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# Coral Reefs and Ocean Acidification

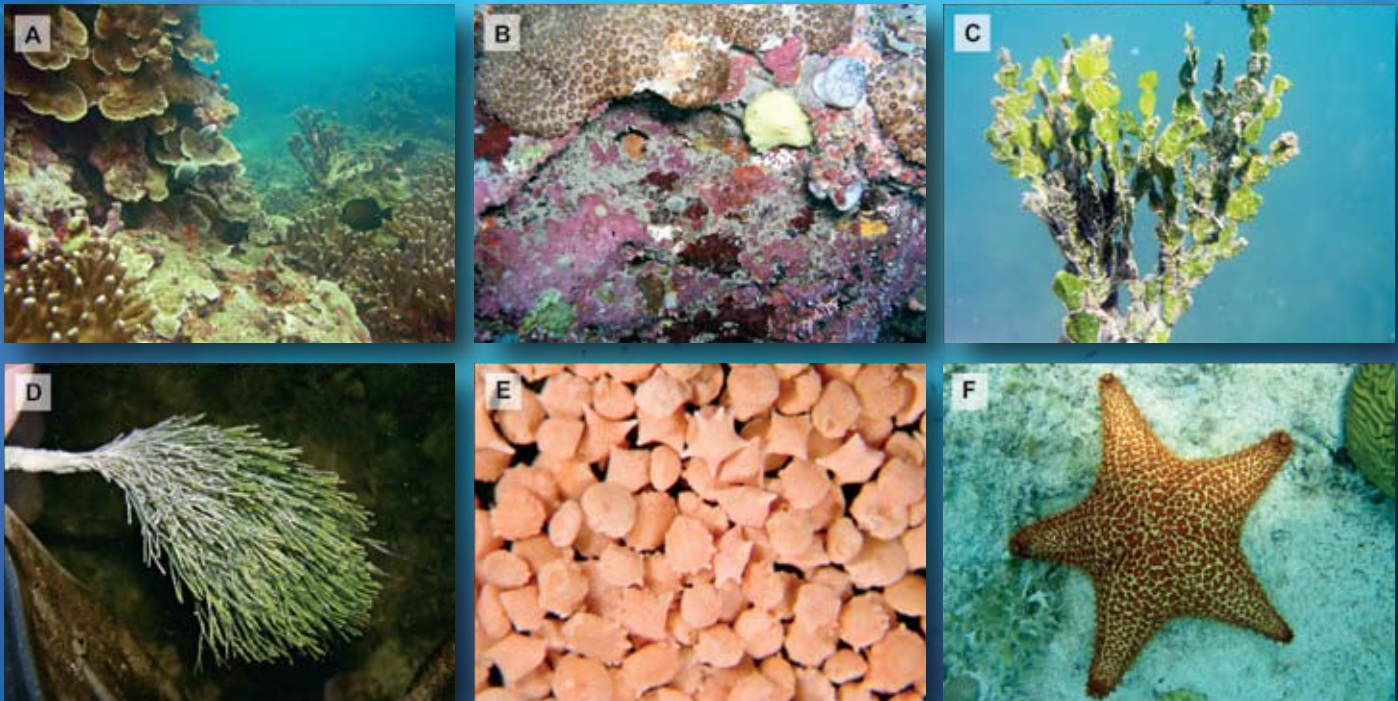


Figure 1. Important calcifying organisms on coral reefs: (A) various reef-building corals on a Samoan reef, (B) coralline algae encrusting rock surfaces on a Samoan reef, (C) *Halimeda* alga from Puerto Rico, (D) *Penicillus* algae, (E) reef sand composed of benthic foraminifera from Warraber Island, Torres Strait (average diameter of foraminifera grains is about 1 mm), and (F) echinoderm from the US Virgin Islands. Photo credits: A,B,C, Nathan Smiley; D, Matt Miller; E, Deirdre E. Hart; F, Chris DuFore



**ABSTRACT.** Coral reefs were one of the first ecosystems to be recognized as vulnerable to ocean acidification. To date, most scientific investigations into the effects of ocean acidification on coral reefs have been related to the reefs' unique ability to produce voluminous amounts of calcium carbonate. It has been estimated that the main reef-building organisms, corals and calcifying macroalgae, will calcify 10–50% less relative to pre-industrial rates by the middle of this century. This decreased calcification is likely to affect their ability to function within the ecosystem and will almost certainly affect the workings of the ecosystem itself. However, ocean acidification affects not only the organisms, but also the reefs they build. The decline in calcium carbonate production, coupled with an increase in calcium carbonate dissolution, will diminish reef building and the benefits that reefs provide, such as high structural complexity that supports biodiversity on reefs, and breakwater effects that protect shorelines and create quiet habitats for other ecosystems, such as mangroves and seagrass beds. The focus on calcification in reefs is warranted, but the responses of many other organisms, such as fish, noncalcifying algae, and seagrasses, to name a few, deserve a close look as well.

