12. Constraints on Predicting Coral Reef Response to Climate Change

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12.1 Introduction and Caveats

Over the last two decades, a primary concern within coral reef science has been the fate of coral reefs in an environment significantly altered by both direct anthropogenic impacts at the regional scale and indirect impacts associated with changes in Earth's atmospheric chemistry. Regional impacts, such as destructive fishing, deforestation, and nutrient loading, can greatly degrade reefs over very short time periods, but in many cases it should be possible to engineer solutions to these problems through mitigative practices such as the formation of marine parks, establishment of fishing regulations, runoff control, etc. The global impacts of greenhouse gas emissions on coral reefs are much more difficult to understand and mitigate. However, unless there are drastic changes in the fossil fuel-based world economy and politics, or engineering breakthroughs that either reduce our dependence on fossil fuels or sequester fossil fuel emissions, atmospheric CO_2 concentration will increase to double the preindustrial concentration by the middle of this century, and other greenhouse gases (CH_4, N_2O, H_2O) will also increase (Houghton et al. 2001). A great challenge within coral reef science is to assess how coral reefs will respond to warmer, more acidic oceanic conditions. This chapter addresses two major global threats facing coral reefs today—increased water temperatures and changing seawater chemistry—by systematically examining current predictions of (1) environmental change, (2) the response of coral reefs to that environmental change, and (3) the likely long-term implications of the response.

Making a reasonable prediction of what will happen to reefs in the future requires knowledge of what future environmental conditions will be like and the rate that future conditions will change, and the response of reef-building organisms to such changes. Unfortunately, neither of these is well constrained, and predictions must be based on analogues, experiments which simulate the environmental change, or modeling efforts. Usually, predictions of future environmental conditions are based on mathematical models, and predictions of organism and community response to these conditions are based on analogues. Although some information about an organism's response to environmental change can also be derived from knowledge of its biochemistry and genetic makeup, this chapter focuses on information obtained from the geologic record of reefs and from climate modeling.

The best way to predict how an ecosystem will respond to environmental change is to look in both space and time for areas or periods with environmental conditions similar to those projected for the future. For example, as a first approximation and based on present-day distributions of ecosystems, ecologists assume that global warming will cause species to migrate poleward in parallel with shifts in ideal temperature regimes, and ecosystems, as a result, to be dismantled to some degree, although the exact nature of that shift is complicated by other environmental and ecological changes (e.g., precipitation, ocean currents, biotic interactions, substrate availability). However, predicting how and in what configuration coral reefs and other tropical ecosystems will migrate in response to global warming is complicated because while the distributions of these ecosystems reflect their lower thermal limits, they do not necessarily reflect their upper thermal limits (because they occur throughout the tropics). If one assumes that coral reef development at higher latitudes is limited by minimum water temperature (and this assumption may not be entirely correct; see Section 12.4), then coral reef ecosystems are likely to expand into higher latitudes. But will reefs also be eliminated from regions that are already near their upper thermal limits? Certainly the geographically extensive mass coral bleaching episodes of the last two decades indicate that reefs are limited by rapid elevation of the normal maximum monthly temperature, but there is little evidence that maximum temperature limits the present-day distribution of coral reefs (Fig. 12.1).

When environmental conditions exceed those that shaped the current ecological map of Earth, one must look to other time periods when similar environmental conditions existed. This requires paleontological records of not only past ecosystems but also the environmental conditions that shaped them. This approach is limited by how well those records are known, which almost always degrades with progressively older time periods. Comparisons of ancient communities with those of today carry additional assumptions related to limitations in paleontological and paleoenvironmental data: (1) decreased temporal resolution with increased age; (2) diagenetic alterations to proxy material; and (3) evolutionary differences in organisms, communities, and ecosystems.

Human-induced changes in atmospheric chemistry are forcing Earth's climate and ocean chemistry toward conditions that have not occurred for hundreds of thousands, and probably millions, of years. In addition, the current suite of reef
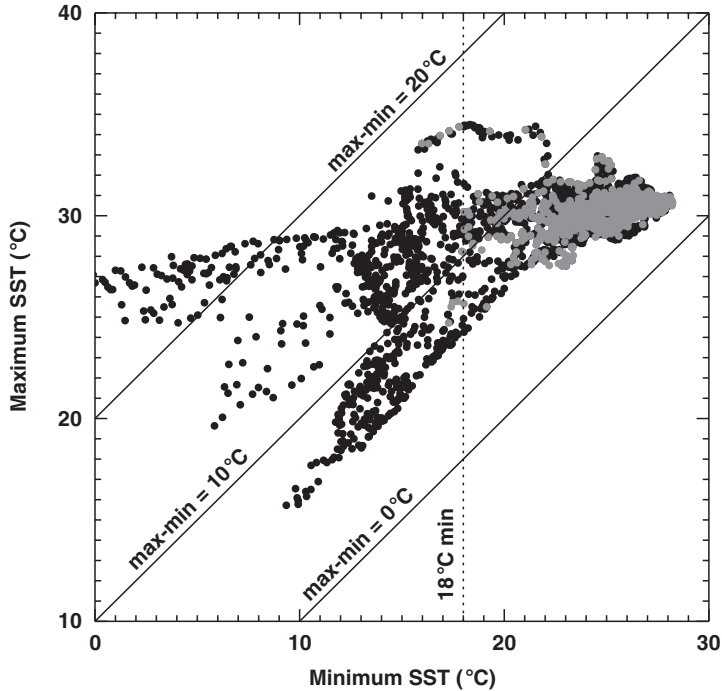
Figure 12.1. Distribution of annual minimum versus annual maximum water temperatures for coral reef regions (gray circles), compared with the distribution for tropical continental shelf waters (black circles). The 18 °C minimum is indicated by a dotted line. No maximum is shown because coral reefs occur in even the warmest waters of the tropics, and hence their maximum temperature tolerance cannot be discerned from this distribution. The diagonal lines designate where annual temperature variation (max–min) of 0 °C, 10 °C, and 20 °C fall on the graph. Most reefs occur where the annual temperature range is less than 10 °C. SST data were extracted from weekly SST data set of Reynolds et al. (2002).

builders has evolved considerably over that time, so that using paleoanalogues to gain insights into how coral reefs will adapt to future environmental change is further limited to observations at the scale of a reef, rather than the scale of a reef-builder. In fact, most of today's important reef-building coral families appeared sometime in the Eocene, and acroporids were not dominant on coral reefs until the Pleistocene (ca. 2 Ma; Wood 2001). Thus, reefs of the early Tertiary (Paleocene and Eocene, ca. 65–35 Ma), when atmospheric CO_2 levels were probably at least 500 ppmV (parts per million volume; this is roughly equivalent to the partial pressure of CO_2 [pCO_2] in the atmosphere expressed in μatm), may provide important clues in terms of certain physical reef characteristics such as calcification rates, distribution patterns, etc., but they are probably less useful as analogues in terms of ecological response. Another way to think of this is to examine the variety of present-day coral reefs: to what extent can we compare Brazilian reefs to "mainstream" Caribbean or Indo-Pacific reefs, which support a different coral fauna?

12.2 Atmospheric CO_2 Concentration

12.2.1 Predictions of Future CO_2 Concentration

According to the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES; Nakicenovic and Swart 2000), atmospheric CO_2 concentrations are predicted to reach between about 555 and 825 ppmV within this century. This wide range in predictions reflects the uncertainty in various inputs used to derive future emissions, such as population growth, development of energy technology, and economic growth. The lower end of the range essentially represents a doubling of the preindustrial concentration and the upper limit a tripling. The uncertainty implied by this range alone is much greater than the known glacial–interglacial fluctuations of CO_2 of about 100 ppmV (Petit et al. 1999).

12.2.2 Records of Past CO_2 Concentration

The best records of past atmospheric concentrations are from ice cores. CO_2 concentrations, sampled directly from air trapped within the ice, can be measured quite precisely, although some caution is warranted because it takes several years for the air to be permanently sealed off from the atmosphere ("diffusional smoothing"), and chemical reactions within the ice can alter the chemistry of the trapped air. The longest record is from the Vostok ice core, which extends back nearly a half-million years (Petit et al. 1999; Fig. 12.2A). This record indicates that over several major glaciations, atmospheric CO_2 concentrations remained between 180 and 300 ppmV. These values are corroborated by leaf stomatal index data for the last interglacial (Eemian; 115–130 ka), which indicate more variable but similarly low atmospheric concentrations (Rundgren and Bennike 2002).

CO_2 data extending back millions of years are scarce. The leaf stomatal index from fossil trees (*Gingko* and *Metasequoia*, both of which have modern counterparts) dating from nearly 60 to 50 Ma, indicates that atmospheric concentrations in the early Tertiary remained between 300 and 450 ppmV, only slightly higher than those of recent interglacials (Royer et al. 2001). However, data from the marine environment (calcium isotopes [De La Rocha and DePaolo 2000], boron isotopes [Pearson and Palmer 2000; Pearson et al. 2001], alkenones [Pagani, Arthur, and Freeman 1999]) all indicate that atmospheric CO_2 concentrations were probably much higher in the early Tertiary and decreased to below 300 ppmV by the Early Miocene (24 Ma; see Fig. 12B). In addition, the GEOCARB model, which hindcasts atmospheric CO_2 levels over the entire Phanerozoic by combining geological, geochemical, biological, and climatological data, suggests early Tertiary CO_2 levels were up to five times those of preindustrial levels (Fig. 12C; Berner 1994, 1997; Berner and Kothavala 2001). Recent isotopic and temperature proxy data from foraminifera (Kennett and Stott 1991; Zachos et al. 2003) indicate that the Paleocene/Eocene Thermal Maximum (an abrupt increase in sea-surface temperatures [SSTs] about 55 Ma) coincides with a sudden increase in greenhouse gas concentration in the atmosphere, as evidenced by negative carbon-isotope excursion of >2.5%, and a deep-sea horizon of carbonate dissolution (Zachos et al. 2005).
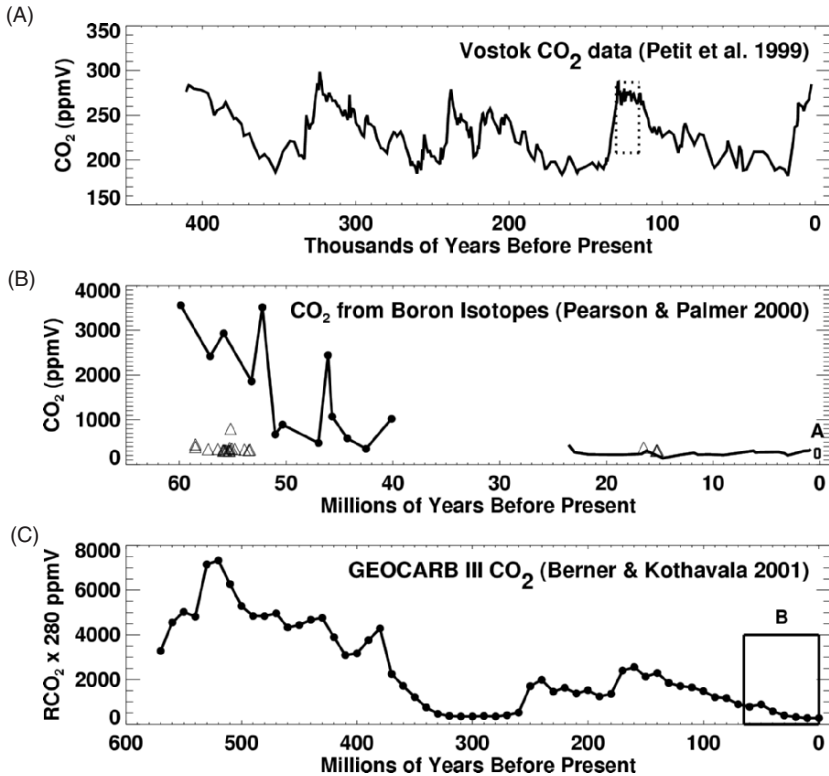
Figure 12.2. Historical atmospheric CO_2 concentrations determined from: (**A**) the Vostok ice core record (Petit et al. 1999); rectangle indicates range of Leaf Stomatal Index (LSI) values from early Tertiary samples (Royer et al. 2001); (**B**) boron isotope data from foraminifera (Pearson and Palmer 2000), with LSI data from late Pleistocene samples shown as triangles (Rundgren and Bennike 2002), and range of (a) indicated by rectangle; (**C**) results from the GEOCARB III model (Berner and Kothavala 2001), and range of (b) indicated by rectangle.

