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Projecting Coral Reef Futures Under Global Warming and Ocean Acidification

John M. Pandolfi,[1,2]* Sean R. Connolly,[3] Dustin J. Marshall,[2] Anne L. Cohen[4]

Many physiological responses in present-day coral reefs to climate change are interpreted as consistent with the imminent disappearance of modern reefs globally because of annual mass bleaching events, carbonate dissolution, and insufficient time for substantial evolutionary responses. Emerging evidence for variability in the coral calcification response to acidification, geographical variation in bleaching susceptibility and recovery, responses to past climate change, and potential rates of adaptation to rapid warming supports an alternative scenario in which reef degradation occurs with greater temporal and spatial heterogeneity than current projections suggest. Reducing uncertainty in projecting coral reef futures requires improved understanding of past responses to rapid climate change; physiological responses to interacting factors, such as temperature, acidification, and nutrients; and the costs and constraints imposed by acclimation and adaptation.

Coral reefs occupy a small part of the world's oceans yet harbor a hugely disproportionate amount of its biodiversity. More than 450 million people from 109 countries live close to coral reefs, which provide important sources of ecosystem goods and services for these communities. But reefs have suffered degradation from human activities associated with overexploitation and pollution on centennial to millennial scales (*1*)—degradation that has accelerated over the past ~50 years (*2*). Global warming and ocean acidification (OA) are compounding these threats. Indeed, past biodiversity crises in reef ecosystems do appear to coincide with episodes of rapid global warming and OA (*3*). Some recent projections of coral reef futures are that present day, ongoing warming and OA will cause rapid, dramatic, and global-scale losses of coral reefs (*4*–*9*). For example, decreasing seawater carbonate ion (CO_3^{2-}) concentrations because of rising atmospheric CO_2 are predicted to lower rates of calcium carbonate ($CaCO_3$) production by corals such that, within decades, rates of reef erosion will exceed rates of reef accretion across much of the tropics and subtropics [e.g., (*5*, *10*, *11*)].

Here, we summarize the most recent evidence for past, present, and predicted future responses of coral reefs to environmental change, with emphasis on rapid increases in temperature and OA and their effects on reef-building corals, which provide much of the habitat framework and structural complexity upon which all reef organisms depend. This new knowledge confirms that coral reefs, at least as presently structured, are indeed threatened by climate change but that current projections of global-scale collapse of reefs within the next few decades probably overestimate the rapidity and spatial homogeneity of the decline. We conclude by considering the implications of a deeper understanding of effects of climate change and OA alongside other anthropogenic effects, such as coastal development and overfishing, for the conservation and management of coral reefs over the next century.

Coral Reef Response to Past Global Change

Long-term changes in Earth's atmosphere and oceans exert considerable control over biotic turnover and evolution through a number of variables, including sea surface temperature (SST), sea level, and mineral saturation state (known as Ω) (Fig. 1). For example, disproportionate extirpation of aragonitic or calcitic taxa from higher temperatures and lower pH during mass extinctions (*12*) substantially influenced calcification in the oceans as biodiversity recovered (*12*, *13*). Long-term steady-state conditions of high atmospheric CO_2 and low ocean pH are essentially decoupled from Ω_{arag} (fig. S1A) because of slow negative geochemical feedbacks, which increase alkalinity, especially calcium availability (primarily caused by increased rock weathering associated with high CO_2). Thus, shallow water tropical reef organisms existed throughout the past 540 million years of the Phanerozoic, through periods of temperature >7°C higher than today, and under CO_2 conditions >6000 parts per million (ppm) (*14*), more than 20 times greater than preindustrial levels (Fig. 1). In contrast to these long-term steady-state