## INTRODUCTION

In the 1970s and 1980s, research on coral reef ecosystems covered two, often separate, tracks: biological and geological. In fact, the *Proceedings of the Third International Coral Reef Symposium*<sup>1</sup>, the outcome of a meeting held in Miami, Florida, in 1977, were cleanly separated into two volumes: “1. Biology” and “2. Geology.” Over time, arguments about the definition of a coral reef (e.g., is reef building a necessary litmus test for defining a coral reef ecosystem?) were reconciled in recognition that coral reef ecosystems exist along a continuum, from nonreef-building coral ecosystems to those that build massive, rapidly accumulating structures. Somewhere along that continuum lies a threshold between coral communities and coral reefs, and across that threshold the coral communities may or may not function similarly. It is not altogether clear that the coral community depends on its own reef building.

What is clear, however, is that

ecosystem functioning *does* affect reef building. Although reef building may not be essential to coral communities, the reef structure provides services to the reef ecosystem by supporting biodiversity and creating more surface area to support the reef community. These services are important, as is the reef function as a breakwater protecting shorelines and creating conditions that promote other productive systems like mangroves and seagrass beds.

Coral reefs are the most widely recognized ecosystem threatened by ocean acidification. Changes in seawater chemistry resulting from increased carbon dioxide uptake by the ocean impede the basic function of calcium carbonate production that is characteristic of many reef organisms, and that provides the foundation of coral reef structure. Ocean acidification, therefore, impacts both the biological and geological components of coral reefs. This article summarizes those impacts and provides a glimpse into what coral reefs may look like in the

future. It explores how ocean acidification might affect coral reef systems at multiple scales, from organism, to coral communities, to reef structure. Feely et al. (2009) provide a review of ocean acidification chemistry.

## EFFECTS OF OCEAN ACIDIFICATION ON REEF ORGANISMS

*How do I affect thee? –*

*Let me count the ways...*

Research on the effects of ocean acidification on marine ecosystems continues to focus on calcifying organisms, and for good reason. Skeletal formation in many organisms that secrete one of the various minerals of calcium carbonate (aragonite, calcite, and high-magnesium calcite) changes when exposed to elevated-CO<sub>2</sub> conditions. On coral reefs, the two main calcifying groups—corals and calcifying macroalgae (Figure 1A, B)—seem particularly sensitive to ocean acidification. However, noncalcifying organisms on coral reefs will also be affected. It is difficult to predict the overall impact on coral reefs of some species being “winners” and others “losers” in a progressively lower-pH ocean, but the loss of reef builders threatens both the biological and geological identities of this ecosystem.

## Reef Builders (Corals and Calcifying Macroalgae)

### History

The pioneers in reef calcification studies have known for some time that calcification by coral reef communities affects seawater chemistry (Smith and Pesret, 1974; Smith and Key, 1975). Some of

<sup>1</sup> The International Coral Reef Symposia have been held every four years since 1969.

the early studies of “reef metabolism” used the alkalinity anomaly technique—a measure of the drawdown of alkalinity over time due to precipitation of calcium and carbonate ions as calcium carbonate—to quantify calcification rates of coral reef communities (Gattuso et al., 1993; Kinsey, 1978, 1985; Smith and Kinsey, 1978). The converse, that seawater chemistry controls coral reef calcification rates, was slower to be recognized (Smith and Buddemeier, 1992). Some of the first studies to test the impact of ocean acidification on marine organisms were conducted on corals and coralline algae (Gattuso et al., 1998; Langdon et al., 2000). The Biosphere 2 studies, in particular, suggested that calcification rates of the coral/algal community correlated best with aragonite saturation state ( $\Omega_{ar}$ ) (Langdon et al., 2000, 2003). This result agrees well with geochemical studies that show that precipitation rates of inorganic aragonite from seawater can be expressed by the empirical equation  $R = k (\Omega_{ar} - 1)^n$ , where  $R$  is the rate of aragonite precipitation,  $k$  is the rate constant, and  $n$  is the order of the reaction (Burton and Walter, 1987). Because changes in  $\Omega_{ar}$  correlate strongly with changes in carbonate ion concentration, the natural inference is that the carbonate ion exerts direct control on calcification rates of corals and coral communities.