12.3 Temperature and Coral Bleaching

Large-scale mass bleaching of corals and other reef organisms is a phenomenon with no known precedent prior to 1982 (Glynn 1993). Many factors have been implicated in these mass-bleaching events (e.g., temperature, UV-B, nutrients, hydrodynamics; see summaries by Hoegh-Guldberg 1999 and Glynn 2000), but water temperature appears to be the primary factor, with solar radiation playing a key role as well (see review by Fitt et al. 2001). Patterns of coral bleaching are consistent with the hypothesis that photosynthesis in corals at elevated temperatures can cause photochemical damage. Bleaching often begins on coral surfaces that receive the most light; and some corals appear to have photo-protective adaptations to slow photosynthesis during light-induced bleaching (Brown 1997).

12.3.1 Predictions of Future Temperature Change

Surface temperatures on the Earth are related to the atmosphere's capacity to act as a greenhouse. Certain gases are transparent to incoming short-wave radiation from the sun but hinder the escape of reradiated long-wave radiation derived from heating of the Earth's surface. Without this natural greenhouse effect, global temperatures would be substantially cooler. Predictions of surface temperature due to the greenhouse effect go hand-in-hand with those of atmospheric CO_2 and other greenhouse gas concentrations. Virtually all SST predictions for the near future are based on projections of atmospheric composition, with changes in CO_2 concentration exerting the greatest increase in radiative forcing (CO_2 exerts about 60% of the current increase in radiative forcing relative to conditions in 1750; CH_4, 20%; halocarbons, 14%; and N_2O, 6%; Houghton et al. 2001).

Atmospheric paleotemperatures are often inferred from paleo-CO_2 records as well (although $\delta^{18}O$ measurements from ice cores provide independent estimates of atmospheric temperature [e.g., Petit et al. 1999]). The CO_2–temperature correlation probably held true for most of the Phanerozoic (the past 560 Myr), but the relationship appears to have broken down for certain brief periods in the early Cenozoic (Royer et al. 2001) and in the Paleozoic (Veizer, Godderis, and Francois 2000; Crowley and Berner 2001). Other factors (e.g., tectonic events) are thought to have been the main influence on global climate during these times (Zachos et al. 2001). For the late Cenozoic, however, warmer climates did prevail during periods of higher atmospheric CO_2.

Records/Analogues of Ocean Temperature and
El Niño–Southern Oscillation

Temperature

For periods prior to the widespread instrumental weather observations (late 19th century) various proxy temperature records are available for atmosphere and ocean. The most common sources of information are: tree-ring width and density, isotopic and geochemical tracers in coral skeletons and foraminifera, and information from cores of marine and lake sediments. The best records of seawater temperature on reefs are from the corals themselves, as recorded by both $\delta^{18}O$ values and Sr/Ca ratios in the annual bands of the skeleton (e.g., McConnaughey 1989; Cole and Fairbanks 1990; Beck et al. 1992). Both techniques can provide high-resolution records of seawater temperatures, and both have been used on living corals as well as fossil corals as old as 130 kyr (Tudhope et al. 2001).

Coral records have provided useful reconstructions of past ocean temperature variability, but like all proxy climate records they are imperfect. Sources of error include problems of separating mutliple environmental effects (e.g., $\delta^{18}O$ can record a mixture of both salinity and temperature), reliance on single coral samples, and variations in signal preservation through time (Bard 2001). Secondary precipitation of inorganic cements can contaminate both the $\delta^{18}O$ and Sr/Ca signals (Müller, Gagan, and McCulloch 2001; Ribaud-Laurenti et al. 2001), even in skeletons of living corals (Enmar et al. 2000); and zooxanthellae can impose a

strong signature on the Sr/Ca signal (Cohen et al. 2002). Despite these potential shortcomings and mismatches with other paleotemperature proxies (Crowley 2000), coral paleo-SST records have proven invaluable at capturing climatic histories such as the variability of the El Niño–Southern Oscillation (ENSO) over the past few hundred years (Dunbar 2000).

One of the main problems with using corals as records of SST is that temperatures are not recorded if a coral discontinues skeletal growth, such as during severe stress or with mortality. The Galápagos record, for example, terminated abruptly during the 1982/1983 bleaching and mass mortality (Shen et al. 1992). The elimination of high-temperature excursions from coral records would certainly bias reconstructions of past temperature variations.

ENSO

The El Niño–Southern Oscillation is the best-understood source of short-term climate variability that significantly affects tropical SSTs and hence coral reefs (see Riegl, Chapter 10; Wellington and Glynn, Chapter 11). During the warm phases of ENSO (El Niño events) large parts of the tropical oceans are unusually warm and have recently been associated with mass coral bleaching events. The cold phases of ENSO (La Niña events) are generally associated with unusually cool SSTs although warmer than normal waters do occur in some areas (e.g., coral reefs lying in the South Pacific Convergence Zone). The response of ENSO to increased greenhouse gases is unclear at present. The El Niño events of 1982 to 1983 and 1997 to 1998 were the strongest since 1950 and probably during the instrumental record period. This does not necessarily indicate, however, that El Niño events are increasing in intensity due to global warming, and the limited data available for years prior to 1950 suggest that similarly intense events occurred in the late 1800s (Enfield 2001). Tudhope et al. (2001) presented coral records spanning the last 130 kyr which show that (1) although ENSO events persisted throughout the glacial/interglacial periods, their intensity waned during colder periods, and (2) current ENSOs are more intense than at any other time in the coral records. Some researchers use these results as evidence that frequency and/or intensity of the ENSO will increase under increased greenhouse gas forcing (but see discussion of modeling ENSO events in the next section).

Modeled Predictions of SST and ENSO

Model Advantages and Limitations

The response of Earth's climate to increased atmospheric greenhouse gas concentrations is complex, and forecasting future changes in surface temperature, precipitation, ocean circulation, and other climate characteristics necessarily rely on mathematical models. These numerical models are primarily based on physics, but many components are parameterized (i.e., the physical processes are formulated as model constants or functional relations) based on empirical observations (e.g., freshwater runoff). A model's accuracy is often judged by how well it simulates conditions of both the present and the recent past, periods for which we have accurate records. Modeled increases in global ocean temperature over the

20th century, for example, show increases consistent with recent analysis of observations (e.g., Levitus et al. 2000).

Given computing constraints, all climate models are limited by both spatial and temporal resolution, as well as by gaps in scientific understanding. For example, one of the most important hurdles in climate modeling today is parameterization of cloud processes and feedbacks. Many aspects of cloud formation and cloud feedbacks to radiative forcing (e.g., albedo) remain poorly understood, so that current cloud parameterizations could be introducing substantial error in climate predictions. Another condition of the Earth system that has been difficult to model, but which could have profound impacts on climate, is the thermohaline circulation. The oceanic "conveyor belt" (sensu Broecker 1987) is driven by the formation of dense (colder and/or saltier) water in polar regions. Some models predict a slowing or virtual shutting down of the thermohaline circulation in response to future climate change (Rahmstorf 1995; Stocker and Schmittner 1997), whereas others predict little change. This large range of predictions arises from rather small differences in temperature and freshwater fluxes of the various models (see reviews by Gent 2001 and Clark et al. 2002).

Nonetheless, global climate models contribute significantly to our understanding of various feedbacks in the climate system, and several large efforts are underway that combine (or "couple") models of the major components of the Earth system—atmosphere, ocean, land, ice—so that they interact simultaneously, allowing feedbacks to occur by passing forcing fields back and forth across the interfaces (atmosphere–ocean, atmosphere–land, ocean–ice, etc.). Earth system models are thus better than analogues at understanding the various *mechanisms* of climate change. They also allow quantification, determination of the limits of change, regional assessments, global coverage, and separation of the effects of covarying parameters.

Modeled SSTs

The Third IPCC Report (Houghton et al. 2001) based its forecasts of future climate on a suite of Earth system models, most of which allowed feedbacks between the major components: atmosphere, ocean, land, and ice. All of the models predict an increase in surface temperature in response to increased greenhouse gas concentrations. Although there is near-consensus that increased greenhouse gas concentrations will cause or are already causing global warming, there is not a consensus on how much the temperature will rise. The range of predicted global temperature increase among models included in the Third IPCC Report is large: 1.4 to 5.8 °C for the period 1990 to 2100 (Houghton et al. 2001). These differences arise from both the differences in the climate models and the range of scenarios of future greenhouse gas concentrations. These same models indicate that warming of tropical SSTs (1 to 3 °C, Houghton et al. 2001) will be less than the global average.

