Chapter 15

Coral Reefs, Climate Change, and Mass Extinction

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The term "extinction" is a loaded phrase when applied to coral reefs. Often, it is applied to coral reefs generically, with the phrase "extinction of coral reefs" appearing regularly in the scientific and popular press (e.g., it appeared more than 15,000 times when typed into the Google search engine, June 4, 2011). This phrase is generally used to describe the disappearance of coral reefs as an ecosystem, which is very distinct from the extinction of a particular coral reef species. This distinction becomes increasingly important when considering the likely outcome for coral reefs and their biodiversity under rapid global change.

Discussions of the characteristics that are likely to influence the vulnerability of species to extinction have appeared several times already in this book. Currently, many marine species are often abundant with large dispersal ranges. These characteristics are such that many marine species are relatively resistant to extinction, especially when compared to many terrestrial species, which are often narrowly distributed with limited dispersal ability. Roberts and Hawkins (1999) list a number of characteristics associated with marine species that make them more or less vulnerable to extinction. In this respect, they explored the influence of parameters that affect population turnover, reproduction, recovery capacity, range and distribution, trophic level, and whether or not a species is common or rare. Under their analysis,

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long-lived and slow-growing organisms that have short dispersal distances and narrow nearshore ranges are at greater risk of extinction than species that are short-lived, fast-growing, dispersed widely, and which have broad geographical ranges (table 15-1).

Reef-building corals tend to be long-lived, slow-growing, reproductive at large size, and immobile as adults (table 15-1). Together with their narrow depth range and nearshore distribution, and their sensitivity to the activities of humans, corals make ideal candidates for extinction. On the other hand, they often have sizable reproduction biomasses and reproduce many times in their lives, with the ability to regenerate and grow asexually from fragments. When in good health, corals are also effective competitors and colonizers with strong larval recruitment. They also have some of the largest geographical ranges of any known animal. For these reasons, they should be relatively less vulnerable to extinction.

Typical coral-dwelling fish, on the other hand, differ from corals in that they are relatively short-lived, mature at small sizes, reasonably mobile but unable to reproduce asexually. According to the Roberts and Hawkins' (1999) framework, typical coral-dwelling fish will also have a degree of vulnerability to extinction but for different reasons. Across the range of organisms that live on coral reefs, there are clearly those that are relatively resistant to extinction versus those that are highly vulnerable. Under a rapidly changing climate, one of the interesting questions becomes: Can we predict which organisms are going to be "winners" and which organisms are going to be "losers" with respect to extinction?

Rapidly Changing Ocean Environments

One of the defining characteristics of our times is that there is no longer anywhere on our planet that humans have not significantly impacted (Halpern et al., 2008). A depressing yet sobering fact, the signature of human activities can be found at the bottom of the deepest oceanic trench and at the top of the highest mountain. For coral reefs, the signature has been unambiguous for some time, with a 1–2 percent decrease in coral cover each year and the loss of 40 percent of coral reefs over the past three decades (Bruno and Selig, 2007).

Both local and global stresses are driving this decline. Local factors include deteriorating water quality (i.e., too many nutrients and

TABLE 15-1. Characteristics that are likely to render marine species vulnerable to extinction (adapted from Roberts and Hawkins 1999).

	Vulnerability			
Characteristics	*High*	*Low*		
Population turnover			*Corals*	*Fish*
Longevity	Long	Short	Long	Short
Growth rate	Slow	Fast	Slow	Moderate
Natural mortality rate	Low	High	Moderate	Moderate
Production biomass	No	High	High	Moderate
Reproduction				
Reproductive efforts	Low	High	Low	Moderate
Reproductive frequency[1]	Semelparity	Iteroparity	Iteroparity	Iteroparity
Age or size at sexual maturity	Old or large	Young or small	Old or large	Moderate
Sexual dimorphism	Large difference in size between sexes	Does not occur	Does not occur	Does not occur
Sex change	Occurs (protandry[2] in particular)	Does not occur	rare	Occurs (but many protogynous)
Spawning	In aggregation is at predictable locations	Not in aggregations	Not in aggregations	In aggregation is at predictable locations
Allee effects[3] at reproduction	Strong	Weak	Strong	Weak
Capacity for recovery				
Regeneration from fragments	Does occur	Occurs	Occurs	Does occur
Dispersal	Short distance	Long-distance	Long distance	Long distance
Competitive ability	Poor	Good	Good	Good
Colonizing ability	Poor	Good	Good	Good

TABLE 15-1. Continued.

	Vulnerability			
Characteristics	*High*	*Low*		
Adult mobility	Low	High	Low	Moderate
Recruitment by larval settlement	Irregular and/or low	Frequent and intense	Frequent and intense	Frequent and intense
Allee effects at settlement	Strong	Weak	Weak	Weak
Range and distribution				
Horizontal distribution	Nearshore	Offshore	Nearshore	Nearshore
Vertical depth range	Narrow	Broad	Narrow	Narrow
Geographic range	Small	Large	Large	Large
Patchiness of population within range	High	Low	Low	Low
Habitat specific	High	Low	High	High
Habitat vulnerable to destruction by people	High	Low	High	High
Commonness and/or rarity	Rare	Abundant	Abundant	Abundant
Trophic level	High	Low	Low	Moderate

[1]Semelparity: Organisms in which the life cycle is characterized by a single reproductive episode before death.
Iteroparity: Organisms in which the life cycle is characterized by multiple reproductive cycles over the course of the life history.
[2]Protandry: Organisms that start off life as males and transform into females. Opposite is protogyny, in which organisms start off life as females and transform later into males.
[3]Allee effects: Situation in which there is a positive correlation between population density and the per capita population growth rate in very small populations.

sediments from disturbed coastal areas adjacent to coral reefs), pollution, destructive fishing using dynamite and cyanide, impacts from shipping, and the overexploitation of key fisheries species (Bryant, 1998; Halpern et al., 2008). These factors have played a dominant role in the the destruction of coral reefs, with the role of climate change being relegated to a secondary and long-term threat. Evidence over the past decade (reviewed by Hoegh-Guldberg et al., 2007), however, reveals that climate change has already affected reefs heavily, and that current trends in the warming and acidification of the oceans will almost certainly destroy coral reefs unless we take action to reduce greenhouse gas emissions.

