Coral Reefs Under Rapid Climate Change and Ocean Acidification


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 faced 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 (3, 6), if not 20 million years (7). During the 20th century, increasing \([\text{CO}_2]_{\text{atm}}\) 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 anthropogenic climate change dwarf even those of the ice age transitions, which are supported by the observation that reefs occur, carbonate-ion concentrations over 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 \([\text{CO}_2]_{\text{atm}}\) 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 (\([\text{CO}_2]_{\text{atm}}\sim 380\) 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 \([\text{CO}_2]_{\text{atm}}\) 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 \([\text{CO}_2]_{\text{atm}}\) (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 \([\text{CO}_2]_{\text{atm}}\) 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 \([\text{CO}_2]_{\text{atm}}\) 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
Fig. 1. (A) Linkages between the buildup of atmospheric CO₂ and the slowing of coral calcification due to ocean acidification. Approximately 25% of the CO₂ 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, [CO₂] atm, and carbonate-ion concentrations reconstructed for the past 420,000 years. Carbonate concentrations were calculated (54) from CO₂ 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 ~ω_{aragonite} = 3.3; [CO₂] 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 [CO₂] atm of more than 500 ppm.

Table 1. Rates of change in atmospheric CO₂ concentration ([CO₂] 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.

<table>
<thead>
<tr>
<th>Period</th>
<th>[CO₂] atm (ppm century⁻¹)</th>
<th>Ratio (relative to past 420,000 years)</th>
<th>Temperature (°C century⁻¹)</th>
<th>Ratio (relative to past 420,000 years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Past 420,000 years (99% confidence interval; n = 282)</td>
<td>0.07 ± 0.223</td>
<td>1</td>
<td>0.01 ± 0.017</td>
<td>1</td>
</tr>
<tr>
<td>Past 136 years (1870–2006)</td>
<td>73.53</td>
<td>1050</td>
<td>0.7</td>
<td>70</td>
</tr>
<tr>
<td>IPCC B1 scenario: 550 ppm at 2100</td>
<td>170</td>
<td>2429</td>
<td>1.8</td>
<td>180</td>
</tr>
<tr>
<td>IPCC A2 scenario: 800 ppm at 2100</td>
<td>420</td>
<td>6000</td>
<td>3.4</td>
<td>420</td>
</tr>
</tbody>
</table>

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
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 fore reefs 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 equilibrium 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.

**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.

**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 framework indicating that acidification and bleaching on reefs, we simplified the coral ecosystem 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°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 in the current rate of increase in [CO₂]atm (>1 ppm year−1), carbonate-ion concentrations will drop below 200 μmol kg−1 and reef erosion will exceed calcification at [CO₂]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).

Fig. 4. Changes in aragonite saturation \(\Omega_{\text{aragonite}} = ([Ca^{2+}]\times[CO_3^{2-}]) / K_{sp\text{aragonite}}\) predicted to occur as atmospheric CO₂ 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 \(\Omega_{\text{aragonite}} > 3.25\) (blue regions in the figure), which is the minimum \(\Omega_{\text{aragonite}}\) that coral reefs are associated with today; the number of existing coral reefs with this minimum aragonite saturation decreases rapidly as [CO₂]atm increases. Noticeably, some regions (such as the Great Barrier Reef) attain low and risky levels of \(\Omega_{\text{aragonite}}\) much more rapidly than others (e.g., Central Pacific).
Whether or not one defines the transition from transports nutrients and sediments into coastal areas. Whether or not one defines the transition from transports nutrients and sediments into coastal areas.

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 \([\text{CO}_2]_{\text{atm}}\) increases, and unmanageable for \([\text{CO}_2]_{\text{atm}}\) 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 coastal countries and developing small island states 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).

Socioeconomic Impacts of Coral Reef Decline

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 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]
can be sustained, with an extra 156,000 km² 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°C 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.

**References and Notes**

26. T. J. Done et al., "Global Climate Change and Coral Bleaching on the Great Barrier Reef, Final report to the State of Queensland Greenhouse Taskforce through the Department of Natural Resources and Mining, Townsville” (2002).
43. UNEP, “Marine and coastal ecosystems and human well-being: A synthesis report based on the findings of the Millennium Ecosystem Assessment” (United Nations Environmental Programme, 2006).
44. UNEP-WCMC, “In the front line: Shoreline protection and other ecosystem services provided by mangroves and coral reefs (United Nations Environmental Programme–World Conservation Monitoring Centre, Cambridge, UK, 2006).
55. This project was supported by the Global Environment Facility, the World Bank, and the University of Queensland through the Coral Reef Targeted Research Program (www.gefcoral.org). We also thank J. Dixon, S. Dove, and D. W. Gledhill for discussions concerning this manuscript. N. Cenacchi for assistance in rendering Fig. 4, and L. Cao for helping with the analysis and preparation of Fig. 3. The manuscript contents are solely the opinions of the authors and do not constitute a statement of policy, decision, or position on behalf of NOAA or the U.S. Government. This paper is dedicated to the memory of Kim Mitchell, who saw the value of and worked hard for the future of the world’s natural ecosystems.

