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## Abstract

Reef building has responded to changes in climate, ocean chemistry, and a variety of other physical and biological factors during the geologic past, as have the taxa involved. Many of the data revealed by the geologic record are also relevant to human impacts on coral reefs today and their success moving forward. This chapter reviews the responses of reefs and reef builders to environmental changes over Earth's history and relates this information to projected changes due to anthropogenic activities going forward. These changes include increasing temperature, ocean acidification, more intense storms, sea-level rise, nutrification, and sedimentation. Past events provide some insights, but are somewhat limited proxies of future impacts, largely because of the perhaps unprecedented current rate of CO<sub>2</sub> release today. Present-day rates of climate change and ocean acidification may be higher than at any point in the geologic past, and may exceed the capacity for corals and other reef builders to tolerate or adapt to the changing environment.

## Keywords

Coral • Reef • Biomineralization • Calcification • Ocean acidification • PETM • Calcite • Aragonite • Climate change

## 9.1 Introduction

Environmental changes can impact the capacity for corals and other calcifying organisms to build reefs. Many of the changes that are projected to occur in response to anthropogenic influences have occurred in the geologic past. This chapter complements the discussion of calcification by modern corals in Chap. 2 and the geologic history of photosymbiosis in Chap. 3 by considering pre-anthropogenic variations in the physical, chemical and biological regime of the world ocean and their effects on the evolution of reefs and reef building organisms through time. It summarizes what is known about how organisms

responded to past climate, ocean chemistry, and other factors and provides insight into how future reefs may react to environmental changes driven by human activities including increasing temperature, ocean acidification (OA), more intense storms, sea-level rise, nutrification, and sedimentation. Relevant reviews include: Stanley (2003), on the evolution of modern scleractinians; Kiessling (2009), on geologic and biologic controls of reef evolution; Pandolfi et al. (2011) on modern aspects of coral reef paleoecology within a historical framework; Hönisch et al. (2012), on geological evidence of OA and its effects over the past ~300 million years; Hansen et al. (2013) on what past climate change might tell us about future impacts to reefs and on the humans that depend on them.

This chapter builds on these discussions and the chronicling of reef history in Chap. 8, tying past events more closely to changing ocean conditions. It also distinguishes between the evolving suite of carbonate-

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producing organisms and the development of the structures they built and inhabited. Chapter 6 points out that, while the two are inextricably linked, reef building involves more than just calcification. Looking to the future, accelerating sea-level rise will challenge the ability of reefs to keep up; the overview in the following pages attempts to put this into the context of reef evolution in the geologic past as well as the possible fate of reefs in the twenty-first century and beyond.

We begin with an overview of the processes that are most intimately tied to coral growth and reef building. We then chronicle the evolution of reefs since the Archean Eon in response to changes in physical and chemical conditions and ecological interactions. Finally, these lessons are applied to possible scenarios in the twenty-first century to provide a contrast between pre- and post-anthropogenic factors related to reef building.

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## 9.2 Physical, Chemical, and Biological Drivers of Reef Building

Reef accretion in tropical and subtropical waters is driven by high rates of calcification, primarily among photosymbiotic corals and calcifying algae, which exceed local rates of reef erosion and dissolution. Not all shallow-water corals are symbiotic, and not all symbiotic corals grow fast enough to build reefs. Conversely, some non-photosynthetic species of primarily deep-water corals can still produce reefs. They tend to be slower-growing than their shallow-water counterparts, but live in environments with lower disturbance, allowing for the accumulation of reef carbonates over time. The ability of shallow- and deep-water corals to create reefs is constrained by environmental and biological factors. Changes in these parameters modulate rates of reef building across space and time.

Organisms cope with changes in their environment through three major mechanisms: migration, acclimatization, and adaptation. In some situations organisms can cope with changing environmental conditions by simply moving from one place to another to find suitable habitat. Sessile species such as adult corals cannot migrate, but their planktonic larvae can disperse, potentially over great distances. A variety of physical (e.g., current velocity) and biological (e.g., planktonic larval duration) factors constrain how fast and far marine organisms can move from one place to another. Successful migration is only possible if suitable habitat exists at the new location. Under global change, there may be nowhere to run, requiring organisms to engage in other responses to survive.

One possibility is acclimatization (also referred to as phenotypic plasticity). This occurs through physiological

or behavioral changes within a *single organism* based on previous conditioning, and occurs *within a single generation*. Another possible option is adaptation (i.e., evolution by natural selection). This occurs due to selective pressure acting on heritable variation within a *population*, and occurs over *one or more generations*. On an evolutionary scale, acclimatization is relatively fast-acting, but is inherently limited in the scope of variation it can generate. Adaptation may require long periods of time to achieve major changes, but it is less constrained in the degree of variation it can generate.

By way of example, a bird with a broken wing which is unable to fly would lose mass in its flight muscles due to a lack of exercise, but would regain that mass after the bone heals and the muscles can be exercised again. That process of losing and regaining muscle mass is acclimatization—the flight muscles undergo physiological changes according to usage. In contrast, turning the forearm of a dinosaur into the wing of a bird is an exquisite adaptation that requires evolution. The rate of evolution is often slow but it can increase dramatically in a rapidly changing environment, given strong selective pressure.