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Unfortunately, this inference is too simple because corals and other organisms exert energy to control their calcification, and because in most reef organisms it is internal and isolated from seawater. In corals, there is no evidence that carbonate ions are transported from seawater to the site of calcification (McConnaughey et al., 2000), so the carbonate ion concentration must affect calcification indirectly, or is simply a covariant of some other aspect of carbonate chemistry that controls calcification rate. Several studies have manipulated seawater chemistry by altering concentrations of  $Ca^{2+}$ ,  $CO_3^{2-}$ ,  $HCO_3^-$ , or pH while holding the others constant in order to tease out which component of the carbonate system elicits a response from corals. Those that manipulated the calcium ion concentration (Gattuso et al., 1998; Marshall and Clode, 2002) did cause a calcification response (note that marine aquarists are certainly aware that calcium supplements speed coral growth), and thus demonstrated the impact of saturation state changes. Ocean acidification, however, does not alter  $Ca^{2+}$  concentration, but rather pH and the concentrations of  $CO_2$ ,  $CO_3^{2-}$ , and  $HCO_3^-$ . All of these change with ocean acidification, and each has been shown to affect calcification either directly or indirectly. Several mechanisms have been proposed to explain why changes in the  $CO_2$  system in seawater affect calcification rate in corals. Cohen and Holcomb (2009) show that corals maintain a high saturation state at the site of calcification, but at low pH this requires extra energy that they don't readily divert from other energy demands. Even within corals, however, it is likely that the calcification process

differs (1) between species, (2) between the life stages of species (note that the mineralogy of the initial calcium carbonate precipitated by larvae is sometimes a rare, highly soluble form), and (3) in some species, between different stages of calcification.

### Calcification

Despite our incomplete understanding of the exact mechanisms that control calcification, decreased skeletal growth in reef-building corals and coralline algae is one of the best-known consequences of ocean acidification (Figure 2). A wide range of responses has been observed, but on average, a doubling of pre-industrial atmospheric  $CO_2$  concentration results in about a 10–50% decrease in the calcification rate of reef-building corals and coralline algae (Kleypas and Langdon, 2006). The good news is the response is reversible (calcification will increase if acidification is reversed). The bad news is it is highly unlikely that ocean acidification can be reversed, and we don't know yet whether corals and coralline algae can adapt to these changes.

Most studies have been conducted in the lab, under nonvarying conditions. This point is important because coral reef waters can naturally exhibit large diurnal swings in pH (e.g., 7.9–8.1; Bates et al., 2001; Suzuki and Kawahata, 2003) and other carbonate system parameters, and it is unclear whether the added suppression of pH by 0.1–0.3 pH units projected for this century would have a significant effect in environments where pH is highly variable. A recent ocean acidification study that simulated future variations in pH conditions in accordance with natural variations on the adjacent reef (Jokiel et al., 2008;

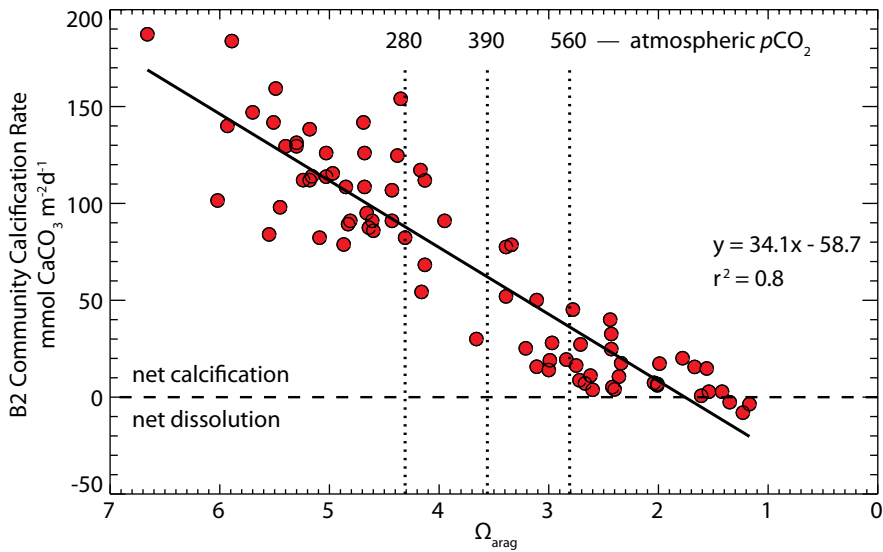


Figure 2. Changes in coral community calcification rate in the Biosphere 2 coral reef mesocosm as a function of decreasing aragonite saturation state (Langdon et al., 2003). Atmospheric  $p\text{CO}_2$  levels that roughly correspond with the  $\Omega_{\text{ar}}$  values are shown: 280 ppm = pre-industrial, 390 = present day, and 560 = 2X pre-industrial. Note that once  $\Omega_{\text{ar}}$  reached a value of 1.0–2.0, the coral community shifted from net calcification to net dissolution. Figure drawn from data provided by Chris Langdon

Kuffner et al., 2008) showed that the calcification responses of corals and coralline algae were similar to those in nonvarying conditions.