Impacts of Global Warming

The atmospheric concentration of carbon dioxide in the earth's atmosphere now exceeds 390 parts per million, which is approximately 100 parts per million higher than the maximal values seen over the past 740,000 years (Petit et al., 1999; Augustin et al., 2004), if not 20 million years (Raven et al., 2005). These changes have driven the average temperature of the ocean up by 0.74 degree Celsius and sea levels by 17 centimeters (7 inches) (IPCC, 2007). Second-order effects have also begun to occur, with evidence of shifting patterns of rainfall, drought, and storm intensity across the tropics leading to complex changes in the conditions surrounding natural ecosystems (Walther et al., 2002; IPCC, 2007).

Even though these changes appear subtle, they have already had a huge impact on coral reef ecosystems. Reef-building corals form intimate mutualistic endosymbioses (in which one organism lives inside the cells of another) with tiny plantlike organisms called dinoflagellates from the genus *Symbiodinium*. The partnership that corals form with these primary producers enables the symbiosis to trap large amounts of solar energy, allowing corals access to an abundant source of energy. As a result of this rich source of photosynthetic energy, reef-building corals are able to precipitate copious quantities of calcium carbonate, which ultimately lead to the formation of the three-dimensional framework of coral reefs (Muscatine, 1990).

The symbiosis between *Symbiodinium* and corals is relatively stable within the normal range of environmental variability. When conditions change too rapidly, or exceed the natural range of environmental

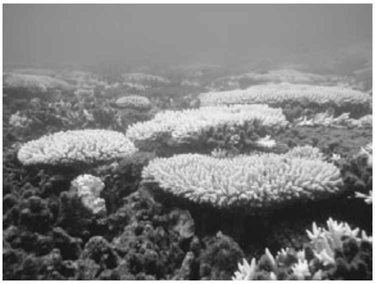

FIGURE 15-1. Small increases in sea temperature can destabilize the symbiosis between reef-building corals and their dinoflagellate symbionts (*Symbiodinium*). A mass bleaching event that affected more than 60 percent of the Great Barrier Reef occurred in 2002, leading to the death of about 5–10 percent of reef-building corals within the Great Barrier Reef Marine Park. Photo: O. Hoegh-Guldberg.

variability, the symbiosis breaks down, with the brown *Symbiodinium* moving rapidly out of the tissues of the coral host (fig. 15-1). This phenomenon is referred to as coral bleaching (Hoegh-Guldberg, 1999). In the early 1980s, coral reefs around the world began to bleach across large areas of the tropics (Glynn, 1983; Lasker et al., 1984; Roberts, 1987), with no precedent in the scientific literature. Work over a number of years revealed that these mass bleaching events were being driven by small increases in sea temperature (Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; Strong et al., 1996) above the summer maximal temperatures for a particular region. This led some to speculate on whether this was connected to climate change (Glynn et al., 1988). These early suspicions were eventually confirmed, with projections of how sea temperature would change under greenhouse forcing revealing that future conditions were likely to be extremely hostile to coral communities (Hoegh-Guldberg, 1999).

Ocean Acidification and Marine Calcification

The increase in atmospheric carbon dioxide has resulted in a greater amount of carbon dioxide entering the world's oceans (fig. 15-2A). When carbon dioxide enters the ocean, it reacts with water to produce a weak acid, carbonic acid. Carbonic acid dissociates producing a bicarbonate ion and a proton, the latter of which reacts with carbonate

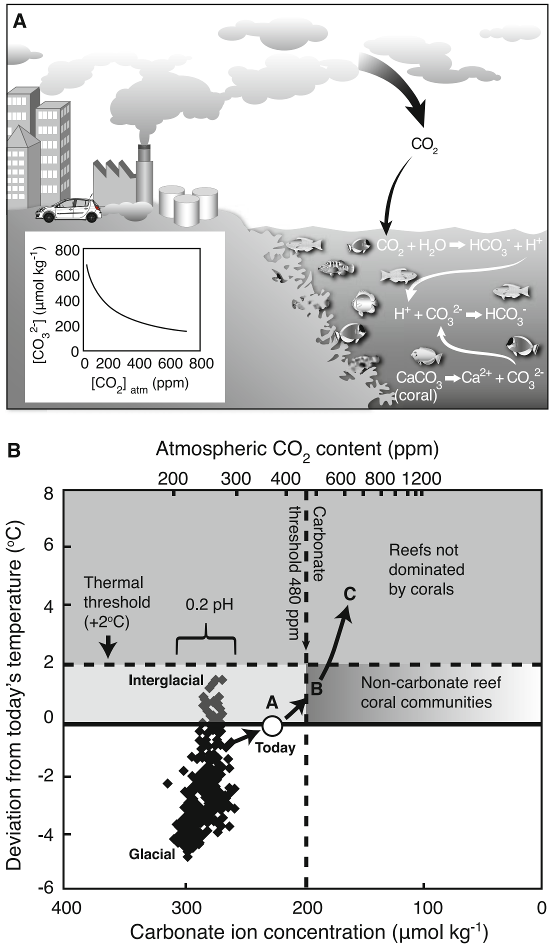

FIGURE 15-2. (A) Ocean acidification is occurring due to the increased amount of carbon dioxide that is entering the ocean. In the ocean, carbon dioxide combines with water to create carbonic acid, which releases a proton that reacts in turn with carbonate ions. The net effect of this is that rising atmospheric carbon dioxide has driven down the concentration of carbonate ions in the ocean. This has already slowed the calcification of corals by around 15 percent since 1990. (B) Reconstruction of the temperature and carbonate ion concentrations of a typical tropical ocean over the past 420,000 years (reconstructed using data from the Vostok ice core series, Petit et al. 1999. See Hoegh-Guldberg et al. 2007 for a full explanation of the methods). Three important features are shown: (i) Present-day values are outside the conditions seen over at least the past 420,000 years. (ii) Rates of change dwarf anything seen over the same period. (iii) Two thresholds, one with temperature and the other with carbonate ion concentrations, will be crossed within the next 40 years. Figures 15-2 and 15-3 reprinted from Hoegh-Guldberg et al. (2007) with permission from *Science Magazine*.

ions, producing bicarbonate and consequently reducing their concentration and availability. The net effect of increasing carbon dioxide in the atmosphere is that it causes a precipitous drop in the concentration of carbonate ions (Raven et al., 2005).