Sometimes the rate of environmental change exceeds the rate at which organisms can migrate, acclimatize, or adapt leaving only one option—to die. Results can range from the death of individuals to the collapse of entire populations, leading to the extinction of species. These events are more common than we might imagine; as Carl Sagan quipped, “Extinction is the Rule. Survival is the exception.” And, even where species are able to survive under environmental change, their ecological roles may shift under the new conditions. At many times in the geologic past, for example, corals survived major environmental perturbations even as coral-reef building ground to a halt.

Whether we are looking into the deep past or the immediate future, it is important to understand the factors which fundamentally impact growth rates of organisms and the reefs that they build. Many of these factors have undergone changes in the past, and can help us to understand natural changes in reefs. However, environmental conditions are changing rapidly due to climate change and other human influences such that migration, acclimatization or adaptation may not be viable options for some species. The following pages will focus on how environmental and biological factors interact to drive changes in reef building. We then examine the rise and fall of reefs and reef biota throughout geologic time, focusing in particular on ocean and climate processes that are most relevant to the present-day situation. Finally, we use these past responses to consider the fate of future reefs as the rate of change in key environmental factors continues to accelerate.

### 9.2.1 Light, Turbidity, and Sedimentation

Calcification in shallow-water, reef building corals is fundamentally a light-driven process and some scleractinian corals have been photosymbiotic since at least the Triassic (Muscatine et al. 2005; Stanley and Helmle 2010; see also Chaps. 3 and 8). The fact that calcification rates of symbiotic corals tend to be higher in the light than in the dark has been known for decades (Kawaguti and Sakumoto 1948; Muscatine and Cernichiari 1969). A variety of possible mechanisms for “light-enhanced calcification” have been offered (see Chap. 2), though the best-supported hypothesis to date involves photosynthesis providing the raw materials needed for calcification, particularly energy-rich photosynthetic products and oxygen (Colombo-Pallotta et al. 2010; Holcomb et al. 2014). Photosynthesis also provides a portion of the precursors needed to synthesize organic matrix molecules, which are critical for the nucleation and growth of calcium carbonate crystals by calcifying organisms (Allemand et al. 1998; Muscatine et al. 2005).

Any factor that clouds the water, such as elevated turbidity from sediment runoff or an increase in plankton, can negatively impact reef building by reducing the amount of light available to drive calcification. Reef building corals growing in clear, oceanic waters may not reach their minimum light requirements until 80 m depth (Lesser et al. 2010), whereas on a turbid reef, similar limits of irradiance can be reached at less than 12 m (Dunne and Brown 1996). In a highly turbid estuary, irradiance may fall below the limits needed to support symbiotic corals within centimeters of the surface, preventing the development of reefs. Sedimentation is a natural process on reefs (Hubbard 1986; Rogers 1990; Anthony and Fabricius 2000), but human activities have led to increased levels of turbidity and sedimentation in some reef areas due to enhanced sediment loading from land-based sources, or dredging (McCulloch et al. 2003; Brodie et al. 2012; Cramer et al. 2012; Pollock et al. 2014). Reduced light penetration due to increased turbidity combined with either direct or indirect effects of excessive sedimentation (e.g., impacts on disease, coral-algal competition, recruitment, etc.) can negatively impact reef building (Hubbard 1986; Cramer et al. 2012; Jokiel et al. 2014; Perez et al. 2014; Pollock et al. 2014). Some coral species are well-adapted to high sedimentation, however, and can continue reef building even under sediment loads that would devastate others (Anthony and Fabricius 2000; Perry et al. 2012).

With increasing water depth, shallow-water coral species become light-limited, but at greater depths their role as reef builders is sometimes taken over by other species of mesophotic corals (30–165 m; Maragos and Jokiel 1986; Locker et al. 2010; Sherman et al. 2010; Weinstein et al. 2014). Mesophotic reef communities are often

distinctive compared to shallow-water assemblages, but many of the coral species are photosynthetic reef builders, as are calcifying algae (reviewed by Kahng et al. 2010). A suite of adaptations are needed for these organisms to thrive under such low irradiance, though these adaptations are not well understood. A few coral species can be found from shallow to mesophotic depths and shift from higher contributions of autotrophy to more heterotrophy along this depth gradient (Lesser et al. 2010). Most corals are more restricted in distribution, either to shallow or deeper waters, presumably because their light tolerances are more limited than in widely distributed species. Descending further still into the water column, beyond the euphotic zone, one eventually reaches cold and dark water where aposymbiotic (i.e., non-photosynthetic) corals build deep-water reefs (reviewed by Roberts et al. 2003; Freiwald et al. 2004; Roberts et al. 2006). These corals rely on light only insofar as it drives the growth of plankton in shallower waters that eventually serves as food for the coral communities in deep water. Even though deep-water corals tend to grow much more slowly than their shallow-water counterparts, they can nonetheless build structural reefs given enough time.