Almost all coupled models indicate greater warming at high latitudes than in the tropics (Fig. 12.3). Despite recent evidence that SSTs during the middle Cretaceous were as high as 33 °C (Wilson, Norris, and Cooper 2002), observations and model results tend to support the "thermostat hypothesis." This hypothesis states that various atmospheric and oceanic feedbacks prevent SSTs in the open
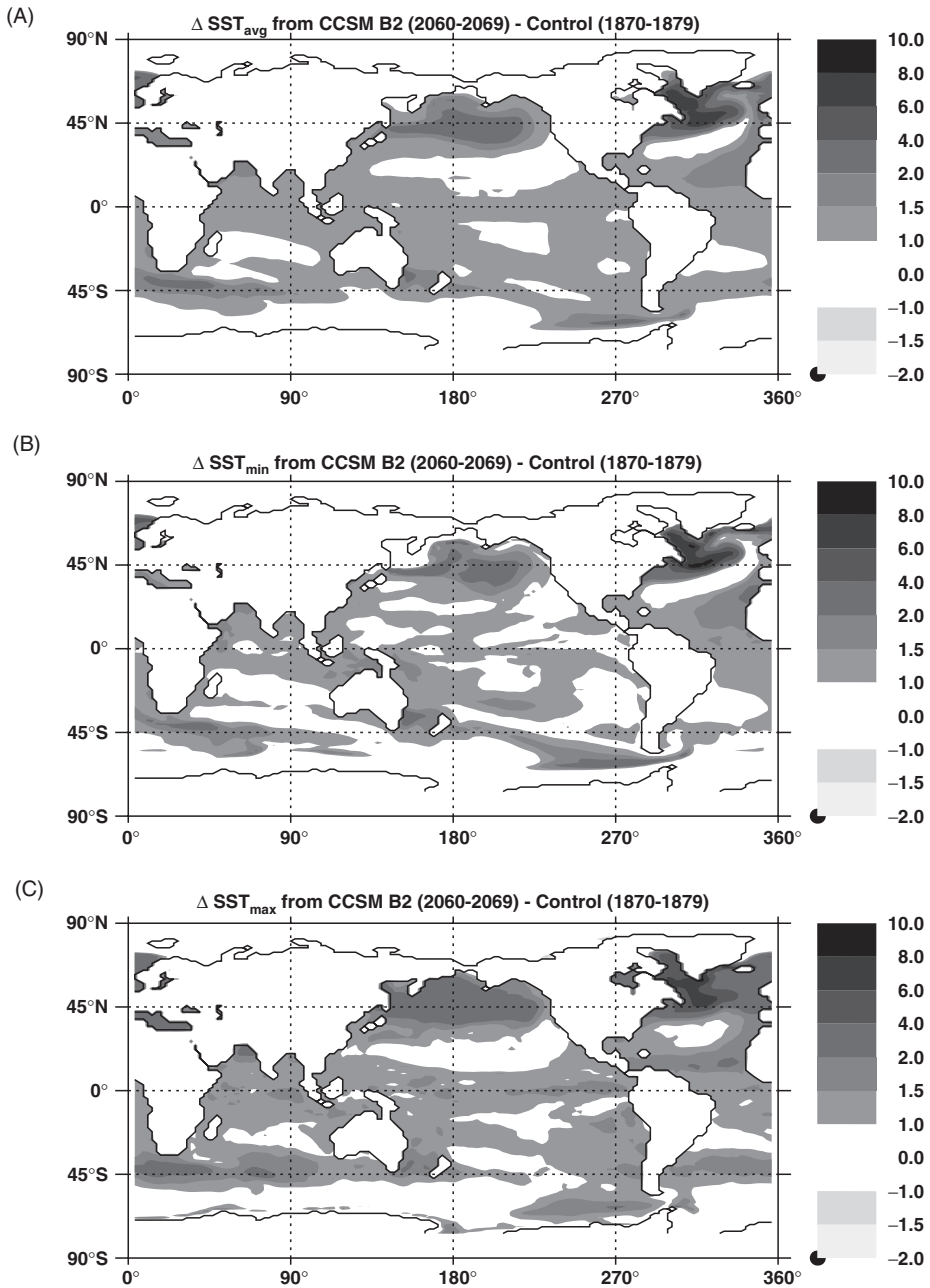
Figure 12.3. Changes in sea surface temperature predicted by the Community Climate System Model version 1.0 (CCSM 1.0; Boville and Gent 1998) of the National Center for Atmospheric Research for the 10-year period 2060 to 2069. Each frame shows the difference between the model run with IPCC's SRES B2 forcings, when atmospheric $CO_2 = 517$ ppmV, and the CONTROL run, in which atmospheric CO_2 was held constant at 280 ppmV. (**A**) Annual average SST; (**B**) annual minimum SST; and (**C**) annual maximum SST.

ocean from exceeding 31 to 32 °C. Three mechanisms for an ocean thermostat have been proposed: (1) evaporative cooling or evaporation–wind–SST feedback (Newell 1979); (2) the cloud–SST feedback or cloud shortwave radiative forcing (Ramanathan and Collins 1991); and (3) ocean dynamics and heat transport (Li, Hogan, and Chan 2000; Loschnigg and Webster 2000). Maximum SSTs today are around 31 to 32 °C in the open ocean, and about 33 to 34 °C in enclosed seas such as the Red Sea. The thermostat may play an important role in how coral reefs fare within a greenhouse earth, because it is likely that the thermostat temperatures vary from region to region, as well as across spatial scales, and consequently reefs that exist in waters that are already near the temperature set by the thermostat may not experience as much warming as reefs in cooler waters.

Modeled ENSO Events

Most global models are not explicitly designed to predict future changes in ENSO, although many predict relatively greater warming of SSTs in the eastern compared with the western tropical Pacific as well as increases in tropical Pacific precipitation (Houghton et al. 2001). Both of these changes are consistent with increased ENSO development or "more El Niño-like conditions." The few coupled ocean–atmosphere models that have been used to examine ENSO sensitivity to atmospheric greenhouse gas concentrations have produced mixed results (e.g., Tett 1995; Knutson, Manabe, and Gu 1997; Timmerman et al. 1999; Otto-Bliesner and Brady 2001). Timmerman et al. (1999) predicted that El Niño conditions will be more frequent and La Niñas more intense with further increases in atmospheric CO_2. In contrast, the ENSO response modeled by E. Brady and B. Otto-Bliesner (unpublished data) was much less sensitive to CO_2 change. Changes in ENSO under $2 \times CO_2$ conditions were insignificant, and under $6 \times CO_2$, ENSO intensity actually decreased. Such results reflect the fact that ENSO frequency and intensity are not merely a function of temperature change, but also reflect the influence of other climatic responses such as monsoons (Otto-Bliesner et al. 2003).

12.3.2 Coral Reef Responses to Rising Temperatures

Regardless of whether there is consensus that the present warming trend is due to increased atmospheric CO_2 forcing, nearly all coral reef scientists agree that mass coral reef bleachings have increased in frequency during the last two decades and are unprecedented within this century and probably for several preceding centuries (Hoegh-Guldberg 1999; Aronson et al. 2000). Recent mass coral bleaching events are clearly associated with anomalously warm SSTs. Given the acceleration in global warming over the same time period there is a strong suggestion that global climate change due to the greenhouse effect is leading to an increased frequency of coral reef bleaching (Lough 2000). These mass bleachings have been shown to be exacerbated by other factors such as subaerial exposure during unusually low tide (Glynn 1984), increased penetration of visible and UV light (Gleason and Wellington 1993), and decreased water circulation (Nakamura and van Woesik 2001). Temperature and the nonanthropogenic exacerbating factors are all associated with climatic features typical of the El Niño phase of ENSO,

and the three most notable recent episodes of coral bleaching occurred during ENSO events: 1982 to 1983, 1987, 1997 to 1998. If mass coral bleaching events continue to increase in frequency, major changes in coral community structure are inevitable (Hughes et al. 2003), and some researchers predict a collapse of coral reef ecosystems over the next few decades (e.g., Hoegh-Guldberg 1999). How reef-building organisms will fare under continued high-temperature stress depends mainly on their ability to adapt to those changes as discussed below.

Records/Analogues of Coral Bleaching

To establish a history of past episodes of bleaching events caused by warm water temperatures, records of both SST and coral bleaching are needed. As mentioned earlier, the best records of past reef-water temperatures are obtained from the corals themselves. Both stable isotopes and Sr/Ca ratios measured chronologically along cores from massive corals can reveal detailed information about past SSTs experienced by those corals. One classic example of this is the record obtained from massive *Pavona* spp. in the Galápagos (Dunbar et al. 1994). The oxygen isotope record revealed that for the time period represented by this record (years 1586–1953) SSTs had remained below that which caused the near-total die-off of Galápagos corals during the 1982 to 1983 bleaching event. Note that this approach is not yet suitable for branching and foliose corals.

Coral bleaching records are much more difficult to obtain. In human recorded history, reports of isolated bleaching events can be found in the literature, but there are no historical records of regional-scale mass bleaching events prior to 1982 (Glynn 1993). Glynn (2000) outlined a variety of markers in the geological record that could be used as indicators of past mass bleaching events, including isotopic and trace-metal markers in coral cores indicative of ENSO events, alterations in skeletal banding, protuberant growths on massive corals (signaling where surviving patches of colonies continued to grow; cf. DeVantier and Done, Chapter 4), and indications of accelerated bioerosion in reef sediments. To date, these have not been used to derive past records of coral bleaching or mass mortality (see review in Wellington and Glynn, Chapter 11).

A combined ENSO-bleaching signal has been derived from coral cores as an excursion in the normal covariance of carbon and oxygen isotopic signals (Carriquiry, Risk, and Schwarcz 1994). Here, the $\delta^{18}O$ signal indicates warmer than normal conditions whereas the $\delta^{13}C$ signal indicated bleaching. This interpretation relies on environmental records of both temperature and salinity, however, and extrapolation to historical times is therefore difficult. Another obvious drawback of a skeletal "coral bleaching signal" is that, like temperature, such a signal is not likely to be preserved when the bleaching leads to coral mortality. There is also evidence that some bleached corals fail to secrete a growth band (Halley and Hudson, Chapter 6). In either case, coral skeletons may underestimate the past frequency and intensity of bleaching.

How corals and coral reefs fared under greenhouse conditions versus icehouse conditions of the last 30 million years is a question not readily answerable with the

paleontological record. In general, corals and other aragonite producers appear to dominate reef-building during cool rather than warm periods of Earth history (Sandberg 1983). The reasons for their dominance may not be strictly related to lower temperature but to some other environmental factor such as the seawater Mg:Ca ratio (Stanley and Hardie 1998). Scleractinian corals were dominant reef-builders in the Jurassic, but rudist bivalves largely displaced them sometime in the Early to Middle Cretaceous. Rosen and Turnsek (1989) also noted that the highest coral diversity in the Cretaceous was shifted poleward to 35° to 45°N. Why were corals rare in low-latitude regions during the Cretaceous, and indeed during many other Phanerozoic periods (Kiessling 2001)? There are many hypotheses for the coral–rudist shift that are based on both environmental and ecological arguments, but there is no strong evidence to favor one hypothesis over another (Gili, Masse, and Skelton 1995; Johnson and Kauffman 2001). Glynn (2000) also raised the interesting hypothesis that some past extinction events could have been caused by mass bleaching. Unfortunately, recent records of coral bleaching are scant and paleontological records of coral bleaching are essentially nonexistent, so the question of whether massive coral bleachings occurred during warm periods in the past cannot be answered yet. It is even more difficult to assess how quickly corals and/or their algal symbionts might adapt to higher SSTs.