**Supporting Online Material**

www.sciencemag.org/cgi/content/full/318/5857/1737/DC1

SOM Text Table S1 References 10.1126/science.1152509
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*To whom correspondence should be addressed. E-mail: oveh@uq.edu.au

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This PDF file includes:

SOM Text
Table S1
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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 (SI) using CO₂ 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°C) and total alkalinity (2300 mmol kg⁻¹). Values of ocean acidity calculated for the 420,000 yr period varied ± 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 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.

<table>
<thead>
<tr>
<th>Feedback mechanism</th>
<th>Exacerbated by climate change</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Competitive interactions between macroalgae and corals</strong>: Macroalgae pre-empt settlement space (S11) and therefore inhibit coral recruitment thereby constraining coral cover and facilitating further algal colonization (S12)</td>
<td>Frequent <strong>mass coral mortality</strong> events (bleaching, disease, hurricanes) facilitate algal colonization because grazing intensity decreases (S13). Note, the reverse process also occurs; coral growth and recruitment</td>
</tr>
<tr>
<td><strong>Competitive interactions between macroalgae and corals:</strong> <strong>algal competition</strong> causes increased post-settlement mortality in coral due to reduced light, flow or growth rate ((S14, 15))</td>
<td><strong>reduce the area available to grazers</strong> which intensifies grazing and can reduce macroalgae.</td>
</tr>
<tr>
<td>Frequent <strong>mass coral mortality</strong> events (bleaching, disease, hurricanes) facilitate algal colonization.</td>
<td></td>
</tr>
<tr>
<td><strong>Competitive interactions between macroalgae and corals:</strong> Macroalgae overgrow adult corals causing direct reductions in <strong>coral fecundity</strong> 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))</td>
<td>Frequent mass coral mortality events (bleaching, disease, hurricanes) reduce larval output of reefs further.</td>
</tr>
<tr>
<td><strong>Calcification rates</strong> of corals are slowed by increased ocean acidification. Results in greater competitive effectiveness of macroalgae relative to corals.</td>
<td></td>
</tr>
<tr>
<td>Thermal stress also reduces <strong>fecundity</strong> in corals ((S20)) which may ultimately reduce <strong>larval supply</strong> and coral recruitment ((S21)).</td>
<td></td>
</tr>
<tr>
<td><strong>Competitive interactions between macroalgae and corals:</strong> Macroalgae may act as vectors of organisms that cause coral disease ((S22)), thereby promoting losses of corals</td>
<td>Coral mortality events promote <strong>algal colonization</strong> and rising temperature may enhance efficacy of disease organisms ((S23)).</td>
</tr>
<tr>
<td><strong>Competitive interactions between macroalgae and corals:</strong> 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</td>
<td>Coral mortality events promote <strong>algal colonization</strong></td>
</tr>
<tr>
<td>Reductions in coral colonization and survival (<strong>coral loss</strong>) lead to a reduction in <strong>reef accretion</strong> and therefore a reduction in <strong>reef rugosity</strong> (structural complexity). This in turn reduces the carrying capacity of reefs for herbivores which require high rugosity to provide <strong>shelter from predators</strong> and sustain high densities ((S25, S26)). A reduction in herbivory continues to enhance the colonization of algae ((S18, S27))</td>
<td>Rate of rugosity loss may be exacerbated by acidification which leads to elevated rates of <strong>bioerosion</strong> and physical erosion because coral <strong>skeletons become weaker</strong> (less densely calcified). Bleaching damage and slower rates of coral recovery will cause <strong>habitat loss</strong> and increase the average <strong>distance among patches of high quality habitat</strong>. This may in turn reduce the <strong>population connectivity</strong> of reef organisms and reduce recruitment ((S28)).</td>
</tr>
<tr>
<td>Certain species of coralline red algae act as <strong>inducers to coral settlement</strong> ((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</td>
<td>Acidification increases energetic cost of calcification in coralline algae reducing their growth rate and increasing susceptibility to disease. Increase in macroalgal <strong>competitors</strong> after coral mortality events exacerbates process further by making the benthos...</td>
</tr>
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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, macroalgaldominated 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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**References**


S3 V. M. Masson-Delmotte et al., Clim. Dynam., 26, 513 (2006)


S14 S. J. Box, P. J. Mumby, Marine Ecology Progress Series 342, 139-149 (2007).
S18. T. P. Hughes et al., Current Biology 17, 1-6 (2007).