### 9.2.2 Temperature

On most contemporary coral reefs, normal seasonal maximum temperatures range from ~27 to 30 °C, though some reefs fall well outside these limits (Kleypas et al. 1999; Jokiel and Brown 2004). On the cool end of the range, the reefs around Lord Howe Island, Australia, reach a normal seasonal maximum temperature of only 24 °C. In contrast, the reefs of the Arabian Gulf reach normal seasonal maximum temperatures of 33–34 °C—a full 9–10 °C warmer (Hughes et al. 2003). This regional variation correlates with differences in coral thermal limits. Corals tend to undergo paling or bleaching (the loss of symbiotic algae or algal pigments) at temperatures 1–2 °C above the normal maximum to which they are accustomed, even at the extremes of 24 °C and 34 °C (Coles et al. 1976; Jokiel and Brown 2004), and both adaptation and acclimatization appear to play roles in setting these limits (Maynard et al. 2008; Barshis et al. 2010; Guest et al. 2012; Barshis et al. 2013). Some equatorial reefs rarely experience temperatures below 27–28 °C whereas high latitude reefs can experience temperatures as low as 18–19 °C for up to several months (Jokiel and Coles 1977; Kleypas et al. 1999; Jokiel and Brown 2004). Some subtropical corals tolerate temperatures as low as 15–16 °C for short periods of time, and exceptional corals in the Arabian Gulf even tolerate brief exposure to temperatures as low as 11 °C (Jokiel and Coles 1977; Coles and Fadlallah 1991). Perhaps the most extreme example of low temperature tolerance among

symbiotic corals is exhibited by *Oulastrea crispata* which is known to survive brief exposure to temperatures as low as 0 °C (Yajima et al. 1986).

While some reefbuilding corals can survive exposure to quite cool temperatures, reef development is exceptionally rare in areas where the temperature drops below 18 °C for more than a few weeks (Jokiel and Coles 1977; Veron 1995). The total annual coral growth rates on cooler, high-latitude reefs may simply be too low to support reef building, though some subtropical corals grow as fast as tropical species (Ross et al. 2015). Other covariates (e.g., nutrient availability, irradiance, herbivory, etc.) probably reinforce the 18 °C isotherm as the lower temperature limit for shallow-water reef building. No such upper thermal limit appears to occur in modern oceans, though anthropogenic climate change may induce a transient upper thermal limit to reef building in the future. Hence, upper thermal limits for reef formation vary from region to region and appear to be flexible over evolutionary timescales, but the lower thermal limit for reef building of 18 °C seems to be more fixed (see Sect. 9.4 below for a discussion of reef building under climate change).

The temperature tolerances of deep-water corals are not as well studied as those of shallow-water corals, but appear to provide equally strong constraints on deep-water reef development. *Lophelia* reefs tend to be associated with water masses that have a temperature of 4–12 °C (reviewed by Roberts et al. 2003; Freiwald et al. 2004; Roberts et al. 2006).

### 9.2.3 Nutrients, Herbivory, and Bioerosion

Shallow-water coral reefs are restricted to oligotrophic and mesotrophic waters where the concentrations of dissolved inorganic nutrients (e.g. ammonium, nitrate, and phosphate) are relatively low. The absolute nutrient concentrations and the availability of particulate organic nutrient sources, however, vary widely on shallow-water reefs, and some communities are subject to anthropogenic nutrient enrichment (reviewed by Kleypas et al. 1999; Szmant 2002; Atkinson 2011). Reefs are also characterized by high biomass and high rates of primary production (reviewed by Atkinson 2011). The role of nutrients in coral-reef building can be summarized as follows: corals and other calcifiers require a supply of nutrients to maintain normal physiological function, but excessive nutrient supply (either due to natural processes or human influence) inhibits carbonate accretion through both direct and indirect mechanisms. Reef organisms are adapted to low and relatively constant supplies of nutrients, but also rapidly take up nutrients during infrequent periods of elevated supply. While this is an efficient use of available resources, it also makes them

sensitive to small increases in nutrients that would not negatively impact many other natural communities (Atkinson 2011).

Under some circumstances, elevated nutrient concentrations have direct, negative effects on coral health and growth (Muscatine et al. 1989; Stimson and Kinzie 1991; Falkowski et al. 1993; Jokiel et al. 1994; Marubini and Atkinson 1999; Ferrier-Pagès et al. 2000; Koop et al. 2001; Loya et al. 2004). Elevated nutrient supply may also interact with other stressors, such as temperature or light stress, leading to negative outcomes for corals (Vega Thurber et al. 2013; Wiedenmann et al. 2013).

In aquarium experiments, where the corals are removed from confounding stressors like adverse light and temperature levels or excessive algae, coral growth can be faster under conditions of modest nutrient enrichment than without it (Godinot et al. 2011; Dunn et al. 2012). DeCarlo et al. (2015) have made similar observations in nature. However, at some point a threshold is reached where higher nutrient supply drives ecological changes (e.g., algal proliferation) that are adverse to coral growth.

In contrast with direct impacts on corals, excessive nutrients inhibit reef building largely through indirect pathways. Nutrient enrichment stimulates the growth and virulence of some coral pathogens, increasing rates of coral loss due to disease (Bruno et al. 2003; Voss and Richardson 2006; Vega Thurber et al. 2013). Elevated nutrients also stimulate the growth of algae, including phytoplankton and benthic macroalgae and microalgae. The latter then may overgrow and kill corals and inhibit coral recruitment. There has been much debate over the relative importance of bottom-up (i.e., nutrient supply) vs. top-down (i.e., herbivory) controls on reef-algae abundance (Hughes 1994; Lapointe 1997; Lirman 2001; Thacker et al. 2001; Szmant 2002; Hughes et al. 2007), but it is clear that both processes are important. When algae have more nutrients they grow faster, and may overgrow and kill corals. If there is insufficient herbivory algae can overgrow and damage corals, and block coral recruitment. With too many nutrients, too little herbivory, or a combination, reefs become choked with algae, and reef building grinds to a halt.