Models of Coral Adaptation to Higher Temperature

Assuming that corals cannot adapt to increasing temperature, future global warming is likely to lead to more frequent mass coral bleaching events. Even without global warming, if ENSO frequency and/or intensity increase, then the probability of mass coral bleachings will also increase, at least in certain geographic areas. The current large-scale bleaching response to increased SSTs indicates that many reef-building corals (either the coral animals, the symbiotic algae, or both) are not adapting adequately to the SST increase. There is, however, evidence that reef-building corals and other symbiotic organisms can adapt to increasing temperatures, either through acclimation (short-term adaptation to environmental change at the individual level), acclimatization (medium-term adaptation), or evolution (long-term adaptation through natural selection; Coles 2001).

The distribution of corals in time and space illustrates this fact. First, scleractinian corals survived the high temperatures of the Cretaceous, although their distribution was shifted to higher latitudes (Kiessling 2001). Second, corals can exist and indeed thrive under extreme temperature regimes. Enclosed regions such as the Red Sea and Persian Gulf support species that tolerate much greater temperature ranges than do their conspecifics in the Indo-Pacific (Coles and Fadlallah 1991). These two examples probably illustrate adaptation over long periods of time, such as adaptation via natural selection.

The "adaptive bleaching hypothesis" (Buddemeier and Fautin 1993; Fautin and Buddemeier 2004) is an adaptive mechanism that acts over shorter time scales. Given that several species of zooxanthellae (and indeed several clades within species) inhabit corals as symbionts, this hypothesis is based on the possibility of a

variety of coral–zooxanthellae combinations, each with a different environmental tolerance for the surrounding environmental conditions. Bleaching could thus be considered an adaptive mechanism if the expelled zooxanthellae are replaced by another species or type of zooxanthellae better suited to the new environment. Baker (2001) suggested the additional hypothesis that because bleaching expels all of the less-tolerant algae, competition with incoming algae is thus eliminated. Manipulation experiments have shown that some corals and anemones that bleached subsequently acquired new algal symbionts better suited to their new environment (Baker 2001; Kinzie et al. 2001). Adaptive bleaching is more difficult to detect under natural conditions, mainly because of the influence of other environmental factors.

There is evidence that corals in some areas are adapting to the recent warming trend. Bleaching on some eastern Pacific reefs was much worse during the El Niño event of 1982 to 1983 than that in 1997 to 1998, even though temperature excursions during the two events were similar, offering evidence for adaptation and perhaps support for the adaptive bleaching hypothesis (Guzmán and Cortés 2001; Podestá and Glynn 2001). Glynn et al. (2001) also found that *Pocillopora* spp. at Gorgona Island in the eastern Pacific fared better in 1997 to 1998 than in 1982 to 1983, and suggested that this reflected evolutionary selection for more heat-irradiance-tolerant individuals that survived the 1982 to 1983 bleaching event. Finally, Brown et al. (2002) demonstrated adaptation in corals exposed to combinations of elevated SST and UV radiation, but without any associated changes in the zooxanthellae.

If one accepts that corals can adapt to increased SST, one must then determine how much and how rapidly they can adapt. Ware (1997) tested how different rates of acclimation might affect the frequency of coral bleaching in the future. He first assumed that corals maintain upper temperature tolerances close to the upper thermal limits to which they are normally accustomed. This is probably a valid assumption given that coral bleaching seems to occur when temperatures exceed the average climatological maximum by about 1 to 2 °C, rather than some absolute value (Coles and Brown 2003). Ware then assumed that the "acclimation temperature" of a coral at a particular location was based on the average annual maximum temperature over some past interval of time. Corals with relatively short acclimation periods (e.g., <25 years, Fig. 12.4) should experience fewer and milder bleaching episodes than those that require longer acclimation periods. Given a long enough temperature versus bleaching record, one could theoretically derive the acclimation period and then use this information to determine the probability that coral bleaching will occur in the future (Ware 1997).

Determining the acclimation period is complicated because (1) there is probably some absolute maximum temperature beyond which corals can physiologically adapt, which is likely to vary across species, and (2) there is probably significant variation in adaptive potential between species and the rate at which they can adapt. Above its absolute maximum, the future of a species will depend on its ability to adapt genetically, through evolutionary processes, and this is also likely to vary across species as a function of gene flow (Hughes et al. 2003). The impact
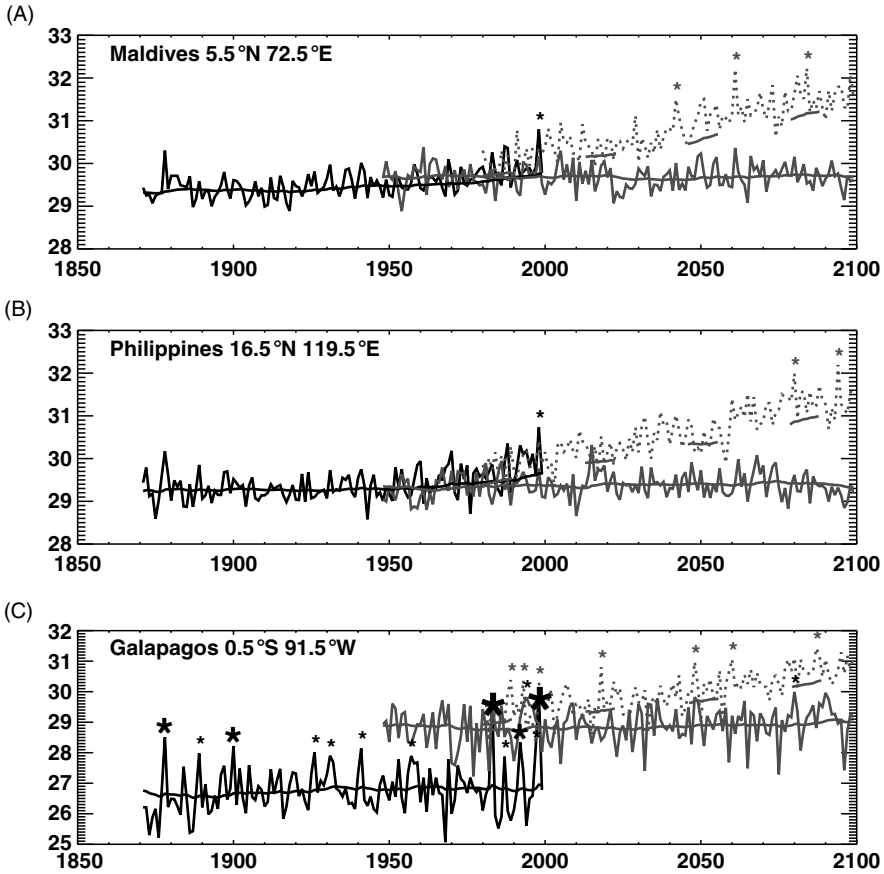
Figure 12.4. Comparison of observed and modeled annual maximum SSTs for three reef regions: (**A**) Philippines, (**B**) Bahamas, and (**C**) Galápagos. Black solid lines for the period 1970–2000 represent annual maxima derived from the HADISST 1×1° lat/lon reconstruction of observed SSTs (Rayner et al. 2003). Gray solid lines show annual SST maxima for years 1948–2000 of the CCSM 1.0 CONTROL integration (atmospheric CO_2 concentration held constant at 280 ppmV). Gray dotted lines show annual SST maxima for years 1980–2100 of the CCSM 1.0 SRES B2 integration, a moderate global warming scenario. The 25-year temperature of acclimation (sensu Ware 1997) is also shown for each SST series. Possible bleaching thresholds are indicated by stars where maximum temperature exceeds the acclimation temperature by 1.0 °C (small star), 1.5 °C (medium star), and 2.0 °C (large star). Even where absolute maximum temperatures are not duplicated by the model (e.g., for the Galápagos), a comparison between the HADISST and CONTROL data shows that the model does a good job of capturing interannual variability of maximum SSTs, which is more limiting to reefs than average maximum temperature.

of temperature *variability* on a coral's ability to adapt is also difficult to assess; a coral may be much better at adapting to increasing temperatures in regions where the annual maxima do not vary much from year to year.

12.4 Seawater Chemistry

12.4.1 Background

The oceans currently take up about about a third of the fossil-fuel-related increases in atmospheric CO_2 (Sabine et al. 2004). The increase in seawater-pCO_2, which is greatest in the well-mixed upper ocean, has measurable effects on seawater pH and the abundance of carbonate ions that are used by organisms that secrete calcium carbonate ($CaCO_3$).

The atmospherically driven acidification of the oceans and the potential effects on $CaCO_3$ precipitation were first raised as concerns several decades ago. Early fears that the normally "$CaCO_3$-saturated state" of the surface ocean would be driven to undersaturation, with grave consequences for marine calcifiers (Fairhall 1973; Zimen and Altenhein 1973), were alleviated by calculations showing that a 10-fold increase in atmospheric CO_2 would be required to achieve $CaCO_3$ undersaturation in surface waters (Whitfield 1974; Skirrow and Whitfield 1975). However, Smith and Buddemeier (1992) pointed out that future changes in the *degree* of $CaCO_3$ saturation state could affect calcification rates on reefs, and many experiments have since illustrated that calcification rates in both corals and coral reef communities are indeed proportional to $CaCO_3$ saturation state (e.g., Gattuso et al. 1998; Langdon et al. 2000; Leclercq, Gattuso, and Jaubert 2000, 2002; Langdon et al. 2003; Marubini, Ferrier-Pages, and Cuif 2003). The acidification of the oceans is therefore an important consequence of increased atmospheric CO_2, because it is likely to affect calcification of corals and algae, and the reef structures that they build.

Seawater pH is largely buffered by the equilibrium chemistry of the carbonate system (Fig. 12.5). Dissolved inorganic carbon (DIC; also called total CO_2 or TCO_2), is partitioned into several different ionic states in seawater, and the relative concentrations of these states constantly adjust to maintain charge balance between total cation and anion concentrations. Dissolving CO_2 in seawater increases TCO_2, but does not alter alkalinity (total charge of cations such as Na^+, Mg^{2+}, Ca^{2+}, etc.). In response to the increased TCO_2, the carbonate system shifts to ensure charge balance by converting some of the CO_3^{2-} (carbonate) ions to HCO_3^- (bicarbonate). The CO_3^{2-} concentration thus decreases as CO_2 is dissolved in seawater. $CaCO_3$ saturation state, a product of the concentrations of both Ca^{2+} and CO_3^{2-} in seawater, therefore, also decreases.