These changes in the concentration of carbonate ions have huge implications for organisms such as corals that precipitate calcium carbonate. A doubling of the concentration of atmospheric carbon dioxide, for example, results in a decrease in the calcification rate of 15–45 percent across a wide range of marine calcifiers such as red calcareous algae to reef-building corals (Kleypas and Langdon, 2006). These changes are now being reported from corals in the field, with studies done on the Great Barrier Reef (De'ath et al., 2009) reporting an unprecedented decrease in calcification of corals in both regions by 15 percent when compared to 1990. Similar observations have been made for corals in Thailand (Tanzil et al., 2009). Given that reef structures are a delicate balance between calcification on one hand and physical and biological erosion on the other, these changes in the calcification rate have the potential to decrease the calcification rate of corals and other calficiers below that required to maintain the carbonate structures of coral reefs (Hoegh-Guldberg et al., 2007). A direct implication of this is that coral reefs will soon reach a point where they are likely to erode and dissolve (Silverman et al., 2009).

When the current geographic distribution of carbonate coral reefs is plotted relative to the aragonite saturation state of seawater, it is clear that coral reefs require a certain concentration of calcium and carbonate ions to calcify at the rate required to maintain coral reefs. The aragonite saturation constant ($\Omega_{aragonite}$) is the ratio of the calcium and carbonate ion concentrations relative to the solubility product of aragonite (the crystal form of calcium carbonate that corals preferentially deposit in their skeletons). Figure 15-3 illustrates how changing the carbon dioxide concentration will essentially shrink the distribution of areas where water contains enough calcium and carbonate for the formation of carbonate coral reefs (i.e., have aragonite saturation in excess of 3.3) to a small band around the equator (at atmospheric carbon dioxide concentrations of 450 parts per million). These conditions are largely eliminated when concentrations rise to 550 parts per million or more. This modelling study illustrates the extreme sensitivity of carbonate coral reef ecosystems to the atmospheric concentration of carbon dioxide (Hoegh-Guldberg et al., 2007).

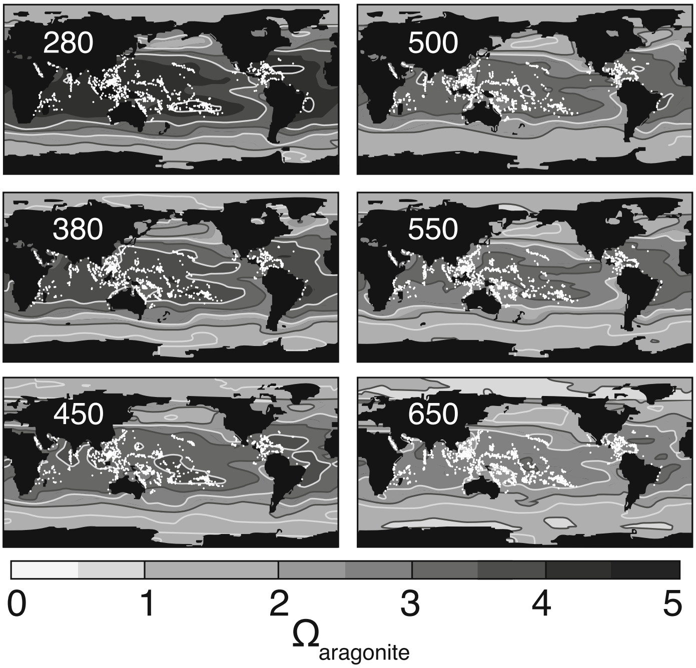

FIGURE 15-3. Distribution of carbonate coral reefs (white dots) relative to the aragonite saturation ($\Omega_{aragonite} = [Ca^{2+}].[CO_3^{2-}]$/Ksp aragonite) calculated for different atmospheric concentrations of carbon dioxide (white number in each box). The aragonite saturation is a measure of the concentration of calcium and carbonate ions relative to solubility of aragonite (the chief form of calcium carbonate deposited by corals and other marine calcifiers). The distribution of today's coral reefs relative to the current aragonite saturation is shown in the panel labeled 380, revealing the association of carbonate coral reefs with waters that have an aragonite saturation of more than 3.3 (darker gray areas). As atmospheric carbon dioxide increases, the distribution of these waters contracts to the equator and more or less disappears when concentrations of atmospheric carbon dioxide rise above 550 parts per million.

Sea-Level Rise and Other Factors

Global sea level is currently rising at the rate of 3.3 millimeters (0.13 inch) per year, and sea level is conservatively expected to rise between 11 and 77 centimeters (4 and 30 inches) by the end of the century (IPCC, 2007). These estimates of sea-level rise are widely considered to be conservative, especially in the light of the recent rapid decreases in land-locked glacial and polar ice mass in Greenland (Cressey, 2007; Steffensen et al., 2008; Zhang et al., 2008) and Antarctica (Barnes and Peck 2008). Under conditions where coral growth is maximal, coral reefs are able to keep pace with comparatively high rates of sea-level rise (Douglas et al., 2000), although this may mean that reef growth may "back-step" in cases of catastrophic rises such as that seen 121,000 years ago (Blanchon et al., 2009). In past periods of rapid sea-level change, corals have been healthy due to the relatively small or nonexistent impact of humans. These assumptions may be invalidated today, when sea-level rise is being accompanied by highly stressful sea temperatures and acidities that are likely to dramatically slow the growth of corals and coral reefs, thereby presenting the specter of deteriorating reefs that "drown" as sea level rises.

There are a large number of other factors that will influence the health of coral reefs into the future. Warmer sea temperatures will drive more intense storm activity (Webster et al., 2005), leading to greater damage to some coral reefs, which when coupled with slowing growth and reduced coral survivorship, may mean that the balance is tipped away from coral-dominated reefs to reefs that are substantially different.