Perhaps most insidious are the effects of nutrient enrichment on bioerosion. The overall rate of reef building depends not just on the constructional processes (e.g., coral growth rates), but equally on the erosional ones (e.g., bioerosion—see Chap. 4). Grazing organisms (primarily parrotfish and urchins) grind away substrate as they consume algae. A diverse array of organisms make a living by boring into the reef itself, and many of these feed on plankton, detritus, or benthic algae. Nutrient enrichment increases the food supply for bioeroders, dramatically enhancing substrate loss in many cases, but not universally (reviewed by Glynn 1997; Chazottes 2002; DeCarlo et al. 2015; Glynn

and Manzello 2015). Higher planktonic food availability often enhances coral growth rates (Ferrier-Pagès et al. 2003; Edmunds 2011; Forsman et al. 2012; DeCarlo et al. 2015), but not as much as it enhances bioerosion. Small increases in nutrient supply are often tolerable or even beneficial for reef builders, and corals may grow fastest under slightly mesotrophic conditions. However, elevated nutrients can still be detrimental to the geological process of reef building due to a larger relative increase in bioerosion (Perry et al. 2014; DeCarlo et al. 2015).

#### 9.2.4 Water Motion and Storm Damage

Water motion is a major factor controlling the exchange of nutrients, oxygen, and other vital compounds between the reef benthos and the overlying water column (Shashar et al. 1993; Kühl et al. 1995; Gardella and Edmunds 1999; Finelli et al. 2006; Atkinson 2011). Flushing of the water overlying reefs also moderates fluctuations in temperature, chemistry, and other parameters that result from local physical and biogeochemical fluxes. As a negative factor, water motion can increase sedimentation rates by re-suspending sediment, but as a positive factor it helps to remove sediment from corals and other surfaces. Water motion is, therefore, a critically important parameter for the healthy function of corals and other benthic reef organisms.

Different coral species are adapted to different flow regimes, with delicate-branching, foliaceous, or fleshy forms (such as *Euphyllia* spp.) well-adapted to gentle flow, whereas many mounding, encrusting, or thick-branching species can tolerate (or even require) much stronger water motion. Coral species are capable of acclimatizing to a range of mean and maximum water flow velocities, but the breadth of this range varies. Jokiel (1978) found that the coral *Pocillopora meandrina* is restricted to turbulent environments in Kāneʻohe Bay, Hawaiʻi whereas the congener *Pocillopora damicornis* is most abundant on semi-protected reefs. These differences in habitat preference parallel different capacities to tolerate high and low extremes in water motion by each species.

Tropical storms can deliver huge amounts of wave energy onto reefs, reducing reef building by physically damaging and killing corals, and by washing away reef carbonates (Chap. 6). Periodic removal of sand and silt, however, benefits reef building by flushing away sediments which would otherwise accumulate and eventually smother the corals (Hubbard, 1986; Hubbard and Miller 1990; Scoffin, 1993; Jokiel 2006). The role of tropical storms in structuring reef communities and the impacts of storms on reef building depend largely on the frequency and intensity of disturbance, which vary substantially over space and time (Hubbard et al. 2008; Hubbard 2011). Many of the

Caribbean islands, the Bahamas, and South Florida, for example, experience frequent hurricanes whereas reefs in the southernmost Caribbean (from roughly Nicaragua to Venezuela and the Dutch Antilles) are only rarely struck by major storms (National Hurricane Center 2014). Branching corals and others with less robust growth forms tend to be more severely affected by hurricanes than are mounding corals, due to their greater propensity to be broken and damaged. Some of the coral mortality associated with storm damage is also driven by secondary disease outbreaks, with the large-scale tissue damage facilitating infection (Knowlton et al., 1981; Miller et al. 2009).

Under anthropogenic climate change, the strength of tropical storms (and possibly their frequency) is expected to increase (Webster et al. 2005; IPCC 2013). Greater storm intensity is a straightforward consequence of higher ocean and atmospheric temperatures. Therefore, storm damage on coral reefs is likely to increase in the future, though the relative importance of this increase will undoubtedly vary. Conversely, tropical storms can also cool shallow waters by mixing them with deeper waters, through evaporative cooling, and by reducing solar input, all of which reduce thermal stress on reefs. The beneficial cooling effects of tropical storms extend up to several hundred kilometers away from the center of the storm, whereas the negative effects from storm damage typically reach <100 km (Manzello et al. 2007). Storm damage is likely to increase in the future, yet tropical storms may also provide reefs with a temporary respite from higher seawater temperatures.

#### 9.2.5 Carbonate Chemistry

Human activities, particularly the burning of fossil fuels, deforestation, and cement production, are releasing CO<sub>2</sub> to the environment. Roughly one-quarter of these emissions are absorbed by the ocean, leading to changes in seawater chemistry (Caldeira and Wickett 2003), a process known as ocean acidification (OA). Interest in understanding the impacts of OA on marine organisms and ecosystems has grown over the last decade. Chapter 2 discusses the effects of carbonate chemistry on modern coral reefs. The effects of carbonate chemistry (including OA) on reef building over geologic time are considered below.