Factors which affect the CO_2 concentration in seawater also affect $CaCO_3$ saturation state. In the surface ocean, the first-order control on CO_2 concentration in seawater is the concentration of CO_2 in the overlying atmosphere, while second-order controls include temperature and biological activity. At regional
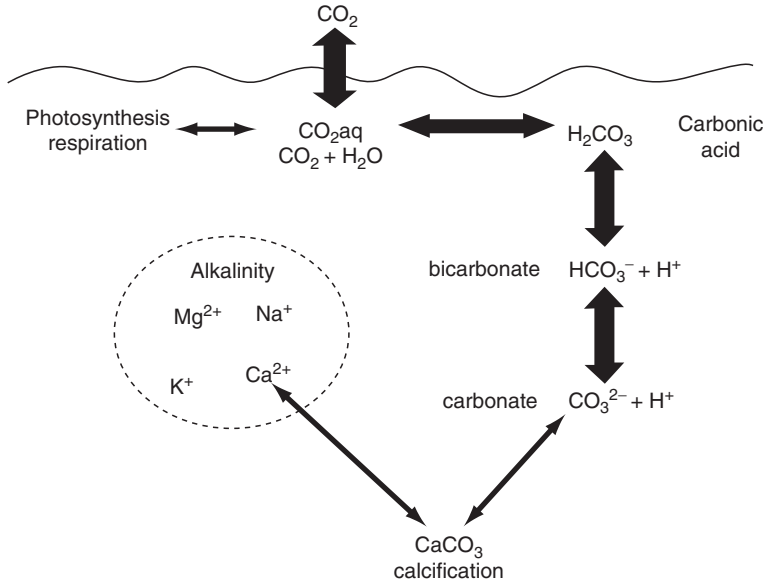
Figure 12.5. The carbonate system in seawater. As CO_2 is driven into the ocean, it quickly forms carbonic acid, which is a weak acid. Most of this rapidly dissociates to either bicarbonate (HCO_3^-) or carbonate (CO_3^{2-}). Total CO_2 (TCO_2) is the sum of HCO_3^-, CO_3^{2-}, and dissolved CO_2 in seawater, while total alkalinity (T_{Alk}) is the excess positive charge in seawater. The proportion of HCO_3^- to CO_3^{2-} adjusts to balance this positive charge. As a first approximation, the carbonate ion concentration can be estimated as T_{Alk}–TCO_2. Note that by adding CO_2, TCO_2 increases and the carbonate ion concentration decreases. From Kleypas and Langdon (2003).

scales, warmer waters hold less CO_2 than colder waters, which explains why tropical waters have higher saturation states than temperate waters. At local scales, photosynthesis and respiration consume and release CO_2 in the water column, respectively. $CaCO_3$ precipitation also affects CO_2 concentration because it reduces alkalinity which causes the carbonate equilibrium to shift toward higher CO_2 concentration. $CaCO_3$ dissolution has the opposite effect (Fig. 12.5).

Compared with the uncertainty of how SST will respond to increasing atmospheric CO_2, the response of ocean chemistry to future CO_2 increases is more predictable, at least over the next 100 years or so. Through processes of air–sea gas exchange, surface ocean seawater chemistry responds relatively quickly to changes in gas concentrations in the atmosphere, reaching equilibrium within about a year. The thermodynamic behavior of the carbonate system in seawater is well characterized, and measured changes in seawater chemistry from large field programs such as the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Survey (JGOFS) are consistent with predicted changes due to increases in atmospheric CO_2 (Sabine et al. 1999, 2002, 2004). Carbon isotopic

measurements from oceanic waters that trace the $\delta^{13}C$ signature from CO_2 emissions derived from fossil fuel burning also support these findings (Quay et al. 2003). Predictions of future carbonate ion concentration in the surface ocean depend mainly on predictions of future atmospheric CO_2 concentrations, and secondarily on predictions of future SSTs (Figs. 12.6–12.9).

The pCO_2 in the surface ocean currently varies between about 80 μatm lower and 120 μatm higher than that of the atmosphere. Regions where surface ocean pCO_2 is lower than atmospheric pCO_2 occur where CO_2 is exported to the ocean interior, either through downwelling or through net biological uptake of CO_2 from the water column. Conversely, surface ocean pCO_2 is higher than that of the atmosphere where upwelling brings deep CO_2-rich water to the surface (the deep sea is isolated from air–sea gas exchange and becomes progressively enriched in CO_2 from the continued decay of organic matter). Upwelling in the eastern equatorial Pacific delivers waters to the surface, with pCO_2 more than 100 μatm higher than that of the atmosphere (Sakamoto et al. 1998). These patterns are reflected in the overall distribution of DIC and alkalinity in the Pacific (Fig. 12.7).

A study by Gattuso et al. (1998) was one of the first to directly test the effects of $CaCO_3$ saturation state on coral calcification, by altering the Ca^{2+} concentration in seawater. Recent experiments on calcification versus saturation state have instead altered CO_3^{2-} through a variety of manipulations of the carbonate system (see review by Langdon 2003). Langdon (2003) determined that calcification rate in the Biosphere 2 coral reef mesocosm responded mainly to CO_3^{2-} concentration rather than to pH or some other carbonate species. However, there is no convenient way to determine CO_3^{2-} concentration directly from seawater and there is no proxy for determining its concentration in the past oceans.
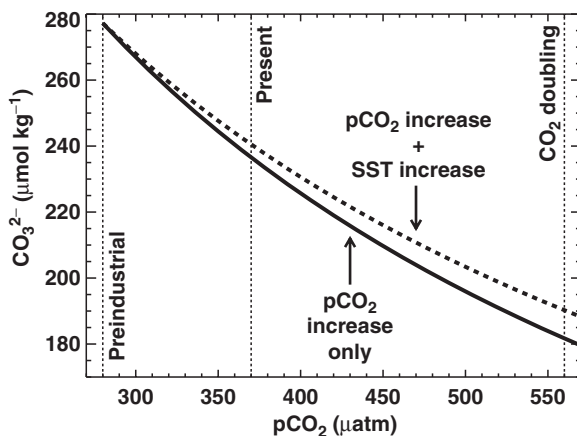

Figure 12.6. Changes in carbonate ion concentration in response to pCO_2 forcing, illustrating the effect of increasing temperature.
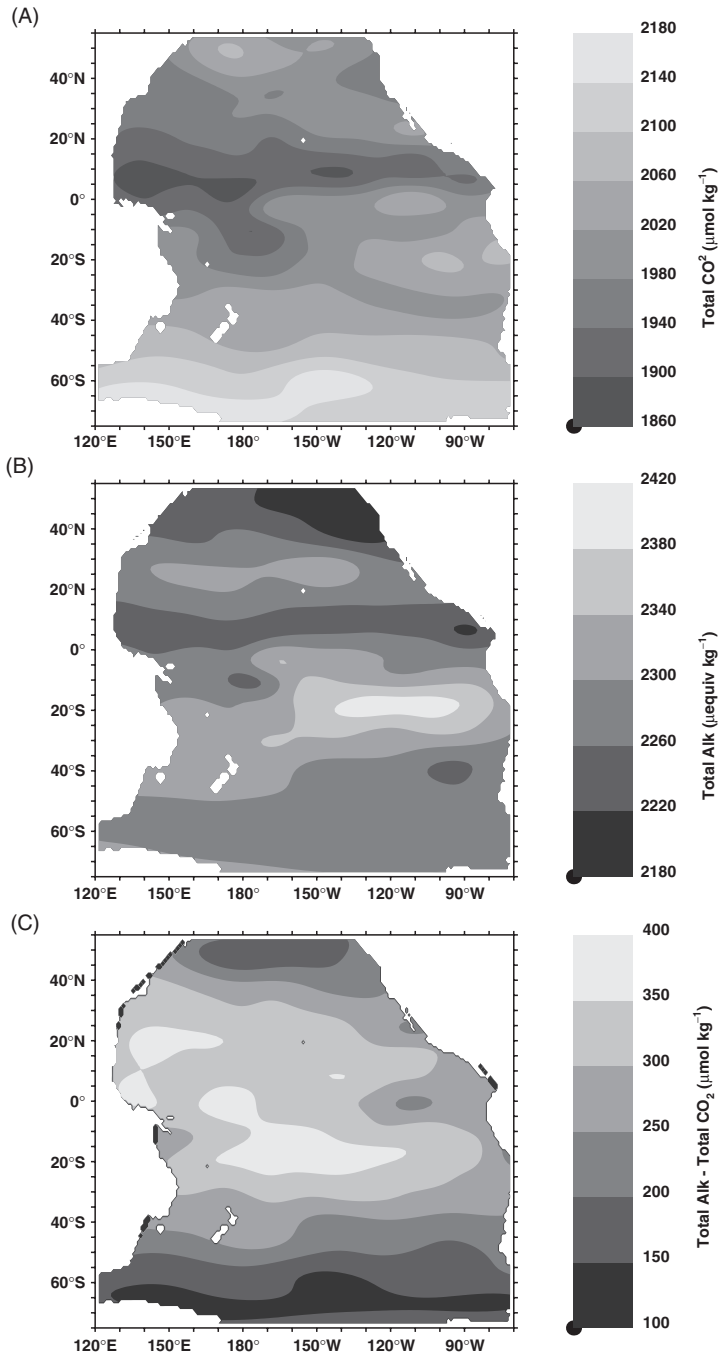
Figure 12.7. Distribution of major carbonate system parameters in the Pacific Ocean: (**A**) TCO_2, (**B**) T_{Alk}, and (**C**) T_{Alk}–TCO_2 as a rough approximation of carbonate ion concentration (see Fig. 12.5 for explanation). Data for panels (**A**) and (**B**) were obtained from a synthesis of the Global Ocean CO_2 Survey conducted over the last two decades (Sabine et al. 1999, 2002).

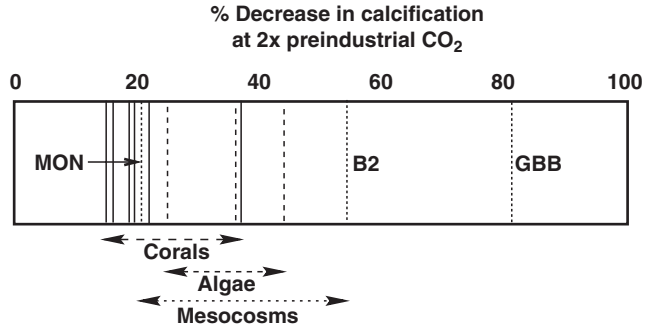**% Decrease in calcification at 2x preindustrial CO$_2$**