Prognosis for the Future of Coral Reefs

In exploring the future of coral reefs, it is instructive to look at the conditions that coral reefs have experienced over the past several hundred thousand years. This type of analysis allows one to understand the range of variability in the past relative to the conditions projected to occur in the future. We recently analyzed (Hoegh-Guldberg et al., 2007) sea temperature (from proxies) and carbonate ion concentrations (from carbon dioxide concentrations) for typical coral reef environments over the past 420,000 years using measurements of ancient atmospheric carbon dioxide and global temperatures derived from the Vostok ice core data series (Petit et al., 1999). This analysis revealed that the key conditions for coral reefs (i.e., temperature and carbonate ion concentration; Kleypas et al., 1999) varied significantly over the past 420,000 years (fig. 15-2) but that current conditions on coral reefs were well outside the envelope in which this variability had occurred. Perhaps even more significant is that fact that the changes that are occuring over decade and century timescales today used to occur over thousands of years in the past (Hoegh-Guldberg et al., 2007).

The trajectory that coral reefs are currently on is rapidly approaching two significant thresholds (fig. 15-2B). The first occurs when tropical seas become 2 degrees Celsius warmer than they were prior to the Industrial Revolution, a condition that we know will cause unsustainable coral bleaching and mortality on an annual basis. The second, which occurs more or less simultaneously, is that oceans will be acidified to the point where they will have carbonate ion concentrations of less than 200 micromoles per kilogram of water. Both field and laboratory studies reveal that the latter is around the point at which coral calcification struggles to keep up with erosion, and hence maintain carbonate reef structures. As a result, many of these all-important structures will crumble and slowly disappear. Hopefully, decisive and effective action to reduce emissions of carbon dioxide will stabilize and eventually reverse the upward trend in atmospheric carbon dioxide.

As a final point in this discussion, it is instructive to consider how coral communities will change over the coming decades. The very rapid rate of rise in atmospheric carbon dioxide is already driving periodic mass mortality events and a slowing of reef calcification. Given that not all corals have the same sensitivity to thermal stress (Hoegh-Guldberg and Salvat, 1995; Marshall and Baird, 2000; Loya et al. 2001; McClanahan, 2007) or even reduced carbonate concentrations (Kleypas and Langdon, 2006), some are likely to be more persistent than others as conditions change. For this reason, massive and encrusting corals (e.g., *Porites, Favia*) may be more prominent on future reefs than branching corals (e.g., *Acropora, Stylophora*), leading to changes in the community structure of reef-building corals and the extinction of some branching coral species. Naturally, given that even these tougher species have their limits, reefs will eventually become largely devoid of corals as ocean temperatures and acidities continue to rise.

These futures are not distant. Three decades ago, the potential extinction of a reef-building coral species would have been unthinkable given the stability of tropical environments and the vast geographic distributions of most species (Veron and Stafford-Smith, 2000). In 2004, however, the US National Marine Fisheries Service received a request from the Center for Biological Diversity to place the Caribbean species of *Acropora* (*Acropora palmata* and *Acropora cervicornis*) on the US Endangered Species list on account of the precipitous decrease in the distribution and abundance of these once dominant coral species. This was finally granted on May 4, 2006. Although the circumstances of a restricted and highly stressed ocean basin such as the Caribbean probably predispose coral species in the Caribbean to extinction (when compared to the vast, moderately stressed Pacific ocean), the listing of these two species represented a wake-up call for coral reef biologists and conservations, who may have been concerned about the loss of functional coral reefs as opposed to the extinction of coral species (Bruckner et al., 2002; Precht et al., 2002; Precht et al., 2004). According to Carpenter (2008), almost one-third of coral species are vulnerable to extinction by climate change and local threatening processes.

The Fate of Coral Reef–Associated Organisms

Rapid changes in the environmental factors associated with climate change, such as sea temperature and acidity, are likely to eliminate coral-dominated reefs (fig. 15-4A) and transform them into vastly different systems that are occupied by very different organisms such as seaweeds. Today, there are a growing number of examples that illustrate what these ecosystems might look like in the future. For example, many areas across the Caribbean have lost almost all of their coral-dominated reefs, leaving behind communities that are vastly different from those of 50 years ago. Naturally occurring coral reefs at high latitudes also give us clues as to what future communities might look like. These areas, like those of the southwest Australia (fig. 15-4B), typically have lower coral cover, which does not contribute enough calcium carbonate to maintain significant reef frameworks. This situation will expand in warmer, more acidic seas, however, with carbonate reef structures beginning to crumble and disappear, as is already happening in some heavily affected areas (fig. 15-4C). As a result of these changes, ecological processes and resources will change radically, leading to changes in the species composition of the organisms that associate with these new reef communities and structures. With this change comes the question of what happens to all the other species that normally associate with coral reefs. Perhaps surprisingly, this question has not been answered adequately for anything more than reef fish at this point. This said, there are a number of "commonsense rules" that appear to apply in terms of which species on the coral reef are more sensitive to global change than others.