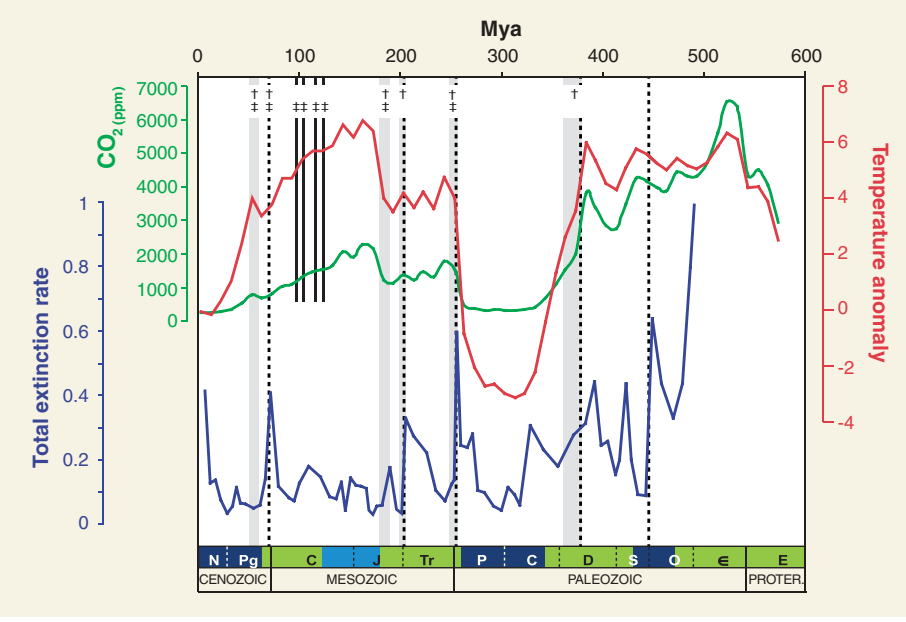

Fig. 1. Summary of major episodes of physical and biological change for reefs through geological time. Curves include global atmospheric parts per million by volume (ppmv) CO_2 (*14*), global mean temperature anomaly in °C (*14*), and total extinction rate (Paleobiology DataBase, http://paleodb.org/cgi-bin/bridge.pl). Greenhouse (green) and Icehouse (blue) periods (*92*) shade the geological time scale (light blue bar denotes no true polar ice caps documented). Vertical dashed gray lines indicate global mass extinction events; vertical gray bars indicate reef crises (*3*); and short vertical black bars indicate ocean acidification events such as ocean anoxic events (OAEs – 120.5 Ma, 111 Ma, 102 Ma, and 93.5 Ma during the Cretaceous) that occurred over time scales too great to affect ocean carbonate saturation states and indeed are not associated with reef decline [after (*15*) and (*3*)]. Evidence for ocean acidification events from (*3*) is indicated by † (derived from physical evidence of pronounced increases of pCO_2), and evidence of ocean acidification events from (*15*) is indicated by ‡ (termed by these authors as "candidate OA events").

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conditions, rapid increases in CO_2 occur too fast for such feedbacks and lead to simultaneous declines in Ω_{arag} (*15*) (fig. S1B). Such departures are more in line with the seemingly unprecedented rate of CO_2 rise occurring now, which would require a millennial-scale time lag before rock weathering restores steady-state saturation states (*15*).

Comparably rapid declines in Ω_{arag} during previous geological intervals have not been documented (*16*), so reef response to these conditions cannot be predicted from fossil sequences. However, reefs have suffered five episodes of severe, global-scale biodiversity loss or cessation of reef growth, termed "reef crises" (*3*) over geologic time. The four most recent reef crises coincided with OA in conjunction with rapid global warming, including two of the "Big 5" Phanerozoic mass extinctions at the end-Permian [251 million years ago (Ma)] and end-Triassic (200 Ma) (*3*) (Fig. 1). An analysis of the inferred physiology of victims versus that of survivors of these biotic crises points to an important role for rapid increases in OA (*12*). Other episodes of increased OA such as the Aptian Ocean Anoxic Event (Fig. 1) (OAE1a, about 120 Ma) occurred on time scales over which carbonate saturation state was well buffered [>10,000 years (*16*)], so the absence of reef decline provides limited information on the consequences of present climate change for coral reefs. The most recent reef crisis, the Paleocene-Eocene Thermal Maximum (PETM; 55.8 Ma), was characterized by rapid SST rise and a similar order of magnitude of CO_2 increase as present, probably consisting of CO_2 release in multiple pulses over 1 to 10 thousand years (fig. S1B). Although a marked faunal shift on continental carbonate platforms, from coral-algal reefs to reefs dominated by large benthic foraminifera, has been associated with this event (*17*), reef assemblages in at least one oceanic setting were unaffected (*18*). Thus, overall evidence from the fossil record indicates that rates of change are crucial for determining ecological outcomes, that reefs are most vulnerable when rapid increases in SST and CO_2 occur together with declines in Ω_{arag}, and that at least some reefs have shown greater resilience to past rapid warming and acidification than previously thought.