#### 9.2.6 Sea-Level Rise

High sea levels lead to the inundation of continents (i.e., marine transgressions) and the generation of shallow, inland seas with resulting formation of huge areas of suitable habitat for shallow-water reef building. Some of the highest rates of reef building and the greatest radiations of marine species

coincided with sea-level highstands in the geologic past (Droser 2003; Kiessling 2006; Servais et al. 2008; Kiessling 2009; Munnecke et al. 2010; see also Chap. 8). The effects of sea-level *rise* on reef building, however, depend largely on how fast the rise is occurring. Under low or moderate rates of sea-level rise, vertical reef accretion can keep pace with or even catch up to the rising ocean. As the reef reaches the surface of the water, it is unable to build any higher, but a moderate rate of sea-level rise allows reefs to continue accreting vertically (Neumann and Macintyre 1985). Once the reef has filled all available accommodation space, it will either build seaward (e.g., in the Caribbean: Chap. 6: Fig. 6.1) or landward in the form of widening reef flats such as those that developed along many Indo-Pacific and GBR reefs after sea level reached its maximum between 8000 and 6000 years ago (Davies and Hopley 1983; Davies et al. 1985; Hopley et al. 2007).

Under high rates of sea-level rise, even rapid reef accretion may be unable to keep up, ultimately resulting in reefs “drowning” below the waves. Tropical oceans around the world are littered with the submerged remains of old reefs. Some of these are the remnants of reefs that were unable to keep up with the rapid sea-level rise that occurred between the last glacial period and the current interglacial. Sea-level rise continues to accelerate with sea level expected to increase by at least 0.5 m, and perhaps as much as 2 m by the end of this century (Jevrejeva et al. 2009, 2012; IPCC 2013). The present rate of sea-level rise ( $\sim 3.3 \text{ mm yr}^{-1}$ ; Church and White 2006, 2011) is in excess of the rate at which many coral reefs can accrete vertically, even under optimal conditions (perhaps more than half of the world’s reefs: see Chap. 6) and conditions are far from optimal on many reefs today due to a variety of anthropogenic stressors. Without limiting climate change, sea-level rise will continue for centuries or millennia and could easily drown most of the world’s present-day coral reefs.

### 9.3 The Rise and Fall of Reefs Through Time

Any rocky promontory can support diverse and productive biological communities, but coral reef organisms build the structures on which they flourish. The sheer abundance and ecological complexity of biogenic reefs during the Phanerozoic Eon, the last 542 million years (Ma), have established their prominence over both space and time.

The history of reefs over geologic time is one of boom and bust, characterized by major episodes of biological turnover and several reef crises (see Chap. 8). Some of these changes correlate with major extinction events, but others have been difficult to explain. Reefs have been successful and repressed during both greenhouse and icehouse climates; they have both flourished and floundered during

times of (likely) high atmospheric  $\text{CO}_2$ . The general evolutionary patterns of reefs and reef builders through geologic time have already been described in Chaps. 8 and 3 stresses the importance of the evolving photosymbiotic association between reef autotrophs and heterotrophs. The following overview focuses on reef responses to past changes in the climatic, oceanographic, and the ecological drivers of reef building detailed above.

#### 9.3.1 The First Reefs

Stromatolites are layered, carbonate structures that formed through the cementation of sediments by mineral precipitation and first appear in the geologic record during the Archean, some 3.5 billion years ago (Ba). Some stromatolites may have formed through strictly abiotic processes, but many were formed through the action of microbial assemblages (Allwood et al. 2007; Lepot et al. 2008). In particular, mats of cyanobacteria and eventually primordial eukaryotes were responsible for the formation of many stromatolites and thrombolites. Such mats and biofilms readily trap sediments. During the daytime the mats consume  $\text{CO}_2$  through photosynthesis, raising the local pH and facilitating the cementation of sediment into a hard structure. Because of the light-dependent nature of this process, stromatolites tend to form in shallow water and to accrete vertically. The oldest stromatolites of confirmed microbial origin date to 2.74 Ba (Lepot et al. 2008), though there is evidence of microbial stromatolites formed 3.43 billion years ago—among the oldest evidence of life on Earth (Allwood et al. 2007).

Following a long run of increasing stromatolite abundance and diversity, they started to decline around 1.25 Ba (Allwood et al. 2007), coincident with the proliferation of metazoan burrowers and grazers. Structures potentially formed by early metazoan burrowers have been reported from 1.1 Ba (Seilacher et al. 1998), though subsequent work has suggested that these were abiotic in origin (Budd and Jensen 2000; Jensen 2003). By the Ediacaran period ( $\sim 565 \text{ Ma}$ ), horizontal burrows formed directly under the microbial mats reflecting clear biotic activity, perhaps to avoid predators (Dzik 2007). Vertical burrowing in the Early Cambrian ( $\sim 542 \text{ Ma}$ ) was patchy and developed at different rates in different places (Dornbos et al. 2004). During the Ordovician ( $\sim 485\text{--}443 \text{ Ma}$ ), metazoan animals underwent a major evolutionary radiation and stromatolites declined further. This pattern continued afterward, with the exception of brief intervals following the end-Ordovician and end-Permian mass extinction events, until metazoans re-established (Sheehan and Harris 2004). Stromatolites still form today, such as in Shark Bay, Australia and the Bahamas, but are restricted to hypersaline lagoons that

discourage metazoans (Playford and Cockbain 1976) or areas where high currents and intermittent burial similarly restrict grazing (Dravis 1983; Dill et al. 1986).

### 9.3.2 The Paleozoic Rise of Metazoan Reefs

The process of cementation associated with early stromatolites was related to a photosynthetically driven increase in pH (i.e., “biologically induced biomineralization”). The earliest evidence of “biologically controlled biomineralization”, in which organisms directly invested energy and resources into biominerals comes from protists as early as 800 Ma (Cohen et al. 2011). These unicellular organisms produced phosphatic biominerals. Throughout the remainder of this chapter, “biomineralization” refers to this latter, direct production of skeletal material.