Figure 12.8. Experimentally derived estimates of calcification response of corals (solid lines), calcareous algae (dashed lines), and whole "communities" in mesocosm and field experiments (dotted lines) to changes in seawater chemistry. Response is standardized to calcification at 2× preindustrial atmospheric CO$_2$ concentrations, as percent decrease relative to that at preindustrial levels. MON = Monaco mesocosm (Leclercq, Gattuso, and Jaubert 2000); B2 = Biosphere 2 (Langdon 2003); GBB = Great Bahama Bank (Broecker and Takahashi 1966). Data are derived from a summary by Langdon (2003) and from Marubini, Ferrier-Pages, and Cuif (2003).
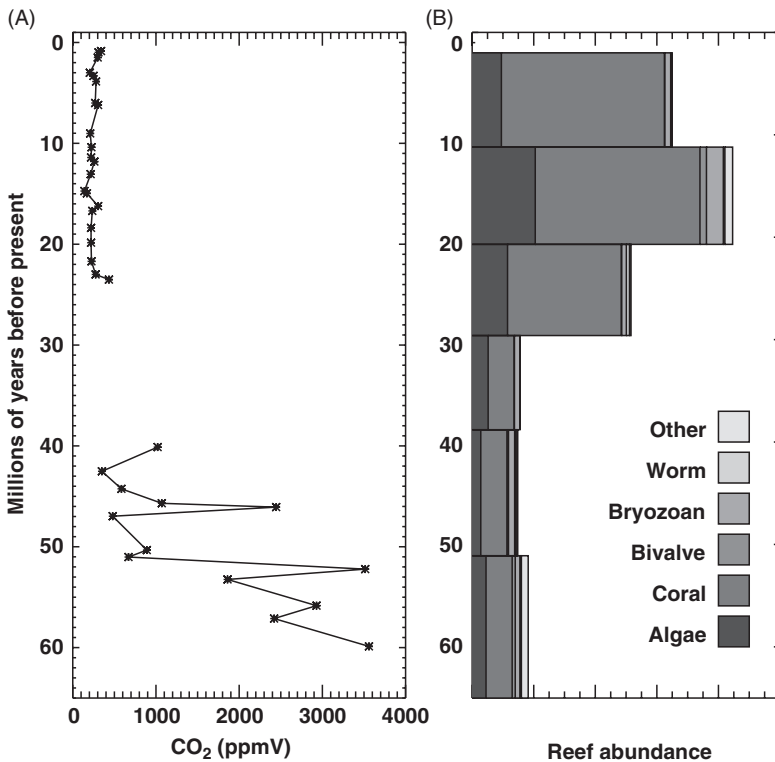

Figure 12.9. (**A**) The Pearson and Palmer (2000) record of atmospheric CO$_2$ for the Tertiary, and (**B**) a compilation of relative reef abundance (cumulative number of reefs in a given period), and the organisms that built them, for the same time period (derived from Kiessling, Flügel, and Golonka 1999; note that absolute numbers of reefs were not provided in their original figure, but bars range from about 30 to 175 reefs). Reef abundance appears to have increased around 30 Ma.

12.4.2 Past versus Future Seawater Chemistry Change

Records/Analogues

The carbonate chemistry of a given parcel of seawater can be determined if any two of the following carbonate parameters are known: pH, TCO_2, T_{AIK}, and pCO_2, as well as temperature, pressure, and salinity of the water. It is now generally accepted by the scientific community that atmospheric pCO_2 was much higher during the Cretaceous and has declined throughout the Tertiary. However, one cannot simply use estimates of atmospheric CO_2 concentration to infer ocean carbonate chemistry during the Tertiary as T_{AIK}, for example, may have also been higher. Records of past ocean chemistry are few, and they rely on proxies of pH and other ion concentrations. A proxy for one of the parameters alone is technically not sufficient to extrapolate the other carbonate parameters, and in such cases a second parameter must be assumed.

Over glacial time scales, there is evidence that ocean pH and CO_3^{2-} concentration were higher during glacial periods (Sanyal et al. 1995; Broecker and Clark 2002), but there is also evidence that ocean pH was relatively stable over the glacial–interglacial cycles (Anderson and Archer 2002). The dichotomy of these results, even over the relatively short time scale of millennia, illustrates the difficulty in reconstructing past ocean chemistry. Despite these problems, Pearson and Palmer (2000) used boron isotopes of deep-sea foraminifera to determine the paleo-pH of the ocean for periods extending back 49 million years. They assumed that ocean alkalinity over that period changed little, and thus used their data to infer atmospheric concentrations over the same period (Fig. 12.2). Broecker and Peng (1982) originally suggested that ocean alkalinity at the last glacial maximum was slightly higher than it is today, but there is no direct proxy for alkalinity, and the assumption of constant alkalinity over time needs to be verified.

Models

Predicting changes in seawater chemistry in the surface ocean over the short term (e.g., 100–200 years) is fairly straightforward. These predictions are complicated, however, by the response of ocean biology to increased pCO_2. Calcification of some of the most important $CaCO_3$ secreters in the oceans (e.g., coccolithophores and foraminifera, as well as reef-building organisms) decreases as pCO_2 increases, while the production of organic carbon could increase, at least in coccolithophores (Riebesell et al. 2000). This not only alters predictions of changes in surface seawater chemistry, but it can also affect our ability to predict changes in the ratio of organic carbon versus inorganic carbon delivered to the deep sea (the "rain ratio"). Changes in the rain ratio in turn affect oceanic uptake of atmospheric CO_2 (Archer et al. 2000a; Sarmiento et al. 2002). Accurately predicting surface changes in seawater chemistry over the next one to two centuries therefore depends primarily on how well we predict how atmospheric CO_2 will change over that time period, and secondarily on how well we predict the biological responses and feedbacks of the ocean.

Attempts to model Pleistocene fluctuations in atmospheric pCO_2 have not adequately captured the mechanisms for the glacial–interglacial differences (e.g., the 80 ppmV increase in pCO_2 since the last glacial maximum). There are many hypotheses to explain these fluctuations, and most concern changes in either the organic carbon pump (storage or burial of organic carbon in the deep sea) or the alkalinity pump (storage or burial of $CaCO_2$ in the deep sea). Even sophisticated models that combine ocean physics, biogeochemistry, and sediment chemistry have been unable to capture the magnitude of glacial–interglacial fluctuations in atmospheric CO_2 concentration (Archer et al. 2000b).

Over longer time periods, additional factors that affect seawater chemistry come into play. For example, deep-sea circulation can enhance CO_2 neutralization through dissolution of deeper-water carbonate; and continental weathering both removes CO_2 from the atmosphere and releases cations that ultimately contribute to ocean alkalinity. However, as demonstrated by results from the Hamburg Model of the Ocean Carbon Cycle (HAMOCC) coupled with a carbonate sediment diagenesis model, these processes would require thousands of years to bring the carbonate system back to preindustrial conditions (Archer, Kheshgi, and Maier-Reimer 1997).

12.4.3 Coral Reef Responses to Seawater Chemistry Change

Natural Chemical Variation on Reefs

Two early field studies tracked the change in seawater carbonate chemistry through time within semienclosed regions: Broecker and Takahashi (1966), on the Bahama Banks; Smith and Pesret (1974), in Fanning Island Lagoon. Both studies found that calcification rates decreased as the calcium carbonate saturation state of the reef waters decreased.

Carbonate chemistry in reef waters is known to fluctuate, sometimes dramatically, in response to both physical forcing and biological processes (Table 12.1). Bates, Samuels, and Merlivat (2001) sampled fCO$_2$ hourly for nearly one month on a Bermuda coral reef flat and found that fCO$_2$ fluctuated greatly (340–470 µatm over the sampling period, with a maximum range of about 60 µatm on any one day). These findings are consistent with measurements of Gattuso et al. (1996) on a reef flat in Moorea (240–420 µatm) and others (Suzuki and Kawahata 1999; Kayanne et al. 2003), where CO_2 rarely exceeded 500 µatm.

Fluctuations in carbonate chemistry of reef waters reflect not only calcification, but also dissolution (Chisholm and Barnes 1998; Halley and Yates 2000). Dissolution of carbonate minerals buffers the carbonate system in seawater because Ca^{2+} and CO_3^{2-} ions are released back into the water column. As saturation state declines, high-magnesium calcite (HMC) is the first mineral to dissolve. As atmospheric CO_2 increases in a system with little exchange with open-ocean seawater, such as in an aquarium or lagoon, buffering due to HMC dissolution cannot bring the system back to preindustrial values, but it can maintain the

Table 12.1. Variation of pCO_2 in coral reef environments. Note that pCO_2 is the partial pressure of CO_2, and fCO_2 is the fugacity of CO_2; the two values are very similar under natural surface seawater conditions

Study	Location	pCO_2 µatm	Comments
Bates, Samuels, and Merlivat (2001)	Bermuda reef flat	340–470	Maximum range of hourly measurements taken over 24 d
Gattuso et al. (1996)	Moorea lagoon	240–420	Maximum range of hourly measurements taken over 3 d
Suzuki and Kawahata (1999)	Palau barrier reef	366–414	Difference between lagoon and open ocean values
	Majuro Atoll	345–370	Difference between lagoon and open ocean values
	South Male Atoll	362–368	Difference between lagoon and open ocean values
Kayanne et al. (2003)	Shiraho Reef (Ryukyu Is.)	200–600	Range of nearly continuous measurements taken over 3 d

seawater saturation state at levels near that of the HMC saturation state. Such a steady state was observed in the Biosphere 2 mesocosm when the CO_3^{2-} concentration approached about 125 µmol kg^{-1}, but this corresponds to more than a doubling of pCO_2, when coral calcification rates would be at least 10% to 20% lower than they were under preindustrial conditions (C. Langdon, personal communication). Numerical modeling designed to examine changes in shallow-water carbonate dissolution and its effect on seawater chemistry found that although dissolution of metastable carbonates was likely, it was insufficient to buffer alkalinity or carbonate saturation state of shallow marine environments (Andersson, Mackenzie, and Ver 2003).

Experiments

Information on possible coral reef responses to changes in seawater chemistry is primarily based on laboratory experiments in which the carbonate chemistry of the seawater is manipulated in various ways (Fig. 12.8; see summary in Langdon 2003). Most of the experiments were performed on single organisms or in aquarium-size mesocosms, and conducted over hours to days. Manipulations of the Biosphere 2 coral reef mesocosm, however, were conducted over weeks to years. All of the experiments, regardless of the size, duration, or type of manipulation, found a reduction in calcification in response to decreased carbonate ion concentration.

Seawater manipulations are difficult in the field, but Schneider and Erez (1999) were able to demonstrate that the calcification response of *Acropora* in the Red Sea was similar to that in laboratory experiments. Halley and Yates (2000) conducted novel field experiments in Hawaii in which they placed large incubation chambers over reef sections and tracked changes in seawater chemistry for more than a day.

They found that as pCO_2 increased in the chambers, calcification rates decreased, but dissolution rates also increased, particularly of HMC. They estimated that on their particular reef the dissolution rate will equal the calcification rate once atmospheric CO_2 concentrations reach double preindustrial levels.

The calcification response of corals and algae thus appears to be affected by changes in the carbonate chemistry of seawater, despite biochemical evidence that corals, at least, exert significant control on the internal chemistry of their tissues (see review by Gattuso, Allemand, and Frankignoulle 1999). The photosynthetic response of zooxanthellae to increased CO_2 concentration is less clear, but it appears that coral zooxanthellae mainly utilize bicarbonate as a substrate for photosynthesis (Al-Moghrabi et al. 1996; Goiran et al. 1996). Zooxanthellar photosynthesis does not increase with increasing pCO_2, and does not appear to be stimulated by the CO_2 released by calcification (Gattuso et al. 2000). However, zooxanthellar photosynthesis does respond to increases in HCO_3^- (Marubini and Thake, 1999; note that HCO_3^- increases as pCO_2 increases). Since zooxanthellar photosynthesis is thought to enhance coral calcification, increased pCO_2 could simultaneously affect calcification in two ways: (1) by decreasing the CO_3^{2-} concentration and (2) by increasing the HCO_3^- concentration. The calcification experiments discussed above (as summarized by Langdon 2003) measured the net effect of both processes, but future experiments should be designed to measure the contribution of each separately.