Since the Last Glacial Maximum (LGM) [~20 thousand years ago (ka)], abrupt changes in global temperatures have occurred repeatedly (*19*), especially between 15 and 10 ka, that have affected tropical SSTs (*20*). Evidence from high-resolution proxy records suggests that tropical SSTs had the potential to repeatedly warm over centennial to millennial time scales (*21*, *22*), in one location at rates comparable to those projected for the coming century [figure 2 in (*23*)]. None of these post-LGM warming episodes appear to have interrupted reef growth, which was substantial throughout the tropical oceans through to the cessation of the Holocene sea level rise around 6 ka (*24*). However, during this time, SSTs were cooler than they are today, there were no rapid changes in greenhouse gases or pH comparable to current, ongoing climate change, and levels of CO_2 remained below 330 ppm.

Ecological Responses to Ongoing SST Increase

Coral reefs are particularly sensitive to increasing temperatures because the major framework builders, scleractinian corals, suffer a breakdown in their symbiosis with zooxanthellae when temperatures are anomalously high. This "coral bleaching" (so termed because corals become white as zooxanthellae are lost), reduces the performance of the coral host, which receives most of its organic carbon from the symbiont. Mass bleaching events, when most of the coral assemblage bleaches, have become more frequent and widespread in the past few decades (*25*). These events are often associated with high mortality (*26*) and depressed colony growth and reproduction among survivors (*27*). Within communities, there is both taxonomic variation (*28*, *29*) and within-species heterogeneity in bleaching susceptibility (*29*) (Fig. 2A). Because the extent of variability in bleaching thresholds itself varies among species, taxonomic differences in bleaching severity may vary among bleaching events (Fig. 2B). Numerous characteristics of coral hosts have the potential to confer differences in bleaching susceptibility, and these characteristics vary substantially within and among coral species (*30*, *31*). Some coral species also harbor multiple strains of zooxanthellae, which confer differential susceptibility of their hosts to bleaching (*32*).

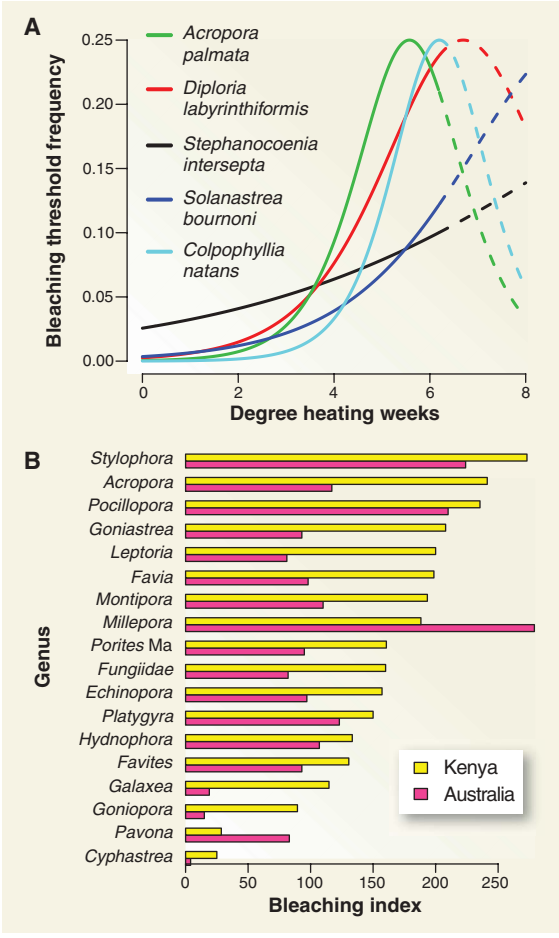

Fig. 2. Bleaching severity differs within and between species, but these differences vary among bleaching events. (**A**) Estimated probability distribution of bleaching thresholds for five species of Caribbean corals, based on logistic regression models fitted to bleaching data from the Florida Keys and Dry Tortugas, under environmental conditions corresponding to the average observed for each species (*29*). The width of the distribution indicates the within-population variation in the temperature at which bleaching is expected to occur. (**B**) Variation in bleaching intensity between Kenya and Australia, during the 1998 mass bleaching event [compare with figure 2 in (*28*)]. Bleaching intensity is a weighted average of the proportion of colonies in different bleaching categories (*28*). Taxa are displayed in rank order of bleaching severity in Kenya. Data provided by A. H. Baird and T. R. McClanahan.