A

B

C

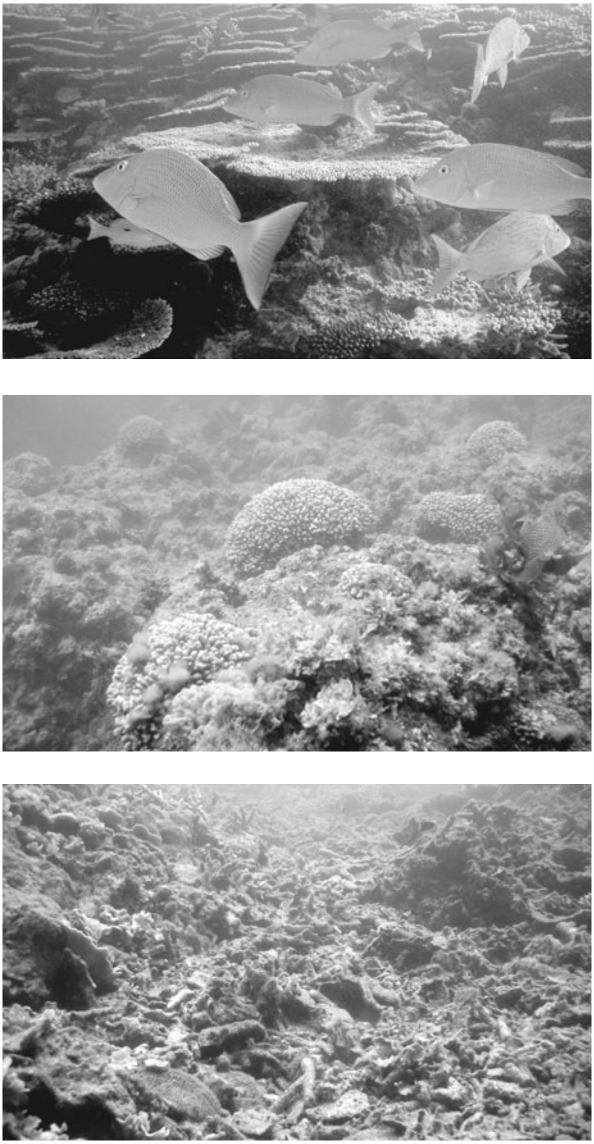

Figure 15-4. Coral reefs are sensitive to climate change. (A) Healthy coral-dominated reef on the Great Barrier Reef in Australia; (B) high-latitude coral reef of Jurien Bay, western Australia, and (C) heavily impacted reef in Karimunjawa, Indonesia, showing the devastated reef framework and dead coral. Photos: O. Hoegh-Guldberg.

Returning to table 15-1, we see that a high level of habitat specificity is associated with increased vulnerability to extinction. This characteristic varies quite significantly across the various organisms that occupy coral reefs. Some organisms have highly specific requirements for habitat and will not be found on reefs that no longer have that habitat. For example, many butterfly fish (Chaetodontidae) require living colonies of corals from the family Acroporidae as habitat for recruitment, protection from predators, and as food (fig. 15-5A). These species tend not to be found on reefs where corals such as *Acroporid* corals have disappeared or are naturally absent (Pratchett et al., 2006). On the other hand, fish such as surgeon fish (fig. 15-5B), scarids, and siganids appear to be somewhat independent or even positively correlated with the loss of coral (Wilson et al., 2008). In this case, the fish involved do not have to eat coral (if they do at all), and have ecological requirements that don't require corals to be present. Not surprisingly, these fish are often found in areas within coral reefs that often do not have high levels of coral cover (e.g., inshore and back-reef areas).

The general principles underlying which species are more vulnerable appear to apply across the board for fish on coral reefs. Wilson and colleagues (2008) visited twenty-one sites across the Indo-Pacific that had been affected by coral bleaching, mass coral bleaching, and other stresses, and which had recovered to varying extents. Using this information, they related fish community composition to the amount of coral cover at the various sites. Fish that were highly tied to coral declined dramatically, while fish that were either omnivorous or herbivorous (and had no specific requirements for coral) did not change or increased (fig. 15-6). Often in these cases, the supply of grazing surfaces and provision of a place to hide from predators will be sufficient. However, one has to be careful with assumptions based on the apparent requirements of the adult phase given that specific requirements can arise in the juvenile stages which are not met by the adult habitat. Munday et al. (2004) has also pointed out that specialist species are far more vulnerable than generalist species, not only because they are specific in their requirements by definition, but they are often in lower abundance and distributed more patchily. Roberts and Hawkins (1999) identified both of these as characteristics conferring vulnerability to extinction (table 15-1). Understanding the direction of change in terms of which species will become vulnerable to extinction will require careful consideration of the full set of ecological requirements of any particular species or group of organisms.

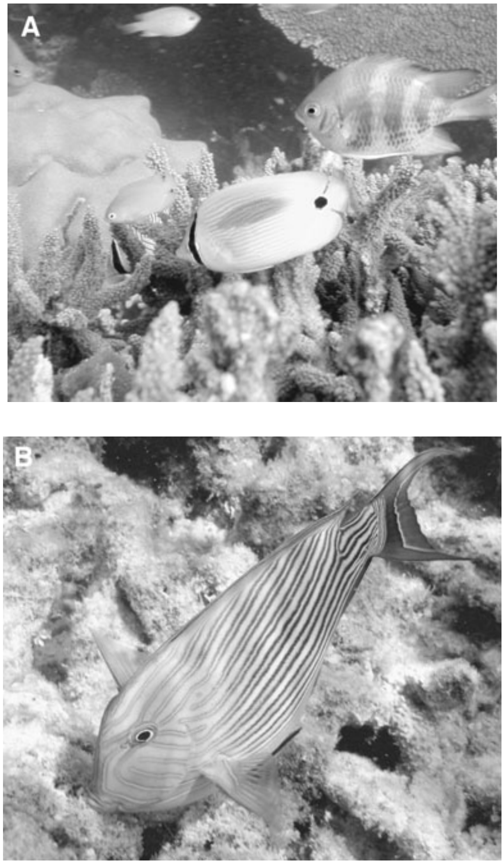

FIGURE 15-5. Coral fish show a broad range of associations with coral communities, from those that are obligatory to those that are not. The requirement for coral may affect their extinction vulnerability. (A) The butterfly fish, *Chaetodon plebius,* has an obligatory relationship with *Acroporid* corals—eating, recruiting into, and hiding among them. (B) Generalists such as the herbivorous surgeon fish, *Acanthurus lineatus,* have a far more facultative relationship with corals, and may show increases in abundance when coral cover decreases. Photos: O. Hoegh-Guldberg.