Paleorecords/Analogues

Geologic Evidence

The dominant form of precipitated $CaCO_3$ has changed several times in the geological past. Such mineralogical shifts are interpreted as markers for major changes in seawater chemistry and/or biota. Two main hypotheses to explain these shifts involve the influence of seawater chemistry on the precipitation of one $CaCO_3$ mineralogy over another. Sandberg (1983) observed that the mineralogy of nonskeletal carbonates has "oscillated" in the Phanerozoic in concert with changes in atmospheric CO_2 and/or sea-level change; in essence, aragonite precipitation occurred when pCO_2 was low ("icehouse" conditions), but did not occur when pCO_2 was high ("greenhouse" conditions). A more recent hypothesis ties the historical calcite:aragonite oscillations to shifts in the magnesium to calcium ratio (Mg:Ca) in seawater (Stanley and Hardie 1998). High Mg^{2+} concentration tends to inhibit calcite precipitation (Berner 1975).

During the Cretaceous and for some time after the Cretaceous–Tertiary (K-T) event and the extinction of rudists, environmental conditions probably favored calcite precipitation. However, reef-building taxa that survived the K-T extinction, scleractinian corals and calcareous algae, secrete skeletons of aragonite or HMC. Indeed, reef building after the K-T event was apparently subdued for some 20 Myr until the Miocene (Kiessling, Flügel, and Golonka 1999; Fig. 12.9), although there are certainly other possible reasons for this delay in reef development, such as the decrease in reef-building taxa in the mass extinction event (Perrin 2002).

Given that atmospheric CO_2 concentrations prior to the Miocene probably remained higher than today, and given that Mg:Ca was probably lower (Wilson and Opdyke 1996), ocean chemistry of the near future cannot be adequately compared to any Tertiary time period (B.N. Opdyke, personal communication). Ocean chemistry of the near future will be extraordinary, mainly because the rapid rate of increase in atmospheric CO_2 will drive the system out of equilibrium. Given time, processes such as weathering will nudge the system back toward steady-state conditions, but in the short term (the next several thousand years) ocean chemistry is likely to be quite different from that of the last 65 Myr.

Recent Field Evidence

Based on experimental data of others (Section 12.4.1), Kleypas et al. (1999) estimated that the average calcification rate on coral reefs might have declined by 6% to 14% as atmospheric CO_2 concentration increased from 280 ppmV to the present-day value of 370 ppmV. However, two studies have shown that calcification rates derived from massive *Porites* in the Great Barrier Reef (GBR) and in Moorea have increased rather than decreased over the latter half of the 20th century (Lough and Barnes 1997, 2000; Bessat and Buigues 2001). Both studies demonstrate a strong linear relationship between temperature and calcification rate, and because temperature and saturation state are strongly correlated in the surface ocean, these studies also offer insight into the relative effects of temperature and seawater chemistry on coral calcification. Since warmer water holds less CO_2, aragonite saturation state increases with increasing temperature (Fig. 12.10A). The Lough and Barnes (2000) analysis of hundreds of *Porites* spp. cores showed that for every 1 °C increase in SST, the calcification rate increased by about 3.5% (Fig. 12.10B), and indeed found a nearly 5-fold increase in calcification rate between *Porites* growing in 23 °C (0.6 g $CaCO_3$ cm^{-2} yr^{-1}) and those growing in 29 °C (2.4 g $CaCO_3$ cm^{-2} yr^{-1}). From a thermodynamic standpoint, at present-day concentrations of atmospheric CO_2, a 1 °C increase in temperature causes about a 2.5% increase in carbonate ion concentration, and by inference from coral calcification-versus-carbonate ion experiments, an increase in calcification. However, the increase in calcification expected from a temperature-induced increase in saturation state can explain only a fraction of the calcification-versus-temperature regressions from the cores (Fig. 12.10B). Simply put, the response of *Porites* calcification to temperature is both biological and geochemical, and the biological response is obviously greater. McNeil, Matear, and Barnes (2004) modeled future coral reef calcification by combining the calcification-versus-SST relationship of Lough and Barnes (2000) and the experimental calcification-versus-saturation state relationship of Langdon et al. (2000). They concluded that increased SSTs in the future will outweigh the effects of decreased saturation state, so that future coral reef calcification will actually increase over the coming century. However, they assumed that coral calcification will increase indefinitely with temperature increase. In reality, calcification in corals peaks near the average summertime temperature, then decreases as temperatures exceed that point (Jokiel and Coles, 1977; Marshall and Clode 2004). Thus, even with the assumption that coral bleaching
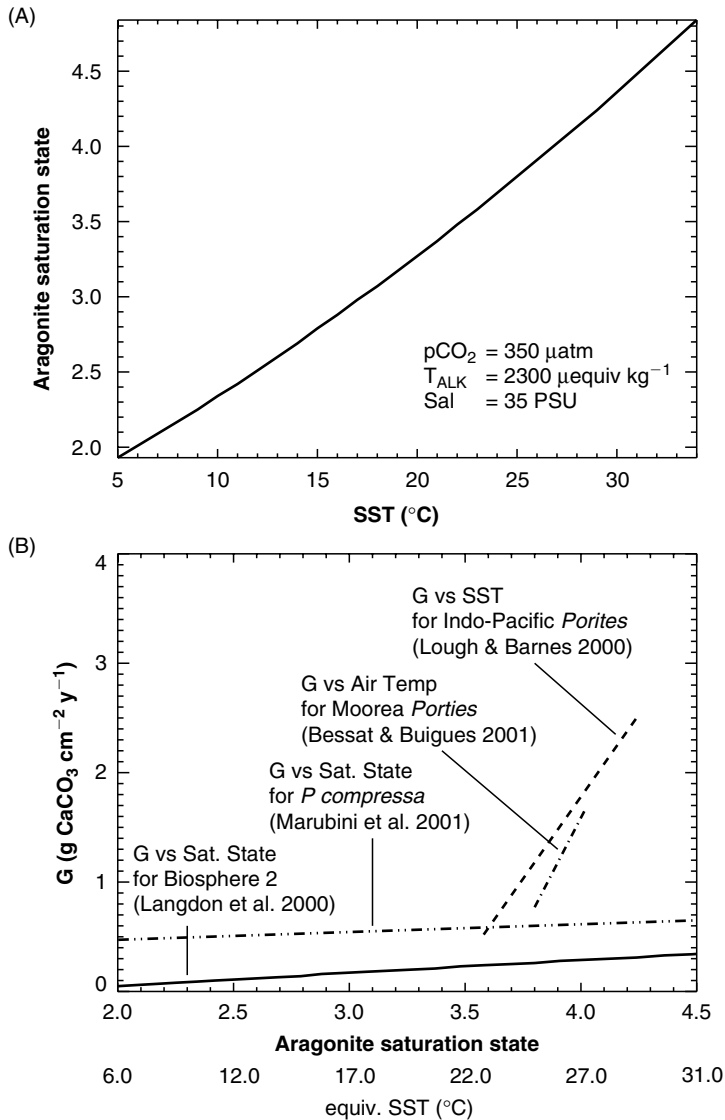
Figure 12.10. (**A**) Aragonite saturation state as a function of SST when other major variables are held constant (pCO_2, total alkalinity, and salinity). Changes in SST explain much of the latitudinal gradient in aragonite saturation state. (**B**) Calcification rate (G) versus aragonite saturation state as inferred from four studies. Note that calcification rate was determined differently in each study, and the results are shown here to illustrate trends and not exact relationships. The solid line represents the G-versus-saturation state relationship determined for long-term (1.9 months to 2.3 years) experiments in the Biosphere 2 mesocosm (Langdon et al. 2000). The dotted-dashed curve represents the G-versus-saturation state relationship for laboratory experiments on *Porites compressa*. The two remaining G-versus-saturation state relationships were inferred from G-versus-temperature relationships

will not occur, while temperature-induced calcification rates may increase in the short term, they are likely to decrease after that (Kleypas et al. 2005). Of course, this suggestion assumes that only temperature and seawater chemistry affect calcification, but in reality other factors should also be considered (e.g., light, water quality, nutrients, food supply). A strong recommendation arising from these results is that future calcification experiments should include both temperature and saturation state as variables. One such study has been performed on *Stylophora pistillata*, with confusing results: at normal temperature, calcification rate did not change with increasing saturation state, but at elevated temperatures, calcification rate decreased by 50% (Reynaud et al. 2003).

Current-day coral reef development is limited at higher latitudes. Coral communities exist at latitudes beyond 30°, but they lose their capacity to build reefs. The calcium carbonate budgets of these coral reef communities must be affected by lower $CaCO_3$ production due to decreased temperature, light, or saturation state; increased $CaCO_3$ removal from increased erosion and off-reef transport, or dissolution; or both lower production and increased removal. Identifying why these communities fail to accumulate calcium carbonate is essential to making predictions of how coral reefs will respond to future changes in seawater chemistry.

12.4.4 Implications for Future Reef Development

With a lowered calcification rate, calcifying organisms would extend their skeletons more slowly and/or make less dense skeletons. Because calcification rates in live specimens are usually measured as either weight changes in individual organisms or via changes in seawater chemistry, how reduced calcification rate is expressed in coral skeletons has rarely been determined and is likely to vary with species. Lough and Barnes (2000) found that slower calcification rates in massive *Porites* were correlated with a decrease in extension rate rather than a decrease in density (density was in fact negatively correlated with calcification rate), while Carricart-Ganivet (2004) found that *Montastraea annularis* maintained its skeletal extension rate despite a change in calcification rate. A reduced extension rate would reduce an individual's ability to compete for space on a reef, whereas reduced density ("osteoporosis") would mean less resistance to breakage, and greater susceptibility to both physical breakdown and bioerosion.