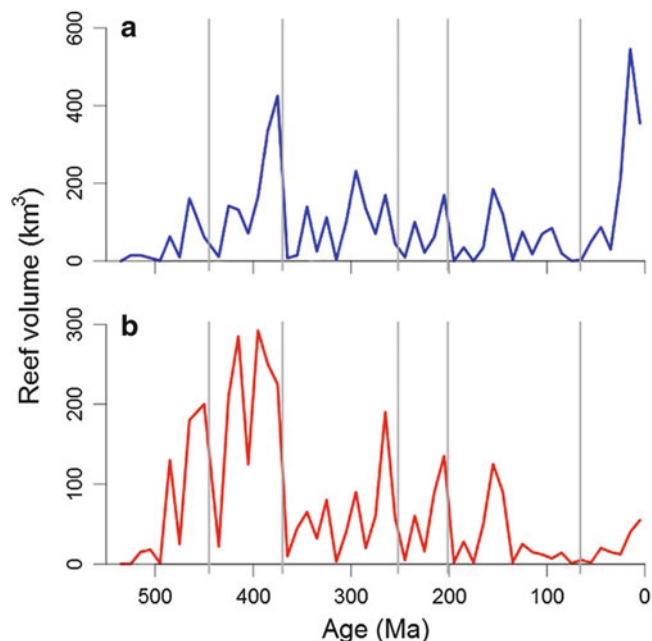
Calcareous, sponge-like organisms were present by ~650 Ma, but biomineralization was relatively rare through most of the Neoproterozoic. During the latter Ediacaran (~580–542 Ma) the size and complexity of metazoans began to increase notably, as did the presence of biominerals. However, it was during the Early Cambrian (~542–510 Ma) that biomineralizing metazoans first became widespread and abundant, allowing them to build reefs. Whether or not this proliferation of calcifying species was a response to increasing predation, it was facilitated by favorable carbonate chemistry conditions (reviewed by Stanley 2006; Ries 2010) and increasingly proved to be advantageous as grazing organisms became more important. Though biomineralization appears to have evolved independently in numerous lineages, some of the genes and many of the basic mechanisms involved appear to be conserved among diverse groups of organisms (e.g., corals, mollusks, vertebrates, etc.). Some of these genes appear to be co-opted from those involved in fundamental metabolic processes, such as calcium and inorganic carbon transport and regulation of intracellular chemistry (Zoccola et al. 2004; Moya et al. 2008; Tambutté et al. 2011; Drake et al. 2013).

The first recognizable coral reefs were built by tabulate and rugose corals, not the scleractinians that build modern reefs. While it’s been suggested that scleractinian corals may have evolved from one or more groups of the Rugosa, this origin is unlikely (see Chap. 8). Both septal development and symmetry are dramatically different in the two coral types. Also, rugose and tabulate corals produced calcitic skeletons, in contrast to aragonitic scleractinians. Hence, rugose, tabulate, and scleractinian corals most likely had different origins and simply show convergence in their roles as reef builders. Recent isotopic data suggests that reef building tabulate corals were photosymbiotic, but the type of algae involved and the nature of the symbiosis are unknown (Zapalski 2013; see also Chap. 3).

The tabulate and rugosan corals from the Ordovician through the Devonian (~485–359 Ma) may have built more abundant and widely distributed reefs than those constructed by modern corals (Kiessling 2006; Fig. 9.1). However, they declined severely following the late-Devonian mass extinction. The contributions of these corals to reef building was greatly curtailed through the Carboniferous and the Permian (~359–252 Ma; Kiessling 2009). Both tabulate and rugose corals disappeared during the Permian-Triassic extinction event.

While tabulate and rugose corals were the major framework builders of many Paleozoic reefs, other organisms contributed significantly to carbonate production and cementation. Microbial cementation was important, but generally decreased after the Cambrian (Kiessling 2009). Various bryozoans produced heavily calcified calcite skeletons, particularly from Ordovician to Devonian time (Boardman and Cheetham 1987). Stromatoporid sponges played an important cementing role on Paleozoic reefs, though there is controversy as to their primary skeletal mineralogy (Stanley 2006).

During the latter Paleozoic, particularly from Carboniferous to Permian time, various groups of algae contributed



**Fig. 9.1** Reef volume ( $\text{km}^3$ ) produced during each interval of the Phanerozoic, plotted in 10 My bins. (a) shows the original series based on preserved, fossil reefs, whereas (b) shows the data transformed to account for biases in the fossil record, particularly reduced preservation of ancient reefs. Note that in both panels the timing of relative peaks and valleys in reef building are maintained, but accounting for biases in the fossil record in panel (b) alters their relative magnitudes. Vertical, grey lines show mass extinctions (Modified from Kiessling 2006)

significantly to reef building. Phylloid algae built substantial aragonitic mounds, similar to deposits formed by codiacean algae (e.g., *Halimeda*, *Udotea*) on modern reefs (Kirkland et al. 1993; Martín et al. 1997; Stanley 2006). Likewise, various sponges contributed significantly to reef building during the latter Paleozoic, with most having primary aragonitic mineralogy (Stanley 2006). Algae with high-Mg calcite skeletons also contributed to building Paleozoic reefs, and some may have been progenitors of modern coralline algae (Stanley 2006). The increased prominence of organisms which produced aragonite and high-Mg calcite skeletons and reduced importance of low-Mg calcitic corals as reef builders during the latter Paleozoic may be related to long-term changes in seawater chemistry, as discussed in Sect. 9.5 below. Bioeroding taxa also experienced major radiations during the Ordovician, which were unmatched until the Jurassic (Taylor and Wilson 2003; Wilson and Palmer 2006).