Calcification rates in scleractinian corals (stony, or hard, corals) and calcifying macroalgae are not only affected by seawater carbonate chemistry, but by other variables such as temperature, light, and nutrients. Temperature has a particularly strong effect, and small increases in temperature can sometimes override the effects of ocean acidification, that is, as long as the temperature increase does not cause bleaching or otherwise compromise coral physiology. When the potential effects of ocean acidification on coral calcification became apparent, scientists looked through the archives of cores taken from massive *Porites* corals, mostly from the Great Barrier Reef, to see if calcification rates had changed over the past century (Lough and Barnes,

2000). There was no indication that coral calcification rates had decreased, at least up to the year 1987, which was the latest age of the corals at the time of coring. If anything, the calcification signal correlated with temperature more than any other variable. Now, data from a new collection of coral cores from the Great Barrier Reef, which extends these records through 2005, indicate a 14% decline in calcification rates between 1990 and 2005 (De'ath et al., 2009), which the authors attribute to excessive temperature increases, ocean acidification, or a combination of the two.

The coral lifecycle includes more than adults, however, and ocean acidification could affect the larval stages of corals and many other reef species. So far, ocean acidification has not been shown to have serious effects on coral gamete production and recruitment, albeit the studies have been few (Albright et al., 2008;

Jokiel et al., 2008). Once settled, however, coral larvae reared in elevated- $\text{CO}_2$  conditions experience depressed growth rates similar to those seen in adults (Albright et al., 2008; Cohen et al., 2009).

Ocean acidification has also been shown to slow calcification rates in calcifying macroalgae, which have long been recognized as important components of coral reef ecosystems. The most common forms are coralline red algae within the phylum Rhodophyta and calcifying green algae within the phylum Chlorophyta. The coralline algae consist of both branching and crustose forms (many of which form unattached living nodules called “rhodoliths”) that produce large quantities of high-Mg calcite (the most soluble form of the common marine carbonate minerals). This group is extremely widespread in the ocean, existing from equatorial to polar regions (Nelson, 2009), and to the deepest depths recorded for benthic photosynthetic species (Littler et al., 1985). Such a broad distribution suggests that this group as a whole has the evolutionary capacity to adapt to a wide range of conditions. Unfortunately, individual reef-building species seem particularly vulnerable to dissolution under increasing  $\text{CO}_2$  concentrations, with no demonstrated ability to adapt. Calcification rates of rhodoliths, for example, decreased by as much as 250% (i.e., net dissolution) in mesocosms with  $\text{CO}_2$  levels elevated by 365 ppm over present-day conditions, and successful recruitment by coralline algae was diminished (Kuffner et al., 2008). Research on other tropical algae indicates that the calcium carbonate they produce can dissolve under elevated- $\text{CO}_2$  conditions (Anthony et al., 2008).

A common coralline algae from the Mediterranean Sea, however, did not show a strong calcification response as long as the algae remained alive, and decreased calcification occurred only when temperature was also elevated (Martin and Gattuso, 2009). Nonetheless, where skeletons were exposed directly to seawater following tissue death, dissolution rates were two to four times faster in elevated-CO<sub>2</sub> conditions. Dissolution of exposed skeletons thus constitutes a significant threat for this group, even if the algae can continue to calcify under high-CO<sub>2</sub> conditions. At a field site near a shallow submarine CO<sub>2</sub> vent in the Mediterranean, a suite of crustose coralline algae species was absent near the vent (where average pH < 7.7), which supports the findings of the laboratory experiments (Hall-Spencer et al., 2008; Martin et al., 2008).

Coralline algae are known to be a favored substrate for settlement of coral larvae and their subsequent metamorphosis and growth (Heyward and Negri, 1999). Thus, the reduction in the surface cover of crustose coralline algae may affect recruitment of other species. Similarly, the branching coralline alga *Amphiroa* is known to induce settlement of bivalve larvae (Williams et al., 2008); this genus is also considered sensitive to ocean acidification as evidenced in the overall community response to ocean acidification in the Biosphere 2 coral reef experiments (Langdon et al., 2000).

The calcifying green algae in the genera *Halimeda* and *Penicillus* (Figure 1C, D) produce large volumes of sand- and mud-sized sediments, respectively, in reef environments. Measured CaCO<sub>3</sub> production rates of *Halimeda* meadows can exceed those of coral reefs

(Freile et al., 1995), and *Halimeda* banks can be large and may be widespread on tropical shelves (Milliman and Droxler, 1996). These structures provide important habitat for many marine organisms. Although the effects of ocean acidification on *Halimeda* and *Penicillus* have not been explicitly studied, multiple studies indicate that calcification in these genera is somewhat passive, being stimulated by the photosynthetic removal of CO<sub>2</sub> from the intercellular spaces (de Beer and Larkum, 2001; Ries, 2009). Thus, an increase in ambient CO<sub>2</sub> concentration is likely to reduce the ability of these species to calcify.