As with bleaching events themselves, there is substantial variation in reef recovery in the aftermath of bleaching events (*25*). Where there is sufficient survival of existing colony tissue, recovery can occur within a few years (*33*), but in other cases no appreciable recovery of coral cover was observed even after 5 to 10 years (*34*, *35*). Most commonly, recovery of coral cover requires about a decade (*25*, *36*). For coral species hosting multiple symbiont strains, shifts to thermally resistant strains are sometimes observed after bleaching events (*37*), although reversion to domination by thermally sensitive strains may occur over several years (*37*), probably because of a trade-off between bleaching resistance and productivity (*38*).

Where coral mortality is accompanied by a loss of habitat structure, the potential exists for negative effects of bleaching on the broader reef community. Mass bleaching can be followed by increases in macroalgae, when herbivores are absent or avoid macroalgal species (*39*), but even when macroalgae are controlled other taxa, such as encrusting sponges, can reduce the space available for coral recruitment (*40*). Fishes and invertebrates that consume or inhabit corals during some part of their life cycle typically decline in abundance after mass bleaching, while roving herbivores such as parrotfishes and surgeonfishes increase (*25*, *41*). Presently, there is limited evidence of systematic changes in the abundance of mesopredators or apex predators or of declines in fisheries yields associated with bleaching, suggesting that any such effects would likely be accompanied by long time lags (*34*, *42*).

Response to Ongoing Ocean Acidification

For coral reefs, the paramount concern about CO_2-induced OA has been its potential impact on rates of biogenic calcium carbonate production by the dominant reef calcifiers: corals and coralline algae. An earlier compilation of data from several single-

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organism and mesocosm experiments and one field study focused on $CaCO_3$ precipitation on the Great Bahama Banks (*43*) suggested that coral and coral reef calcification declined linearly with declining aragonite saturation state, reaching zero when $\Omega_{arag} = 1$ (solid line in Fig. 3) (*44*). On the basis of these data, a 40 to 83% decline in reef calcification was predicted by 2065 C.E. (*44*). Moreover, a subsequent study based on the sensitivity of net community calcification to Ω_{arag} on a northern Red Sea reef predicted a global shift in coral reefs from net accreting to net dissolving when atmospheric CO_2 doubles to 560 ppm (*11*). These projections fueled concern that coral reefs are under threat of imminent collapse from OA.

However, a considerably expanded data set (*45*–*51*) incorporating more recent findings reveals that the calcification response to changing Ω_{arag} among individual coral species, coral mesocosms, and in situ reef communities, although consistently negative, is highly variable and often nonlinear (Fig. 3). Although calcification is strongly sensitive to Ω_{arag} in some experiments, it did not change significantly in others where corals were exposed to CO_2 levels between two and three times greater than preindustrial concentrations (*45*, *46*, *52*) or levels that declined below the aragonite saturation threshold ($\Omega_{arag} = 1$) (*45*). In a few instances, calcification increased under moderately elevated partial pressure of CO_2 (pCO_2) (*46*, *48*, *53*), as has also been observed for some coralline algae, crustacea, and echinoderms (*45*). Sensitivity of calcification to decreases in Ω_{arag} appears to be reduced when (i) studies are conducted over weeks or months (*45*, *46*, *50*, *53*)] as opposed to <1 day (*44*, *54*) or (ii) corals are reared under nutritionally replete conditions by feeding or elevating inorganic nutrient concentrations (*44*, *45*).

