R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, M. E. Hatziolos

*To whom correspondence should be addressed. E-mail: oveh@uq.edu.au

This PDF file includes:

SOM Text
Table S1
References

Supporting Online Material

1. Calculations associated with Fig. 1B.

Temperature and carbonate-ion concentrations were reconstructed for the past 420,000 years using the Vostok Ice Core data (*5*). Carbonate concentrations were calculated (*S1*) using $CO_{2\ atm}$ and temperature deviations from today's conditions using the Vostok Ice Core data set and assuming constant salinity (34 ppt), mean sea temperature ($25^{o}C$) and total alkalinity (2300 mmol kg-1). Values of ocean acidity Calculated for the 420,000 yr period varied $\pm$ 0.1 pH unit. Present day values (and those of 100 years ago) are also shown, but were derived from other sources (*8*) given that the Vostok Ice Core data ends 2300 y BP. Surface ocean carbonate ion concentrations during glacial times may have been slightly greater (by 20-25 μmol kg^{-1}) than indicated here owing to an elevation of alkalinity during glacial periods linked to glacial ice formation and the dissolution of carbonate minerals that compensated for increased storage of carbon in the deep sea (*S2*). Furthermore, there is uncertainty with regard to the relationship between Antarctic and tropical paleo-temperatures. Here, we assume that paleo-temperature changes estimated for the Antarctic (8) exceed tropical temperature changes by a factor of 2 (*S3*). Assuming less polar amplification would yield higher estimates for glacial carbonate-ion concentrations; however, even without any assumed polar amplification of temperature changes, estimated glacial carbon-ion concentrations are greater than modern carbonate-ion concentrations.

2. Calculations associated with Figure 4.

To calculate ocean chemistry changes, we prescribed IPCC SRES A2 emissions (*S4*) in the University of Victoria (UVic) Earth System Climate Model version 2.8 (*S5*). Ocean chemistry is computed as per the protocol of Ocean Carbon Model Intercomparison Project (http://www.ipsl.jussieu.fr/OCMIP). We add deviations from year 1994 as predicted by the model to ocean chemistry as observed for year 1994 (*S6*). Reef locations are from ReefBase (*S7*).

3. Table S1. Feedback Mechanisms Causing Threshold (Catastrophe) Dynamics

Reef ecosystems are particularly susceptible to the emergence of alternative stable states of the ecosystem (*S8-11*). Stable states are reinforced by ecological feedbacks that 'attract' or drive a reef towards to a particular state and then maintain the ecosystem within a specific state. The following table lists some of the feedback mechanisms that are suspected to occur on coral reefs and highlights how they are exacerbated by climate change. Text highlighted in bold relates to labels on the feedbacks figure (**Fig. 4**) in the main text.

Feedback mechanism	Exacerbated by climate change
Competitive interactions between macroalgae and corals: Macroalgae pre-empt settlement space (*S11*) and therefore inhibit coral recruitment thereby constraining coral cover and facilitating further algal colonization (*S12*)	Frequent **mass coral mortality** events (bleaching, disease, hurricanes) facilitate algal colonization because grazing intensity decreases (*S13*). Note, the reverse process also occurs; coral growth and recruitment

	reduce the area available to grazers which intensifies grazing and can reduce macroalgae.
Competitive interactions between macroalgae and corals: algal competition causes increased post-settlement mortality in coral due to reduced light, flow or growth rate (*S14, 15*)	Frequent **mass coral mortality** events (bleaching, disease, hurricanes) facilitate algal colonization.
Competitive interactions between macroalgae and corals: Macroalgae overgrow adult corals causing direct reductions in **coral fecundity** because of absent coral (*S6-18*) and indirect chronic reductions in fecundity because of competition (*S18, 19*). Reduced fecundity reduces demographic rates of colonization in corals, reinforcing shift towards algae. Note that rate of algal-coral overgrowth is poorly understood and varies dramatically among the taxa involved (*S20*)	Frequent mass coral mortality events (bleaching, disease, hurricanes) reduce larval output of reefs further. **Calcification rates** of corals are slowed by increased ocean acidification. Results in greater competitive effectiveness of macroalgae relative to corals. Thermal stress also reduces **fecundity** in corals (*S20*) which may ultimately reduce **larval supply** and coral recruitment (*S21*).
Competitive interactions between macroalgae and corals: Macroalgae may act as vectors of organisms that cause coral disease (*S22*), thereby promoting losses of corals	Coral mortality events promote **algal colonization** and rising temperature may enhance efficacy of disease organisms (*S23*).
Competitive interactions between macroalgae and corals: Macroalgae exude polysaccharides that may stimulate bacterial growth near corals causing local hypoxia and coral mortality (*S24*). Note, mechanism not demonstrated in situ and probably highly dependent on flow regime	Coral mortality events promote **algal colonization**
Reductions in coral colonization and survival (**coral loss**) lead to a reduction in **reef accretion** and therefore a reduction in reef **rugosity** (structural complexity). This in turn reduces the carrying capacity of reefs for herbivores which require high rugosity to provide **shelter from predators** and sustain high densities (*S25, S26*). A reduction in herbivory continues to enhance the colonization of algae (*S18, S27*)	Rate of rugosity loss may be exacerbated by acidification which leads to elevated rates of **bioerosion** and physical erosion because coral **skeletons become weaker** (less densely calcified). Bleaching damage and slower rates of coral recovery will cause **habitat loss** and increase the average **distance among patches of high quality habitat**. This may in turn **reduce the population connectivity** of reef organisms and reduce recruitment (*S28*).
Certain species of coralline red algae act as **inducers to coral settlement** (*29*). Reductions in the cover of encrusting coralline red algae caused by increases in the cover of carpeting macroalgae that trap sediments reduces the availability of settlement substratum for corals, thereby	Acidification increases energetic cost of calcification in coralline algae reducing their growth rate and increasing susceptibility to disease. Increase in macroalgal **competitors** after coral mortality events exacerbates process further by making the benthos

facilitating proliferation of algae (*S30*)	increasingly hostile to encrusting corallines
Failure of recovery of the urchin, *Diadema antillarum*, in much of the Caribbean may be driven by feedbacks. Hostile, macroalgal-dominated reefs possess high densities of microinvertebrates that prey upon settling urchin spat causing a bottleneck in urchin colonization because of high **post-settlement mortality** (i.e. macroalgae are a **predator refuge** for juvenile urchins). In contrast, macroalgae are scarce at high densities of adult urchins (*S31*). Thus, urchins can maintain high-quality habitat for urchin survival but only once grazing levels are high. Modest urchin recovery would enhance the health of many Caribbean reefs (*S32*).	Acidification may further reduce urchin survival by reducing test strength and / or enhancing vulnerability to disease because of increased **energetic requirements of calcification**. Reductions in rugosity, which are exacerbated by climate change (above), increase the post-settlement mortality of urchins and increases in macroalgae after bleaching-induced coral mortality also add to density of urchin predators.
Recruitment of corals declines because of **Allee effects** which reduce **fertilization success** and reduce levels of larval supply (*S33*). The problem is then exacerbated because Allee effects may become more severe as **coral density declines** because of reduced recruitment (and other factors – see main text)	Frequent mass coral mortality events reduce the density of adult corals and enhance the severity of Allee effects further. **Chronic stress** caused by bleaching also causes **reduced fecundity** in corals (*S20*)

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