The role of secondary cementation and its response to changes in seawater chemistry could be an important factor in determining both the density of coral skeletons and overall reef calcification rates. Secondary cementation here refers to the inorganic precipitation of aragonite and HMC that occurs within skeletons

Figure 12.10. (*continued*) derived from coral cores, by applying the aragonite saturation state-versus-SSTrelationship shown in (**A**) (note that the temperatures equivalent to the aragonite saturation state on the x axis are shown). The Lough and Barnes (2000) G-versus-SST regression was derived from several hundred *Porites* spp. cores from the Great Barrier Reef and Indo-Pacific. The Bessat and Buigues (2001) G-versus-air temperature regression was derived from a single *Porites lutea* colony from French Polynesia.

and reef structures after the original $CaCO_3$ deposition by organisms. Marine cements are prevalent on most reefs. They contribute to reef building by increasing reef resistance to erosion and by simply adding $CaCO_3$ to the structure. Buddemeier and Oberdorfer (1997) estimated that secondary cementation on Davies Reef, a middle-shelf reef on the GBR, contributes about 100 g $CaCO_3$ m^{-3} yr^{-1}. This is much slower than biological precipitation, but over time, secondary cementation in corals and within reefs can thus contribute significantly to the total reefal $CaCO_3$ (Enmar et al. 2000). In general, secondary cementation within reefs increases with the degree of hydrographic exposure (Marshall 1985), and this is reflected both within individual reefs and across the shelf within reef provinces. Because inorganic precipitation of $CaCO_3$ is primarily controlled by thermodynamic rather than biological factors, a reasonable hypothesis is that secondary cementation will decrease in response to increased pCO_2. However, whether future increases in pCO_2 will result in decreased reef cementation, and whether decreased cementation affects reef growth overall, remain essentially unknown.

Reef building itself is the net sum of carbonate deposition, primarily via $CaCO_3$ precipitation, less its removal through erosion, off-reef sediment transport, and dissolution. A reduction in $CaCO_3$ precipitation by whatever means—organism mortality, lowered calcification rates, lowered cementation rates, increased dissolution rates—ultimately lowers the net carbonate deposition on a reef, and thus its reef-building potential (see review by Kleypas, Buddemeier, and Gattuso 2001). The structure of slower-growing reefs would, therefore, be at a greater risk from a reduction in calcification rate than faster-growing reefs.

Regional Effects

Carbonate accumulation on some reefs is naturally low, due to either a low $CaCO_3$ production rate or a high $CaCO_3$ removal rate. High-latitude reefs are often considered marginal in terms of their reef-building capacity, and their slow reef-building state is thought to be a consequence of cooler temperatures, shallower light penetration, or lower saturation state (Kleypas et al. 1999). Although ocean warming will likely allow the migration of corals poleward by a few degrees latitude, future changes in seawater chemistry may drive carbonate budgets in these areas to levels below that required for reef building (Guinotte, Buddemeier, and Kleypas 2003).

Some reefs that are considered marginal may experience less change in surface ocean chemistry than others. Upwelling regions, for example, tend to be dominated by the chemistry of the upwelled waters. Upwelled waters of high pCO_2, for example, strongly affect the Galápagos reefs (other factors such as low temperature and high nutrients are also important). The pCO_2 of these waters can exceed 500 µatm (120 µatm higher than current atmospheric pCO_2). The Galápagos reefs, and other reefs which are dominated by upwelling, may actually be less affected by changes in seawater chemistry in the future. In fact, the Galápagos and other eastern Pacific reefs may provide present-day analogues for studying reef response to increased pCO_2. These reefs tend to be slow-growing and are poorly cemented (Cortés 1997; Glynn and Macintyre 1977). Following the 1982 to 1983 bleaching and mass mortality event in the Galápagos, the reef

structure was nearly destroyed by bioerosion (Glynn 1988; Eakin 1996, 2001). This leads one to question whether the extremely rapid loss of $CaCO_3$ on Galápagos reefs was influenced by their poor cementation or increased dissolution under the naturally higher pCO_2 conditions.

12.5 Sea-Level Rise

Sea-level rise as a consequence of global warming is not considered a major threat to coral reef development. This is because the projected rise of 0.1 to 0.8 m by the end of the 21st century (Houghton et al. 2001) is two orders of magnitude less than the 120-m rise since the last glacial maximum. Reefs are not, therefore, considered to be directly threatened by sea-level rise, at least in terms of "drowning" due to decreased light-dependent calcification rates in deeper water. However, indirect effects of sea-level rise could have an impact on some reefs, in cases in which nutrients and sediments released from newly flooded coastlines will lead to degradation of water quality (Neumann and Macintyre 1985).

12.6 Summary and Conclusions

Future increases in greenhouse gas emissions will create a suite of environmental conditions that lie outside those experienced by modern humans. The current rapid rate of increase in atmospheric CO_2 concentration is effectively a shock to Earth's climate system and to the carbonate system in seawater, because the rates at which natural feedbacks can return these systems to equilibrium are far slower than the rate of atmospheric CO_2 increase. This chapter considers possible future coral reef environments by systematically looking at future projections of atmospheric CO_2, sea-surface temperature, and seawater chemisty, and by examining whether analogues for these projections occur, either within present-day environments or in the past.

Predicting coral reef responses to future climate change and changing seawater chemistry is hampered by uncertainty at multiple levels. Uncertainty begins with projections of future CO_2 emissions (Table 12.2). The range of projected greenhouse-gas emissions varies greatly because of the difficulty of predicting future population growth, economic growth, political stability, and technological advances. Additional uncertainty arises from climate modeling efforts; modeled increases in average global surface temperature, as reported in the Third IPCC Report (Houghton et al. 2001), range between 1.4 and 5.8 °C. This range reflects variations in different global climate models as well as future greenhouse-gas emission scenarios. Finally, predicting coral reef responses to warming SSTs is fraught with uncertainty as to how coral reef organisms and ecosystems will respond to these changes as well as other possible changes in regional climates (e.g., changing frequencies and intensities of ENSO events; tropical storms, rainfall and river runoff, etc.). Predicting changes in seawater chemistry is considerably easier than predicting temperature changes but there remains considerable

Table 12.2. Summary of preindustrial versus projected values for several climate-change-related variables that can affect coral reefs. Analogues from both present-day and the past environments are listed

Variable	Preindustrial values	Projected values	Present-day analogues	Past analogues	Notes
Atm. CO_2	280 ppmV	555–825 ppmV	None	Early Tertiary, Cretaceous	Records most reliable for past 400 kyr. Older records rely on chemical and biological proxies.
Max. SST	30–31 °C (higher in enclosed seas)	31–33 °C? (higher in enclosed seas)	Red Sea / Persian Gulf (34 °C)	Early Tertiary, Cretaceous	Role of ocean "thermostat" in mediating maximum SST is uncertain. Higher latitudes will experience greater change.
$[CO_3^{2-}]$	200–350 μmol kg^{-1}	150–250 μmol kg^{-1}	Extratropics	Early Tertiary?	Knowing atmospheric CO_2 concentration alone is insufficient for determining carbonate equilibria in seawater; also need pH, TCO_2, or alkalinity. Effects of other seawater chemistry parameters, e.g., Mg/Ca, probably play a role in precipitation of various carbonate mineralogies
Sea-level rise	Stable	< 1 m	Reefs in subsiding regions	Holocene, Pleistocene glacial–interglacial sea-level rise	Sea level per se is not considered a threat to reefs. Sea-level-related increases in coastal erosion and nutrient inputs considered a threat to some reefs.

uncertainty as to how calcifying organisms will respond to seawater-chemistry changes, particularly in combination with other environmental changes.

Present-day environments can offer some clues about how reefs will survive in the future. Corals in semienclosed seas already tolerate higher-than-normal SSTs, as do corals in tidal pools. The reasons for their higher temperature tolerance— whether it is through acclimation, acclimatization, or adaptation—could provide clues to the time scale of coral adaptation to future temperature increases. Similarly, non-reef-building coral communities that already exist under high pCO_2 conditions (e.g., high-latitude reefs and the Galápagos) may provide clues about the importance of carbonate saturation state to reef building.

The most recent time period of Earth history that had atmospheric CO_2 concentrations similar to those of future projections appears to be the early Tertiary, sometime prior to the Miocene and the onset of major glaciations. Can reef scientists look to the early Tertiary as a guide to what future reefs will look like? Reefs did exist during this period of higher SSTs and higher atmospheric CO_2 concentrations. However, high atmospheric CO_2 alone does not mean that the carbonate-ion concentration of the early Tertiary oceans was lower. Higher alkalinities, for example, would have counteracted the effects of higher pCO_2. Because of this incomplete knowledge of the carbonate system of past oceans, the question of whether coral reefs ever existed under lower carbonate-ion concentrations cannot yet be answered. Another difficulty with using this time period as an analogue for future reef environments has to do with reef ecology. Reefs prior to the Miocene were likely quite different from those of today; the acroporids, for example, were not yet major reef components.

Warming SSTs and changes in ENSO frequency and/or intensity are probably the most significant projected climate changes that will affect coral reefs. It is almost certain that average tropical SSTs will continue to increase in the future by an average of 1 to 3 °C. Even with an SST thermostat of 30 °C, many parts of the tropical ocean have maximum SSTs significantly below this threshold and could experience continued warming. Increases in SST maxima experienced by some corals will exceed their capacity to adapt, and mass coral bleaching is likely to occur with increasing frequency on those reefs. Whether ENSO frequency or intensity will increase in response to global warming is still uncertain. Attempts to quantify the potential effects of future SST increases on coral bleaching rely not only on broad assumptions about future changes in SST extremes and variability, but also on assumptions about the abilities of corals to adapt to increases in SST. Predictions, therefore, range from almost no bleaching mortality, through changed coral reef community structure (favoring more thermally resistant species), to the total collapse of reef ecosystems. Current-day observations drive predictions of future coral reef response to bleaching. Records of past coral bleaching have proven elusive, either because bleaching was rare in the past or because it is still too difficult to detect within the coral skeletal record. It is clear, however, that the occurrence and magnitude of mass coral-bleaching events have increased in recent decades with only a relatively modest SST warming in comparison to that projected by the end of this century.

   Possible effects of changes in seawater chemistry on reef communities and on reef building are largely based on geochemical arguments. Essentially all of the experiments that have manipulated seawater chemistry and measured effects on corals, calcifying algae, and coral reef mesocosms indicate that calcification approaches a linear response to decreased carbonate saturation state. This suggests a strong geochemical control over calcification. In contrast, calcification rates derived from cores of *Porites* heads illustrate a stronger response to temperature changes than to declining saturation state, at least within two separate regions. Regardless of the biological factors that control $CaCO_3$ precipitation, it is very likely that dissolution will increase on reefs as atmospheric CO_2 concentrations increase. At the very least, $CaCO_3$ budgets will decrease on coral reefs overall (particularly if coral cover on reefs declines) and reef building will decrease.

   Reef scientists are not likely to lower the uncertainty of predictions about the future Earth climate system, but future research *can* lower the uncertainty about reef responses to changes in climate and atmospheric chemistry. Some of the best analogues for reef responses to changes in climate and atmospheric chemistry can be found on present-day Earth, by looking at reefs living in high-temperature semi-enclosed seas and in regions with naturally low carbonate saturation states. Although the closest paleo-analogue for our future climate appears to be the early Tertiary, the current uncertainties associated with estimates of atmospheric CO_2, tropical SSTs, seawater chemistry, and reef ecology for that time period are too poorly constrained to provide an adequate analogue for predicting the future of coral reefs within the next decade or so. The urgent need to understand reef response to climate change, and to design effective mitigative and managerial strategies, will need to rely more heavily on present-day observations and experimental manipulations.

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