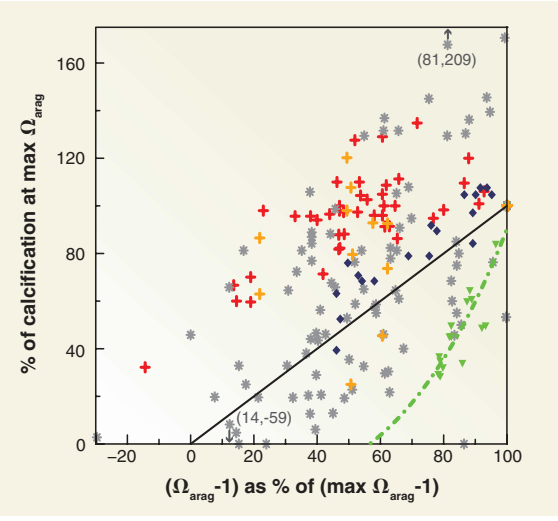

Fig. 3. Calcification response to changes in Ω_{arag} observed in experiments and in nature. Experiments using Ca to manipulate Ω_{arag} and those reporting >80% mortality under elevated CO_2 are excluded. Data are grouped as follows: (i) CO_2 invasion experiments at ambient temperature [seven studies (*45*–*49*, *52*, *53*), red crosses], and CO_2 invasion experiments at elevated temperature [three studies (*46*, *47*, *53*), orange crosses]. In all CO_2 invasion experiments, corals and coral reef organisms were exposed to treatment conditions for longer than 1 week. (ii) Non-CO_2 invasion experiments using different combinations of acid and base to manipulate Ω_{arag}, DIC, and pCO_2 [seven studies (*44*, *50*, *51*, *54*, *82*, *93*, *94*), gray asterisks]. Periods of exposure vary from hours to years. (iii) Field data from Gulf of Eilat (*58*) (green triangles) and Great Bahamas Bank (*43*) (blue diamonds). The horizontal axis is scaled to ($\Omega_{arag} - 1$) rather than Ω_{arag} because the first-order saturation-state model of (*44*) predicts that calcification is proportional to ($\Omega_{arag} - 1$), and this scaling facilitates comparing the model prediction (solid line) with the empirical data (points). The range of Ω_{arag} conditions for each experiment varied significantly, and, in several instances, corals were exposed to saturation states significantly higher (and lower) than those under which they grow naturally. Here, we set (maximum $\Omega_{arag} - 1$) in each experimental and field study at 100% and the calcification response is represented as percent of calcification recorded under the maximum Ω condition. The dash-dot green line is the fitted calcification model from (*58*).

Although a component of the documented variability in responses to acidification may be linked to differences in experimental technique, it also likely reflects real variability in the sensitivity of coral calcification to Ω_{arag} and flexibility in the ability of some corals to maintain calcification rates over a broad range of Ω_{arag} conditions. There are several potential explanations for such variable responses. For example, adaptation might result in the evolution of OA-hardy genotypes, either highly efficient calcifiers or those that direct more of their energetic budget to calcification. Also, given the right combination of environmental factors, such as abundance of food or high levels of inorganic nutrients, some corals might be able to divert excess energy to calcification and offset, at least partially, the impact of elevated CO_2 over a defined range of Ω_{arag}.

In fact, the energetic cost of calcification, currently poorly understood, may be key to predicting the response of corals and other reef calcifiers to future OA. Hypercalcifiers, including corals, probably utilize all forms of seawater carbon by using a combination of enzymes and proton pumps to convert CO_2 (aq) and HCO_3^- to carbonate ions for rapid calcification. However, this process is energetically costly, and, in a high-CO_2, higher dissolved inorganic carbon (DIC) ocean, well-nourished corals may be better equipped to convert excess HCO_3^- to CO_3^{2-}. Evidence from some experiments supports this (*55*, *44*). Conversely, poorly nourished or energetically depleted corals [including bleached or partially bleached corals (*47*)] will likely display heightened sensitivity to OA. At the community level, responses of other reef organisms to OA, such as increased productivity of algae (*56*), could alter the intensity or consequences of corals' interactions with other benthic taxa.

Experimental observations appear consistent with measurements of annual calcification rates in field corals that suggest high interspecific variability in calcification rates over natural gradients in Ω_{arag} (*57*). Nevertheless, striking inconsistencies remain between experimental and field observations that must be reconciled if predictions of future OA impacts on coral reef ecosystems are to be improved. Most importantly, a field study of community calcification (*58*) (green symbols in Fig. 3) implies community calcification responses to changes in Ω_{arag} that are considerably stronger than expected from either single-organism or mesocosm experiments. Efforts to understand this discrepancy, particularly the role of dissolution (*59*), are paramount to improved predictions of future OA impacts on reef ecosystems on a global scale.