### 9.3.3 Origination and Diversification of the Scleractinia

Scleractinian corals have been a component of the primary framework builders of reefs since the Middle Triassic (~245 Ma), but their origins are debated. Scleractinian corals were already diverse and differentiated at the level of suborder by the time they were able to build significant reefs (Wells 1956). Thus, either an earlier origination and/or a major evolutionary radiation is necessary to explain their sudden rise as reef builders in the geologic record.

Romano and Palumbi (1996) used genetic evidence to place the origins of the Scleractinia further back in the geologic past. From these data they inferred that modern scleractinians are represented by two major groups: the “Complex” and “Robust” clades. Based on molecular clocks, their divergence was estimated to have occurred on the order of 300 million years ago—well into the Paleozoic. More recent molecular evidence has revealed a wider diversity of extant scleractinians than previously known. Kitahara et al. (2010) and Stolarski et al. (2011) confirmed the basic correctness of distinctive Complex and Robust clades which diverged in the Paleozoic, and identified additional scleractinian clades. The “Basal” scleractinian clade, represented by the solitary, deep-sea families Gardineriidae and Micrabaciidae, was estimated to have diverged from the Complexa and Robusta by ~425 Ma, whereas divergence of the Complexa and Robusta was estimated at ~415 Ma. A Paleozoic origination of scleractinians helps to reconcile the geologically sudden appearance of diverse suborders in the Middle Triassic as well as the occurrence of “scleractiniamorph” fossils in the Paleozoic (Stolarski et al. 2011). The oldest scleractiniamorphs are known from the

Ordovician, ~450 Ma. They are indistinguishable from later scleractinians in terms of septal insertion and are morphologically similar to Basal scleractinians (Stolarski et al. 2011). Thus, it appears that scleractinians originated and began calcifying in the Paleozoic. Further, scleractiniamorphs are bona fide Paleozoic scleractinians that apparently did not engage in reef building until the Middle Triassic. Unfortunately, Paleozoic scleractinians (or scleractiniamorphs) may have left a poor fossil record of their early evolution.

The “Naked Coral Hypothesis” proposes that the geologically sudden reappearances of coral skeletons and subsequent gaps in the fossil record may have been the result of the temporary loss of skeletons during periods when environmental conditions were unfavorable for calcification. These so-called “naked corals” would not have left a fossil record until a resumption of calcification when conditions improved (Stanley and Fautin 2001; see also Chap. 8). Medina et al. (2006) found that the non-calcifying Corallimorpharia form a genetic clade nested within the Scleractinia, supporting this idea. They estimated that corallimorphs diverged from scleractinians during the mid-to Late Cretaceous (~132–110 Ma), when coral-reef building was depressed globally. However, new genetic data from Kitahara et al. (2010) and Stolarski et al. (2011) suggest that the Corallimorpharia and Scleractinia represent distinct, monophyletic clades from closely related sister groups. Further study is needed to determine whether these two are closely related but distinct sister groups, or if corallimorphs are instead scleractinians that lost the capacity to calcify at some point in the geologic past (Kitahara et al. 2014), making them truly “naked corals.” Whatever the outcome it is possible that periodic “reef gaps” favored reduced skeletons during times when environmental conditions were unfavorable for calcification.

### 9.3.4 Reef Building Through the Mesozoic

Scleractinians were extremely successful reef builders from the Middle to the Late Triassic (~245–201 Ma: Stanley 2003). This may have been facilitated by the establishment of photosymbiosis. Stable isotope data and growth bands suggest that at least some scleractinians were photosymbiotic by the Middle Triassic (Muscatine et al. 2005; Stanley and Helmle 2010; see also Chap. 3). The coral species that dominated Triassic reefs were distinctive from those on modern reefs. They were primarily phaceloid-dendroid, uniserial (i.e., one polyp per branch), and had non-porous skeletons (Stanley 2003). In contrast, many dominant corals on modern reefs have complex, branching morphologies, are multiseriate (i.e., many polyps per branch), and have porous skeletons.



Following their success during the Triassic, scleractinians suffered severe extinction coincident with the broader Triassic-Jurassic mass extinction. Reef building remained relatively low during the Early Jurassic, but expanded substantially during the Late Jurassic to earliest Cretaceous (~160–140 Ma; Stanley 2003; Stanley 2006; Kiessling 2009). During this time, they likely exceeded modern rates of reef formation (Kiessling 2006; Fig. 9.1). However, coral reef building was relatively low during much of the Cretaceous, and became significantly depressed during the latest Cretaceous (~80–66 Ma) when coral extinction rates increased dramatically. This Late Cretaceous extinction was second only to the Triassic-Jurassic mass extinction event in terms of scleractinian extinction rates and faunal turnover (Kiessling and Baron-Szabo 2004).