### Other Calcifying Organisms on Reefs

Many calcifying taxa in addition to corals and calcifying macroalgae produce calcium carbonate skeletons, often in large quantities. Although the effects of ocean acidification on some of these taxa have been investigated, rarely have the studies focused on coral reef species. A brief summary of what we know about ocean acidification on these calcifying groups follows.

*Calcareous benthic foraminifera* are important contributors to reef sediments, sometimes producing the bulk of carbonate sands in shallower environments (Hohenegger, 2006; Figure 1E). Data from previous ocean acidification events identified in the geologic record (e.g., deep-sea sediment cores) indicate that calcifying benthic foraminifera are vulnerable to ocean acidification. Approximately 40% of benthic foraminifera species went extinct at the Paleocene-Eocene Thermal Maximum (55 million years ago), which included a strong ocean acidification event (Zachos

et al., 2005; Kump et al., 2009), and calcifying foraminifera went extinct at the Permian-Triassic boundary (around 250 million years ago) although the agglutinated forms did not (Knoll et al., 2007). Note that these extinction events also coincided with elevated temperatures and hypoxia, so it is difficult to discern which environmental change was the smoking gun. However, experiments that exposed both calcareous and noncalcareous benthic foraminifera to high CO<sub>2</sub> levels confirm that calcareous species are indeed sensitive to high CO<sub>2</sub> perturbations while noncalcareous species are not (Bernhard et al., 2009).

*Mollusks* are also important reef organisms, particularly the shelled forms such as gastropods and giant clams. Ocean acidification research has focused on pteropods, squid, and a variety of bivalves and gastropods; surprisingly, none of the studied species has been from coral reefs. Based on existing studies on nonreef-dwelling mollusks (Gazeau et al., 2007; Green et al., 2004; Miller et al., 2009; Talmage and Gobler, 2009), it might be expected that some, but not all, species will produce thinner shells and/or suffer reduced recruitment rates under elevated-CO<sub>2</sub> conditions.

Many *echinoderms*, including starfish (Figure 1F), brittle stars, sea urchins, sand dollars, crinoids, and holothurians, have important functions in the reef. For example, the corallivorous crown-of-thorns starfish can strip a reef of most of its live coral tissue; the grazing of many sea urchins keeps algal growth in check; and echinoderms, in general, are responsible for a large portion of global calcium carbonate flux (Lebrato et al., in press). All echinoderms secrete high-Mg calcite skeletons (in the case

of holothurians, the skeleton has been reduced to small ossicles embedded in their tissues). Examination under a polarizing microscope shows that each skeletal component is composed of a single crystal. The greater solubility of the high-Mg calcite skeletons of echinoderms, and their limited control on internal acid-base chemistry (Kurihara, 2008; Miles et al., 2007), suggests that this group is highly vulnerable to ocean acidification. This vulnerability appears to be the case in some species, but some echinoderms live on or within sediments, and thus may be adapted to lower-saturation-state conditions. A temperate brittle star, for example, calcified more under elevated-CO<sub>2</sub> conditions although at the expense of other tissues (Wood et al., 2008), and a temperate starfish fed more and grew faster (Gooding et al., 2009).

Within the phylum echinodermata, ocean acidification studies have focused more extensively on larvae than on adults. Larval echinoderms produce an amorphous phase of CaCO<sub>3</sub> that is highly soluble (Politi et al., 2004). Larval development in most species reared in elevated-CO<sub>2</sub> conditions has been stunted, delayed, or even malformed (Clark et al., 2009; Kurihara and Shirayama, 2004). Genomic studies on larvae of the purple sea urchin revealed that gene expression in this species demonstrated a response not only in biomineralization but also in cellular stress response, metabolism, and self-destruction of cells (Todgham and Hofmann, 2009).

Many *other important taxa* on reefs produce CaCO<sub>3</sub>, such as some crustaceans, some polychaete worms, octocorals, and even soft corals. Although the

contribution of these taxa to carbonate production is small, their functioning in the reef system could be impacted if their ability to produce their shells or skeletons is impaired.

### Noncalcifying Organisms

Many organisms on reefs are not calcifiers, yet their responses to ocean acidification can be quite important. Seagrasses, for example, are widely recognized as potential winners with ocean acidification. Several studies show that in nutrient-replete conditions, the growth of seagrasses increases significantly in elevated-CO<sub>2</sub> conditions (Palacios and Zimmerman, 2007). Although seagrasses could potentially expand on reef flats and displace corals and other calcifiers, recent studies indicate they could benefit calcifiers, as some coralline algae calcify faster in the proximity of seagrasses, due to the drawdown of CO<sub>2</sub> from the water column (Semese et al., 2009). Elevated CO<sub>2</sub> may also stimulate growth in other noncalcifying macroalgae, such as was found in *Porphyra yezoensis* and two *Gracilaria* species (Gao et al., 1991, 1993), and particularly in algae that use CO<sub>2</sub> rather than bicarbonate for photosynthesis, such as *Lomentaria articulata* (Kübler et al., 1999).