There is probably little doubt that similar results would be obtained for coral-dependent invertebrates and the many other organisms that associate with coral reefs. Information beyond that about fish and corals, however, is extremely limited (Przeslawski et al., 2008). Several previous studies have focused on benthic crustacea associated with living coral colonies. These studies have revealed that the species composition of decapod crustacea (shrimps and crabs)

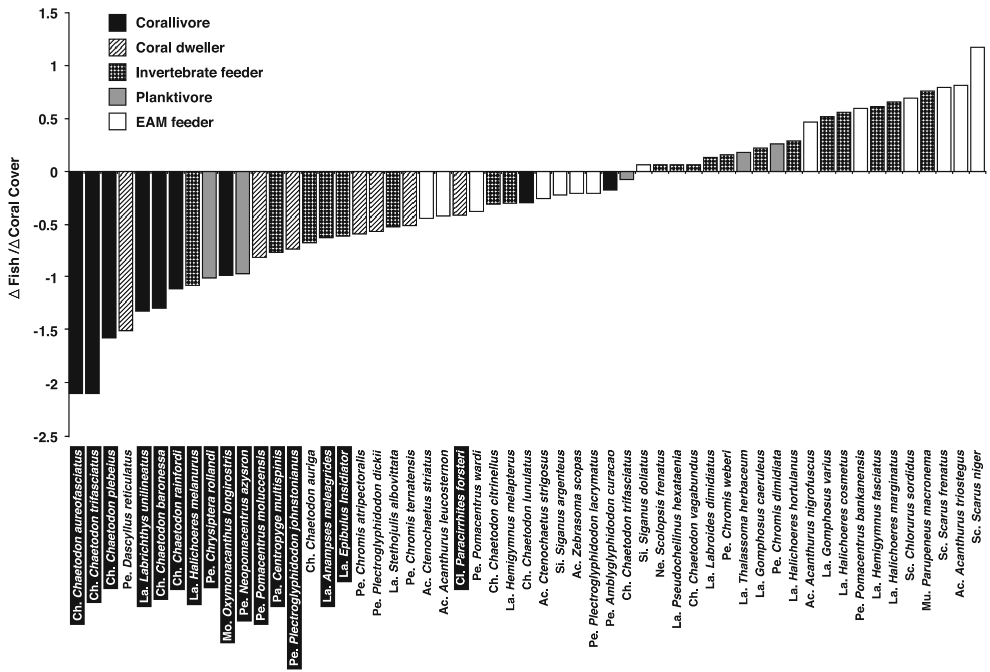

Figure 15-6. Response of coral fish species to a decline in coral cover measured for Indo-Pacific coral reefs. Bars that drop below the *x*-axis represent fish whose abundance decreased as coral cover decreased, while those above the *x*-axis represent fish species that increase their abundance in situations of low coral cover. Key ecological characteristics of each fish species are depicted by different patterns on the bars. Species names in black indicate differences to zero (95% confidence intervals). EAM = epilithic algal matrix. Reprinted with permission of Blackwell Publishing Ltd.

responds to the coral colony size, the surrounding habitat, and behavioral interactions between species (Abele and Patton, 1976; Black and Prince, 1983; Gotelli et al., 1985). When the host coral colony dies, the infaunal community shifts from a dominance of predominantly symbiotic species to small facultatively associated normal symbionts (Coles, 1980; Glynn, 1993). Preston and Doherty (1990) analyzed the agile shrimp fauna living in live and dead colonies of a single species of reef-building coral, *Pocillopora verrucosa,* on the central Great Barrier Reef in Australia. Their study highlights the potentially enormous diversity of coral-dependent organisms, with the identification of more than twenty species of coral-dwelling shrimp that regularly inhabited colonies of *P. verrucosa,* with three species being coral specialists (obligates). Clearly this complexity within complexity is just the tip of the iceberg with a very clear message that the loss of corals and the structures that they build are very clear threats to a poorly known yet sizable component of marine biodiversity.

Until advances are made in the taxonomy of the multitude of species that live in and around coral reefs, estimates of the number of species that are highly vulnerable to extinction through the loss of coral-dominated reef systems will be speculative at best. However, one might list the following characteristics of coral reef species that would make them a high risk for extinction.

- Obligatory dietary requirement for coral or coral-dependent organisms. Many fish and invertebrates depend on living coral as part of their diets. The loss of corals as a food source would directly threaten these organisms with extinction (Moran, 1986; Rinkevich et al., 1991; Turner, 1994; Graham et al., 2007; Pratchett et al., 2008; Wilson et al., 2008).
- Commitment to a settlement cue that is dependent on coral or involves a requirement for live coral by new recruits. This is widespread on coral reefs with highly specific settlement preferences (Sale et al., 1984; Feary et al., 2007) and often involves homing in on particular coral species or genera (Gotelli and Abele, 1983; Gotelli et al., 1985; Öhman et al., 1998).
- Requirement for complex three-dimensional reef structure to hide from predators. Many organisms on coral reefs require their three-dimensional structures, which provide a complex set of hiding places for coral reef organisms (Pratchett et al., 2008). Where corals have disappeared due to human stresses

(fig. 15-5C) or storms, much of this three-dimensional topology and complexity also disappears.

- Need for close spacing of coral habitat to be able to access mates. Although corals can reproduce asexually by fragmentation (Highsmith, 1982; McKinney, 1983), and could theoretically exist for centuries without undergoing sexual reproduction, many organisms require access to the opposite sex. In order to be able to persist, these organisms require coral colonies to be within close proximity to each other to have access to mates (Abele and Patton, 1976; Black and Prince, 1983; Gotelli et al., 1985; Roberts and Hawkins, 1999; Cowen et al., 2000; Sale, 2002; Cowen et al., 2006).

The shaping of coral reef ecosystems by reef-building corals necessarily dictates that many species are dependent on the health and presence of these organisms. Although similar relationships hold for other marine communities such as rocky shores, kelp forests, and sea-grass beds, the sheer number of species involved in coral reefs (i.e., 1 million–9 million species) means that the projected loss of corals and the reef structures due to climate change will have huge consequences for tropical and indeed global biodiversity.

Species Extinction Versus Functional Extinction

As pointed out earlier, the phrase "extinction of coral reefs" is used frequently in both public and academic discourse as part of the concern for the future of coral reefs with rapid climate change. The phrase implies that coral reefs and the species that live on them will disappear if we continue down the current enhanced greenhouse pathway. Many coral reef organisms, however, have characteristics that make them relatively invulnerable to extinction. This suggests that many coral reef organisms will survive even if coral reefs as the functional ecosystem do not. What will be fascinating (though disturbing) for future generations of biologists is how these new assemblages will take shape and function. Beyond this, the functional extinction of coral reef ecosystems remains a serious crisis for humanity. Coral reef ecosystems support enormous numbers of relatively disadvantaged people living along tropical coastlines through the provision of subsistence food sources, income, and coastal protection. The loss of functional coral reef ecosystems represents a severe threat to these people and their societies. It is hoped that there will be a global commitment not to let this disturbing future unfold.