The Role of Evolution

Evolution can buffer populations from environmental change (*60*) or accelerate species decline. Coral reef organisms will evolve in response to the increased thermal stress and OA associated with climate change, but the impact of this evolution is unclear (*61*). For corals specifically, the issue is complicated by symbiosis: The interdependency of mutualists, such as the coral host and symbiont, can affect rates of evolution (*60*). The symbiont suffers greater mortality because of thermal stress than does the host (*62*), so, from an ecological perspective, the symbiont is often viewed as the weaker link [but see (*63*)]. From an evolutionary perspective, however, the generation times of corals are orders of magnitude greater than those of symbionts, so symbionts may show faster evolutionary responses than their hosts. Nevertheless, the generation times of many coral species do not preclude rapid genetic evolution of the host in response to climate change as well: Other organisms have undergone rapid evolution in response to anthropogenic stresses within just a few generations (*60*). Furthermore, the modular nature of corals means that somatic line mutations could provide additional sources of variation such that evolution can occur within a single generation (*64*).

Phenotypic plasticity in thermal tolerances (acclimation or acclimatization) is an additional source of variation in the response of coral reef organisms to climate change (*65*). Because phenotypic plasticity allows organisms to cope with environmental change in the absence of genetic change, it has been argued that phenotypic plasticity will not influence reef organisms' evolutionary responses to climate change (*66*). However, models suggest that phenotypic plasticity enhances both the persistence and the evolution of organisms facing rapid environmental change (*65*). Assemblages that experience greater variability in SST appear less susceptible to bleaching (*67*), as do assemblages that have recently

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experienced substantial bleaching (*68*), phenomena that may be partly due to acclimatory responses. One example is the shift to more thermally tolerant symbiont strains after bleaching events (*37*). This suggests that some acclimation to increasing temperatures is already occurring, and it is likely that this plasticity will also enhance adaptation to warmer conditions. However, constraints and trade-offs will undoubtedly limit the phenotypic responses of coral reef organisms. For instance, the ability of hosts to "shuffle" symbionts to more thermally tolerant strains may be genetically constrained (*69*); indeed, corals on one reef may be incapable of acquiring such strains, even when conspecifics on nearby reefs can (*70*). Furthermore, although phenotypic plasticity in response to climate change should facilitate adaptation, phenotypic plasticity is costly (*65*), with implications for physiological performance or the ability to cope with further change. Whether such costs are common on reefs remains unclear.

Like acclimatory responses, evolutionary responses of reef organisms to climate change will be influenced by the nature and severity of genetic constraints. Populations can only adapt when there is sufficient genetic variation on which selection can act and the traits under selection are not correlated with other traits that affect fitness (often termed genetic trade-offs) (*71*). Such trade-offs have been shown to preclude adaptation to climate change despite substantial genetic variance in the traits under direct selection (*71*). In coral reef organisms, there are very few estimates of standing genetic variation in traits that are likely to be under selection under climate change regimes (*31*, *72*) and little information about genetic trade-offs associated with these traits, which have critical implications for potential adaptation to climate change (fig. S2). For example, among coral symbionts, there is a strain-level trade-off between bleaching resistance and holobiont growth rates (*73*), suggesting that genetic constraints may limit the scope and trajectory of evolution in response to climate change. Similarly, simultaneous adaptation to rapid warming and acidification may be constrained if these two selection pressures act on reef organisms in contrasting ways. Genetic constraints not only affect the magnitude of the response to selection via trade-offs with fitness—they can affect the direction of the response to selection and lead to important changes in other, seemingly unaffected traits (fig. S2). Thus, as corals and reef-associated species evolve to cope with climate change, unanticipated demographic and phenotypic consequences are likely.

Projecting Coral Reef Futures

Because bleaching causes mortality of corals and reduces energy available for growth and reproduction among survivors, increases in its frequency and intensity can confidently be expected to reduce coral cover. The most pessimistic projection is for global-scale losses of coral reefs resulting from annual mass bleaching events (*4*). More recent mathematical modeling that incorporates adaptation of thermal tolerance under varying emissions scenarios suggests that a wide range of outcomes is possible, from a complete collapse of coral cover by the middle of this century to maintenance of comparable levels of cover to 2100 and beyond (*74*). The outcome will depend on the extent of thermal adaptation and aggressive emissions reduction: Both appear necessary to avoid extended declines in coral cover to very low levels (*74*).