One of the most interesting effects of ocean acidification concerns “euendolithic” algae, that is, algae that bore into reef skeletal material. At double CO<sub>2</sub> levels, these algae bore more deeply into skeletal material, dissolving nearly 50% more carbonate in the process (Tribollet et al., 2009). If this response is universal on reefs, then increased dissolution by these little known but pervasive microscopic algae could alone push many reefs

from a state of reef building to one of reef destruction.

Most reef fish have not been considered vulnerable to ocean acidification, but one study looked at the effects of pH changes on the chemosensory ability of larval clownfish to locate suitable habitat (Munday et al., 2009). Surprisingly, larvae subjected to lowered pH levels appeared to lose their ability to distinguish between favorable (e.g., their host anemones) and unfavorable (e.g., mangrove) habitats.

### SPECIES INTERACTIONS AND ECOSYSTEM SHIFTS

A main concern about the effects of ocean acidification on coral reefs is that it appears to affect many groups of reef organisms, particularly corals and coral-line algae, the “ecosystem engineers” of reefs. The loss of these keystone species affects many other species associated with them. When corals die in bleaching events, the species that depend on them are also impacted, and the effects trickle through the reef ecosystem. These changes can degrade the reef’s resilience (i.e., its ability to withstand disturbance) even while it appears visibly healthy, until at some point it can no longer sustain even minor disturbances, and becomes vulnerable to an ecological “regime shift,” that is, a rapid transition to a different ecosystem state (Figure 3). The classic example of such a regime shift occurred on a Jamaican coral reef; it was driven by the loss of both fish herbivores and sea urchin herbivores (through overfishing and disease, respectively), which allowed the ungrazed macroalgae to overgrow the reef (Hughes, 1994). Other regime shifts have been observed on coral reefs in Australia (Hatcher, 1984) and in the



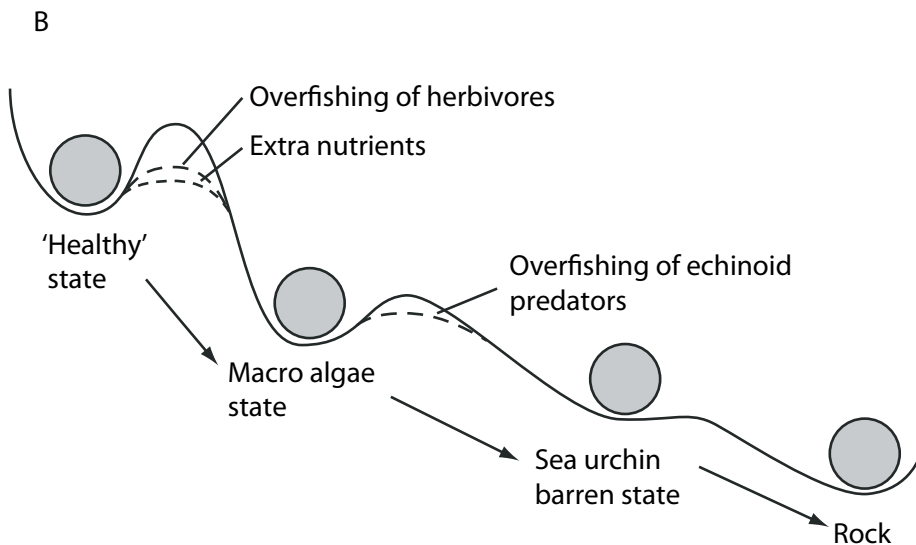
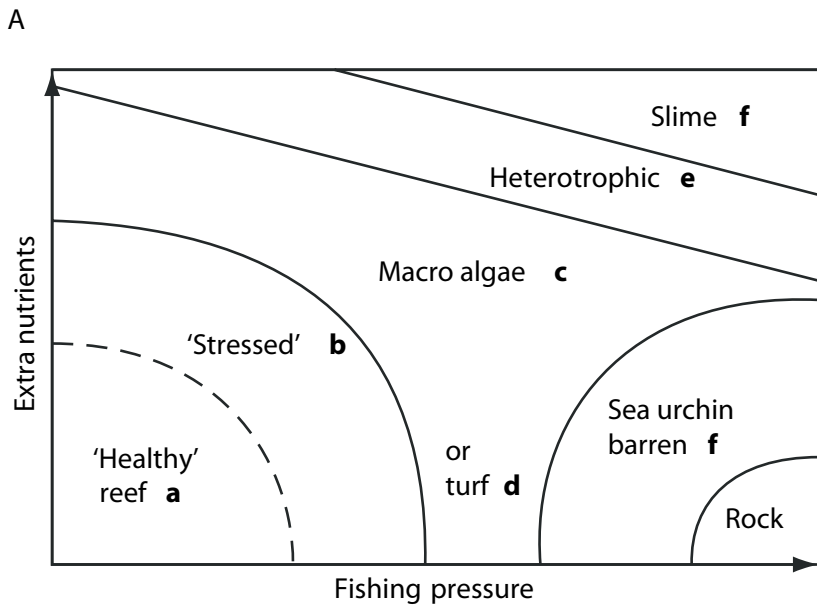