REFERENCES

Abele, L., Patton, W. 1976. "The size of coral heads and the community biology of associated decapod crustaceans." *Journal of Biogeography* 3: 35–47.

Augustin, L., Barbante, C., Barnes, P. R. F., Barnola, J. M, Bigler, M., Castellano, E., Cattani, O., et al. 2004. "Eight glacial cycles from an Antarctic ice core." *Nature* 429: 623–628.

Barnes, D. K. A., Peck, L. S. 2008. "Vulnerability of Antarctic shelf biodiversity to predicted regional warming." *Climate Research* 37: 149–163.

Black, R., Prince, J. 1983. "Fauna associated with the coral *Pocillopora damicornis* at the southern limit of its distribution in Western Australia." *Journal of Biogeography* 10: 135–152.

Blanchon, P., Eisenhauer, A., Fietzke, J., Liebetrau, V. 2009. "Rapid sea-level rise and reef back-stepping at the close of the last interglacial highstand." *Nature* 458: 881–884.

Bruckner, A., Hourigan, T., Moosa, M., Soemodihardjo, S., Soegiarto, A., Romimohtarto, K., Nontji, A., and Suharsono, S. 2002. "Proactive management for conservation of *Acropora cervicornis* and *Acropora palmate*: Application of the U.S. Endangered Species Act." *Proceedings of the Ninth International Coral Reef Symposium* 2: 661–665; Bali, 23–27 October 2000.

Bruno, J. F., Selig, E. R. 2007. "Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons." *PLoS ONE* 2: e711.

Bryant, D. 1998. *Reefs at Risk: A Map-Based Indicator of Threats to the World's Coral Reefs*. Washington, D.C.: World Resources Institute.

Carpenter, K., Abrar, M., Aeby, G., Aronson, R., Banks, S., Bruckner, A., Chiriboga, A., et al. 2008. "One-third of reef-building corals face elevated extinction risk from climate change and local impacts." *Science* 321: 560–563.

Coles, S. 1980. "Species diversity of decapods associated with living and dead reef coral *Pocillopora meandrina*." *Marine Ecology Progress Series* 2: 281–291.

Cowen, R., Lwiza, K., Sponaugle, S., Paris, C., Olson, D. 2000. "Connectivity of marine populations: Open or closed?" *Science* 287: 857.

Cowen, R., Paris, C., Srinivasan, A. 2006. "Scaling of connectivity in marine populations." *Science* 311: 522.

Cressey, D. 2007. "Arctic melt opens Northwest passage." *Nature* 449: 267.

De'ath, G., Lough, J. M., Fabricius, K. E. 2009. "Declining coral calcification on the Great Barrier Reef." *Science* 323: 116–119.

Douglas, B., Kearney, M., Leatherman, S. 2000. *Sea Level Rise: History and Consequences*. International Geophysics Series, Vol. 75. New York: Academic Press.

Feary, D., Almany, G., Jones, G., McCormick, M. 2007. "Coral degradation and the structure of tropical reef fish communities." *Marine Ecology Progress Series* 333: 243–248.

Glynn, P. 1993. "Coral reef bleaching: Ecological perspectives." *Coral Reefs* 12: 1–17.

Glynn, P. W. 1983. "Extensive bleaching and death of reef corals on the Pacific coast of Panama." *Environmental Conservation* 10: 149–154.

Glynn, P. W., D'Croz, L. 1990. "Experimental-evidence for high-temperature stress as the cause of El-Niño-coincident coral mortality." *Coral Reefs* 8: 181–191.

Glynn, P. W., Cortes, J., Guzman, H. M., Richmond, R. H. 1988. "El Niño (1982–1983) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific." In *Proceedings of the Sixth International Coral Reef Symposium,* edited by J. H. Choat, et al., 237–243. Townsville, Australia: 6th International Coral Reef Symposium Executive Committee. Vol. 11.

Gotelli, N., Abele, L. 1983. "Community patterns of coral-associated decapods." *Marine Ecology Progress Series. Oldendorf* 13: 131–139.

Gotelli, N., Gilchrist, S., Abele, L. 1985. "Population biology of *Trapezia* spp. and other coral-associated decapods." *Marine Ecology Progress Series. Oldendorf* 21: 89–98.

Graham, N. A., Wilson, S. K., Jennings, S., Polunin, N. V., Robinson, J., Bijoux, J. P., Daw, T. M. 2007. "Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems." *Conservation Biology* 21: 1291–1300.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., et al. 2008. "A global map of human impact on marine ecosystems." *Science* 319: 948–952.

Highsmith, R. 1982. "Reproduction by fragmentation in corals." *Marine Ecology Progress Series. Oldendorf* 7: 207–226.

Hoegh-Guldberg, O. 1999. "Climate change, coral bleaching and the future of the world's coral reefs." *Marine and Freshwater Research* 50: 839–866.

Hoegh-Guldberg, O., Salvat, B. 1995. "Periodic mass-bleaching and elevated sea temperatures—bleaching of outer reef slope communities in Moorea, French-Polynesia." *Marine Ecology Progress Series* 121: 181–190.

Hoegh-Guldberg, O., Smith, G. J. 1989. "The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* and *Seriatopra hystrix*." *Journal of Experimental Marine Biology and Ecology* 129: 279–303.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., et al. 2007. "Coral reefs under rapid climate change and ocean acidification." *Science* 318(5857): 1737–1742.

IPCC. 2007. *Synthesis Report*. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Kleypas, J. A., Langdon, C. 2006. "Coral reefs and changing seawater chemistry." In *Coral Reefs and Climate Change: Science and Management. AGU Monograph Series, Coastal and Estuarine Studies,* vol. 61, edited by Phinney, J., Hoegh-Guldberg, O., Kleypas, J., Skirving, W., and Strong, A. E., 73–110. Washington, D.C.: Geophysical Union.