Most researchers predict coral species that are more susceptible to severe bleaching, such as the branching *Acropora* that form much of the habitat complexity of Indo-Pacific reefs, to be reduced in abundance relative to species that exhibit less sensitivity, such as slower-growing genera with massive or encrusting growth forms (*75*). Projection models that characterize interactions between idealized susceptible and resistant coral morphotypes reproduce such predicted changes (*74*, *76*), as do observations of community change after bleaching events (*77*). However, because bleaching-susceptible species often have faster rates of recovery from disturbances, their relative abundances will not necessarily decline; indeed, such species could potentially increase in abundance, depending on how demographic characteristics and competitive ability are correlated with thermal tolerance (*78*) and on the response of other benthic taxa, such as algae. Moreover, the shorter generation times typical of more-susceptible species (*79*) may also confer faster rates of evolution of bleaching thresholds, which would further facilitate maintenance of or increases to the relative abundance of thermally sensitive but faster-evolving species (*74*).

Early projections of contraction in the global distribution of reefs because of OA had their basis in part in the observation that present-day reefs are confined to regions where the neighboring open ocean has an Ω_{arag} above ~3.3 (*80*). However, temperature and Ω_{arag} are strongly correlated at global scales (*80*), making the attribution of geographical limits to reef growth to critical levels of Ω_{arag}, rather than lower thermal limits, problematic. A more recent projection has its basis in a calcification model parameterized by field studies of calcification's response to medium-term (~2-year) fluctuations in calcification and Ω_{arag} (*58*) (dashed green line in Fig. 3) and predicts that most of the world's reefs will be compromised once atmospheric CO_2 reaches 560 ppm (*11*). The model [equation 3 in (*11*)] assumes that calcification at the skeleton surface declines to zero as Ω_{arag} approaches 1.0, as with abiogenic $CaCO_3$ precipitation. However, corals are known to calcify at rates far exceeding the abiogenic $CaCO_3$ precipitation rate (*81*); corals may still calcify when $\Omega_{arag} < 1$ (*45*, *82*), and the calcification response underpinning these modeled projections exhibits much greater sensitivity to Ω_{arag} than has been apparent in other reef localities [figure 1 in (*11*)] or in many laboratory experiments where much greater variability in reef and coral response to changing Ω_{arag} occurs (Fig. 3).

There is no unified explanation that reconciles the broad range of implications that experimental studies of individual colonies, experimental mesocosms, and field studies have for changes in calcification rates on coral reefs over the next century. In particular, it is not clear whether the high sensitivity of calcification to Ω_{arag} assumed in current projections (*5*) occurs because the calcification response is influenced by other physical variables that covary with Ω_{arag} (temperature, light, nutrients) over the temporal scale of the field studies used to calibrate the models (*58*) or because the whole-reef response is dominated by processes other than coral calcification (e.g., calcification by other organisms or the dissolution kinetics of the reef matrix). Evidence from other field studies does suggest geographical variation in the community calcification response [e.g., figure 1 in (*11*)] that may be related to these factors.

An additional source of uncertainty concerns interactions between OA and other environmental variables. Any exacerbation of OA-induced reductions in calcification by high temperatures, reductions in coral cover because of mortality from bleaching, or reductions in nutrient or heterotrophic energy acquisition that reduce the energy available for calcification could accelerate declines in calcification at the whole-reef scale over the next century (*47*, *53*). Episodic depletion of energy reserves associated with increased coral bleaching (*83*) and chronic reductions in ocean productivity caused by increases in stratification and reductions in mixed-layer depth in the tropics (*84*) are two potential drivers of such reductions. Indeed, even without coincident acidification, large-scale depletion of coral cover associated with mass bleaching has caused periods of net reef dissolution (*85*).