Figure 3. Regime shifts in coral reefs. (A) Conceptual model showing the effects of overfishing and excess nutrients on reef state. With increasing fishing pressure and/or nutrient pollution, the coral community enters a stressed state with a loss of resilience and increased vulnerability to a rapid shift to a different state, such as an algal-dominated, sea-urchin-dominated system. (B) Diagram of how environmental changes enable transitions to new ecosystem states. The dotted lines illustrate the loss of resilience that increases the likelihood of shifting to a different state (redrawn with permission from Macmillan Publishers Ltd: *Nature* [Bellwood et al., 2004], © 2004). The exact effects of ocean acidification will be different than those imposed by pollution or overfishing, but the process of how diminishing resilience increases the likelihood of a regime shift is the same.

(e.g., reef building, grazing, filter feeding, sediment turnover) will collapse, leading to a regime shift. It is difficult to predict how future regime shifts will proceed, particularly because ocean acidification is occurring alongside other stressors like temperature increases and overfishing. Previous regime shifts on reefs were usually to ecosystems dominated by macroalgae, but shifts to soft corals and skeletonless relatives of reef-building corals called corallimorpharians have also occurred (Norström et al., 2009).

### REEF BUILDING

Reef building—the accumulation of calcium carbonate framework and sediments—is almost certain to change in the future, because both carbonate production (almost entirely biogenic) is likely to decrease, and its removal (via mechanical transport of material off the reef and chemical dissolution) is likely to increase. The severity of the impact of ocean acidification on coral reefs will depend, in part, upon a delicate balance among calcification, carbonate sediment dissolution, and transport of sediment away from the reef. An important question is whether reef growth will be able to sustain the reef structure, or rather shift to a state of erosion. However, like inept accountants, most scientists concentrate on what goes into the reef and not on what is removed! Observed dissolution rates on many reefs can be quite high (Yates and Halley, 2006), particularly in areas where high-Mg calcite is common, and particularly at night, when CO<sub>2</sub> accumulates in the water column because photosynthesis has ceased while respiration continues. In some areas where water mass residence time is relatively long (on the order of days as opposed to

eastern Pacific (Hunter and Evans, 1995) and Indian oceans (Graham et al., 2006). As ocean acidification proceeds, more and more species will be affected. Some species will be losers (e.g., corals) and

some will be winners (e.g., seagrasses), but the higher the proportion of species that are affected (including winners and losers), the higher the probability that some major function of the ecosystem

hours), sediment dissolution may buffer decreasing seawater pH and provide some “relief” to calcifying organisms. However, most reefs are well flushed with open ocean seawater and will not be afforded this type of protection (Andersson et al., 2007). Furthermore, loss of reef sediment may be exacerbated for eroding reefs as lagoonal and other back-reef areas that are naturally protected by reef structure become exposed to higher wave energy, currents, and sediment transport.

The threshold where coral reefs shift from net production/accretion to net dissolution/erosion will vary greatly from reef to reef. These variations depend on a complex interplay of factors

such as metabolic performance due to community composition, seasonal variation in calcification and dissolution rates, variation in sediment composition, degree of biologic control on calcification and dissolution mechanisms, and mixing rates of water masses overlying substrate areas. As ocean acidification proceeds, slow-growing reefs that already have a balanced carbonate budget will be the first to shift from a reef-building to a reef-erosion state (Figure 4). In general, reefs at higher latitudes have lower net growth rates because the waters are colder, more acidic, and perhaps because of shallower light penetration in the winter (Kleypas et al., 1999). They may also have higher

dissolution rates. Reefs at higher latitudes tend to be less well developed than those in warmer, more tropical regions, but even reefs in the warm tropics may accumulate only slowly if, for example, they grow in turbid waters or if storms transport much of the excess carbonate off the reef.