Kleypas, J. A., McManus, J. W., Menez, L. A. B. 1999. "Environmental limits to coral reef development: Where do we draw the line?" *American Zoologist* 39: 146–159.

Lasker, H., Peters, E., Coffroth, M. 1984. "Bleaching of reef coelenterates in the San Blas Islands, Panama." *Coral Reefs* 3: 183–190.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., van Woesik, R. 2001. "Coral bleaching: The winners and the losers." *Ecology Letters* 4: 122–131.

Marshall, P. A., Baird, A. H. 2000. "Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa." *Coral Reefs* 19: 155–163.

McClanahan, T. R. 2007. "Western Indian Ocean coral communities: Bleaching responses and susceptibility to extinction." *Marine Ecology Progress Series* 337: 1–13.

McKinney, F. 1983. "Asexual colony multiplication by fragmentation: An important mode of genetic longevity in the Carboniferous bryozoan *Archimedes*." *Paleobiology* 9 (1): 35–43.

Moran, P. 1986. "The *Acanthaster* phenomenon." *Oceanography and Marine Biology* 24: 379–480.

Munday, P., Jones, G., Sheaves, M., Williams, A., Goby, G. 2007. "Vulnerability of fishes of the Great Barrier Reef to climate change." *Climate Change and the Great Barrier Reef* 357–391.

Muscatine, L. 1990. "The role of symbiotic algae in carbon and energy flux in reef corals." In *Ecosystems of the World*, vol. 24, *Coral Reefs*, edited by Z. Dubinsky, 75–87. Amsterdam: Elsevier.

Öhman, M., Munday, P., Jones, G., Caley, M. 1998. "Settlement strategies and distribution patterns of coral-reef fishes." *Journal of Experimental Marine Biology and Ecology* 225: 219–238.

Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J. M., Basile, I., Bender, M., et al. 1999. "Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica." *Nature* 399: 429–436.

Pratchett, M., Wilson, S., Baird, A. 2006. "Declines in the abundance of *Chaetodon* butterflyfishes following extensive coral depletion." *Journal of Fish Biology* 69: 1269–1280.

Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinnerm, J. E., Bellwood, D. R., Jones, G. P., Polunin, N. V. C., McClanahan, T. R. 2008.

"Effects of climate-induced coral bleaching on coral-reef fishes—Ecological and economic consequences." *Oceanography and Marine Biology: An Annual Review* 46: 251–296.

Precht, W., Bruckner, A., Aronson, R., Bruckner, R. 2002. "Endangered acroporid corals of the Caribbean." *Coral Reefs* 21: 41–42.

Precht, W., Robbart, M., Aronson, R. 2004. "The potential listing of *Acropora* species under the US Endangered Species Act." *Marine Pollution Bulletin* 49: 534–536.

Preston, N., Doherty, P. 1990. "Cross-shelf patterns in the community structure of coral dwelling Crustacea in the central region of the Great Barrier Reef. 1. Agile shrimps." *Marine Ecology Progress Series* 66: 47–61.

Przeslawski, R., Ahyong, S., Byrne, M., Worheide, G., Hutchings, P. 2008. "Beyond corals and fish: The effects of climate change on noncoral benthic invertebrates of tropical reefs." *Global Change Biology* 14: 2773–2795.

Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J., Turley, C., Watson, A. 2005. *Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide*. London: Royal Society.

Rinkevich, B., Wolodarsky, Z., Loya, Y. 1991. "Coral-crab association: A compact domain of a multilevel trophic system." *Hydrobiologia* 216: 279–284.

Roberts, C., Hawkins, J. 1999. "Extinction risk in the sea." *Trends in Ecology and Evolution* 14: 241–246.

Roberts, C., Ormond, R. 1987. "Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs." *Marine Ecology Progress Series. Oldendorf* 41: 1–8.

Roberts, L. 1987. "Coral bleaching threatens Atlantic reefs: Unexplained changes are occurring in some of the most productive ecosystems on the planet, the Caribbean coral reefs." *Science* 238: 1228–1229.

Sale, P., Douglas, W., Doherty, P. 1984. "Choice of microhabitats by coral reef fishes at settlement." *Coral Reefs* 3: 91–99.

Sale, P. F. 2002. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. San Diego: Academic Press.

Silverman, J., Lazar, B., Cao, L., Caldeira, K., Erez, J. 2009. "Coral reefs may start dissolving when atmospheric CO_2 doubles." *Geophysical Research Letters* 36: L05606, doi:05610.01029/02008GL036282.

Steffensen, J. P., Andersen, K. K., Bigler, M., Clausen, H. B., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., et al. 2008. "High-resolution Greenland ice core data show abrupt climate change happens in few years." *Science* 321: 680–684.

Strong, A. E., Barrientos, C. S., Duda, C., Sapper, J. 1996. "Improved satellite technique for monitoring coral reef bleaching." *Proceedings of the Eighth International Coral Reef Symposium*, Panama, 1495–1497.

Tanzil, J., Brown, B., Tudhope, A., Dunne, R. 2009. "Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005." *Coral Reefs* doi:10.1007/s00338-008-0457-5.

Turner, S. 1994. "The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs." *Oceanography and Marine Biology* 32: 461–530.

Veron, J. E. N., Stafford-Smith, M. 2000. *Corals of the World*. Townsville, Queensland: Australian Institute of Marine Science.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J. M., Hoegh-Guldberg, O., Bairlein, F. 2002. "Ecological responses to recent climate change." *Nature* 416: 389–395.

Webster, P. J., Holland, G. J., Curry, J. A., Chang, H. R. 2005. "Changes in tropical cyclone number, duration, and intensity in a warming environment." *Science* 309: 1844–1846.

Wilson, S. K. 2006. "Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient?" *Global Change Biology* 12: 2220–2234.

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. C., Sweatman, H. P. A. 2008. "Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing environment." *Journal of Animal Ecology* 77: 220–228.

Zhang, J., Lindsay, R., Steele, M., Schweiger, A. 2008. "What drove the dramatic retreat of arctic sea ice during summer 2007?" *Geophysical Research Letters* 35: L11505, doi:11510.11029/12008GL034005.