Projections are useful exercises to help plan for future uncertainty in a dynamic system. There is abundant evidence indicating sensitivity of coral reefs to accelerated rates of warming and acidification conditions, including the historical record; bleaching; and the interactive effects of rising SST, OA, and reductions in oceanic productivity. This evidence has played a key role in many predictions that the disappearance of coral reefs on a global scale will be irreversibly under way within a matter of decades (*4*–*6*, *8*, *9*). However, recent evidence including studies of the late Paleocene fossil record (*18*) and species-specific responses to bleaching and OA [in experimental and field (*57*) settings] and recent work highlighting the role of phenotypic plasticity in evolution and the potential for rapid adaptation indicate that this view about the time scale of reef response may not adequately take account of reef organisms' capacity for coping with stress and their potential for adaptation. Moreover, range expansions of corals in response to warming temperatures have been recorded (*86*–*88*), but we presently lack good estimates of the potential rates of such range expansion under rapid environmental change and models that incorporate such shifts into projections. Such physiological, evolutionary, and biogeographic responses are not free from costs or constraints, but they will influence the nature of reefs' responses to climate change. Thus, reef degradation resulting from climate change alone is likely

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to be a more spatially, temporally, and taxonomically heterogeneous process than some projections suggest (*5*, *8*, *11*) and could even be slowed where management of local pressures, such as coastal development and overfishing, provides greater opportunity for reefs to cope with increasing ocean temperature and decreasing pH. Incorporating an explicit consideration of these issues should improve our ability to project the consequences, and manage the impacts, of ongoing climate change.

Management Considerations

Managing for future climate change impacts on coral reefs needs integration with our understanding of other ongoing anthropogenic stresses such as overfishing and pollution (*1*, *75*). There have been numerous calls to maximize the ecological resilience of coral reef communities to anthropogenic stress, including climate change (*75*). Because the rate at which the environment changes strongly affects whether and in what form coral reefs will persist (*65*), actions that slow the rate of climate change will diminish its impacts and maximize the potential for coral reefs to recover and even adapt.

Substantial evolutionary change can occur over the decadal time scales relevant to reef managers (*60*), but only if there is sufficient evolutionary potential within a population. When environments change rapidly, extinction risk declines with increasing genetic variation. Consequently, actions that decrease genetic variation will erode the capacity of coral reef organisms to adapt to climate change. Larger, well-connected populations generally have greater capacities to evolve than smaller, poorly connected populations (*89*). Thus, human impacts, such as fishing, pollution, and habitat destruction, that fragment populations or decrease population sizes will not only have immediate ecological effects, they will also reduce the potential of coral reefs to adapt to warmer, more acidic conditions. Similarly, genetic bottlenecks, that is, populations that have reduced genetic variation because of a past period of strong selection, have reduced capacity to evolve in response to additional changes (*89*).

The non–climate-related threats already confronting coral reefs are likely to reduce the capacity of coral reefs to cope with climate change. For instance, bleaching susceptibility is exacerbated by coastal runoff (*90*). Collapses in herbivory from overfishing could also increase the risk that mass bleaching events will lead to transitions to algae-dominated reefs, but this has yet to be clearly documented (*91*). Thus, in addition to climate policy, local reef management strategies designed to mitigate non–climate-related stressors, such as Marine Protected Areas, fisheries management, and marine spatial planning, may also increase the potential of coral reefs to cope with climate change. All of these actions are well aligned with current conservation management practices, and, in that regard, the best and most achievable thing we can do for coral reefs currently to deal with climate change is to seek to manage them well. However, slowing rates of climate change and reducing the strong selection imposed by anthropogenic impacts such as fishing and coastal development will remain critical to facilitating the long-term persistence of coral reef ecosystems.

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78. Consider a simple modification to the two-species Lotka-Volterra competition model to incorporate density-independent mortality from bleaching: $dN_i/dt = r_iN_i(K_i - N_i - \alpha_{ij}N_j)/K_i - Bc_iN_i$, where N_i, r_i, and K_i represent the abundance, intrinsic growth rate, and carrying capacity of species i (i = 1,2) and α_{ij}, the relative competitive effect of species j on species i. B represents bleaching severity, and c_i is a coefficient relating bleaching severity to the species-specific mortality rate induced by bleaching. Species 2 increases in abundance as bleaching intensity increases if $r_2/r_1 > c_2K_2/(c_1\alpha_{21}K_1)$. Species 2 can increase in abundance as bleaching intensity increases if it has a sufficiently greater ability to rapidly exploit available space (i.e., it has a sufficiently higher r), relative to its relative bleaching susceptibility (c_2/c_1). This occurs because increased bleaching mortality has two effects on a species: It directly reduces a species' abundance, but it also increases available space for colonization because of increased mortality of the species' competitor.
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