Only a few studies have focused on determining  $p\text{CO}_2$  thresholds for coral reef communities that mark the critical point when rates of carbonate sediment dissolution are equivalent to rates of calcification, and above which dissolution exceeds calcification. Average  $p\text{CO}_2$  thresholds for reef communities in these studies ranged from approximately 560–654 ppm (Yates and Halley, 2006;

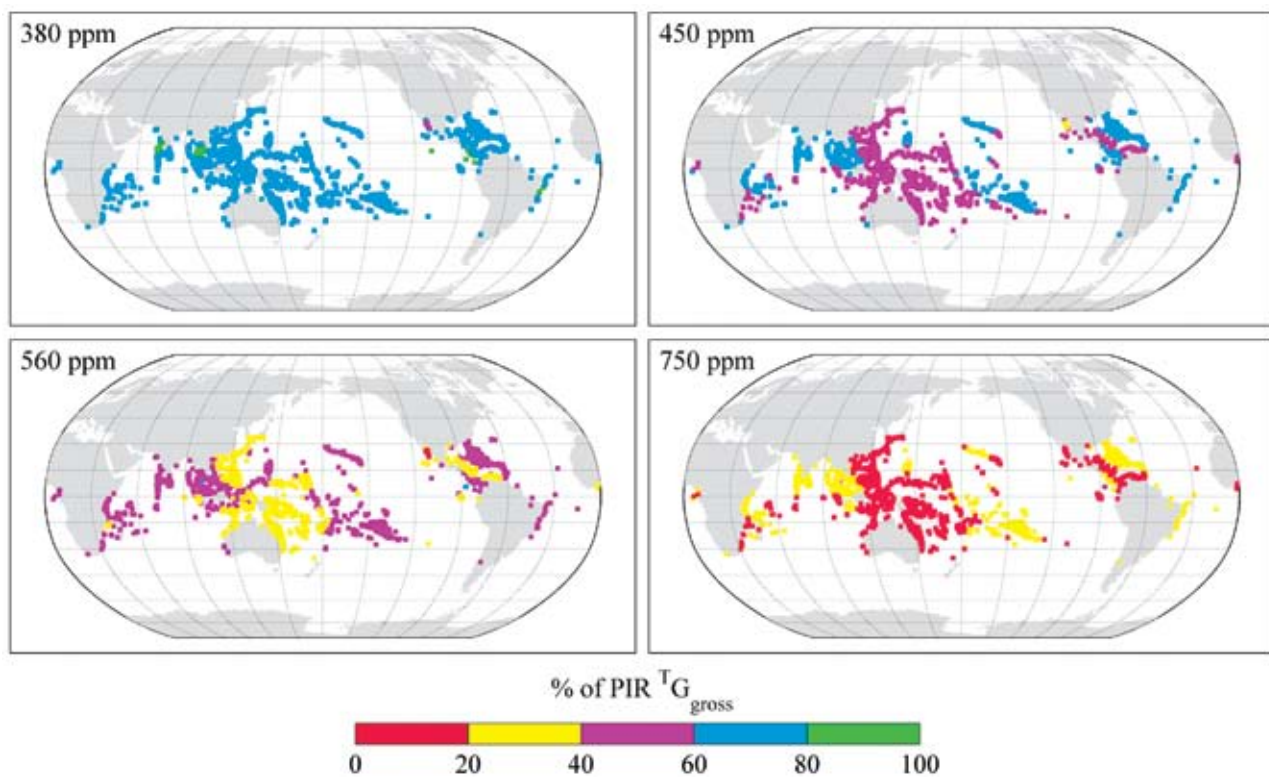



Figure 4. Calculated changes in reef building for coral reefs worldwide at four different atmospheric  $p\text{CO}_2$  stabilization levels, based on the combined effects of predicted changes in saturation state and temperature on coral community calcification. The values are expressed as a percentage of pre-industrial calcification rates (when atmospheric  $\text{CO}_2$  levels were 280 ppm); PIR = pre-industrial rate;  $TG_{\text{gross}}$  = temperature-dependent gross calcification. Note that this calculation assumes constant coral cover = 50% (but see Silverman et al. [2009] for projections that include changes in coral cover). Reprinted from Silverman et al., 2009, with permission from the American Geophysical Union



Silverman et al., 2009), but show a high degree of variation that is not yet fully understood. One projection of future net carbonate production (production minus dissolution) on reefs estimated that almost all coral reefs will be in a state of net dissolution once atmospheric CO<sub>2</sub> concentrations reach 560 ppm (Silverman et al., 2009), a level that is projected to occur around the year 2050.

What does degradation of reef structures mean for coral communities? While coral communities can remain viable on eroding substrates, recent studies show that reef surfaces, which are typically rough and irregular, are becoming “flatter” (Alvarez-Filip et al., 2009). Loss of architectural complexity will decrease habitat diversity, which in turn will lead to decreased biodiversity. The loss in biodiversity, particularly in combination with loss of coral reef species through bleaching, disease, and overexploitation, threatens the persistence of coral reef and fish communities in the future (Jones et al., 2004). The future level of reef persistence as a function of ocean acidification alone is largely unknown, but the likelihood of fewer coral reefs in the future is high.

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