The decline of corals during the Cretaceous was coincident with a proliferation of coccolithophores (Stanley 2006) and the rapid rise to prominence of rudist bivalves at a time when tropical temperatures were significantly elevated. Rudists secreted a combination of aragonite and low-Mg calcite and they came to dominate many tropical reef environments during much of the Cretaceous. While it has been argued that rudists competitively excluded scleractinian corals on reefs during this interval (Kauffman and Johnson 1988), competitive exclusion seems unlikely for several reasons. First, rudists and corals appear to have had distinct (though overlapping) paleoenvironmental preferences. Rudists were gregarious settlers on soft sediments, similar to many bivalves and tubeworms, whereas most corals required stable, hard substrata (Gili et al. 1995). Second, coral generic diversity remained high throughout most of the Cretaceous, inconsistent with their being out-competed by rudists (Stanley 2003; Kiessling 2009). Finally, reef building by rudists collapsed at the end of the Cretaceous, more than 1 million years before the Cretaceous-Paleogene extinction event, yet corals did not return to dominance. Indeed, extensive coral-reef building did not occur until much later in the Cenozoic, long after the extinction of the rudists.

The Cretaceous-Paleogene mass extinction resulted in heavy losses among many groups, notably the (non-avian) dinosaurs, but was comparatively mild in its effects on scleractinians. Kiessling and Baron-Szabo (2004) suggest that the high rates of extinction experienced by corals during the latest Cretaceous (~70 Ma) may have left remaining species more tolerant of adverse environmental conditions, and more likely to survive through the K-Pg boundary.

As in the Paleozoic, various calcifying sponges were major contributors to reef building during much of the Mesozoic (Stanley 2003; Stanley 2006; Kiessling 2009). Calcifying algae of various types were also important contributors to Mesozoic reefs, though to a much lesser extent than on Carboniferous and Permian reefs, or later

Cenozoic reefs (Kiessling 2009). Microbes contributed significantly to reef building during the Triassic and Late Jurassic, especially at mesophotic depths (Stanley 2003), but became far less important from the Cretaceous onwards (Kiessling 2009).

### 9.3.5 Coral-Reef Building Through the Cenozoic

Compared to the latest Cretaceous, coral-reef building increased noticeably during the Paleogene, but still remained at rather modest levels (Kiessling and Baron-Szabo 2004). Over recent years, a great deal of interest has been placed on understanding the causes and consequences of the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma) as a possible analogue to modern climate change and ocean acidification from human activities (e.g., Zachos et al. 2005). Reef building decreased dramatically at the PETM, whereas coral extinction rates increased only modestly (Kiessling and Baron-Szabo 2004). By the Late Eocene (~35 Ma), a larger increase in coral extinction rates roughly coincided with the onset of Antarctic glaciation and rapid climate cooling (Lisiecki and Raymo 2005; Zanazzi et al. 2007). However, coral-reef building was little affected (Kiessling and Baron-Szabo 2004) and increased rapidly during the late Oligocene (~25 Ma). While reef building has continued at relatively high levels over the last ~20 Ma, it never returned to the levels seen in the Triassic and Late Jurassic (Kiessling 2006; Fig. 9.1).

Most recently, a modest increase in coral extinction rates occurred during the Pliocene and Pleistocene (~5–1 Ma), coinciding with the closure of the Isthmus of Panama and the initiation of Pleistocene glacial-interglacial cycles (see Chap. 6). This extinction was especially profound in the Caribbean and Western Tropical Atlantic where more than 40 % of the coral genera (18 of 43) and perhaps 60 % of the coral species went extinct (Johnson et al. 2008; van Woesik et al. 2012). Of the 18 genera that disappeared at this time, six experienced global extinction while 12 are still extant in the Indo-Pacific (*Alveopora*, *Caulastraea*, *Galaxea*, *Gardinoseris*, *Goniopora*, *Isopora*, *Pavona*, *Pocillopora*, *Psammocora*, *Stylophora* and *Trachyphyllia*). It is particularly noteworthy that reef building shows no relationship with coral-species diversity in the Caribbean over the last 28 Ma (Johnson et al. 2008). Reef building was relatively widespread in the Caribbean during the late Oligocene when coral species diversity is estimated to have been on the order of ~70 species. From the late Oligocene to the Early Pliocene coral species diversity roughly doubled to ~130 species, though reef building became rare and highly localized across the region. Approximately 60 % of these coral species went extinct during the Pliocene and Pleistocene, and

the regional coral diversity was reduced to ~50 species. Subsequently, reef building again became widespread across the Tropical Western Atlantic. Both the regional coral extinctions and low rates of reef building may have been driven largely by changes in regional upwelling (Edinger and Risk 1994) and associated fluctuations in temperature, nutrient supply, and seawater chemistry. Extensive reef building resumed only after upwelling diminished.

Unlike in earlier reef buildups, microbes and calcifying sponges contributed very little to the structure of Cenozoic reefs. In contrast, calcifying algae (and especially corallines) made major contributions to reef structure, especially since the Eocene. Indeed, modern reefs are often referred to as coral-algal constructions. A variety of other calcifiers including forams, molluscs, echinoderms, etc. also contributed to reef building over the Cenozoic, but corals and coralline algae have been by far the most important contributors to the reef framework and the carbonate incorporated into the reef structure.

Perhaps the most important development in the Quaternary (2.6 Ma to present) was the rise to prominence of the coral genus *Acropora*. The earliest known fossil *Acropora* comes from the Late Paleocene (~54 Ma), in Somalia (Carbone et al. 1994). However, it is not until the Late Oligocene (~25 Ma) that the genus is first recorded as dominating a reef community, in Greece (Schuster 2002). Some have argued that the genus has undergone a recent evolutionary radiation with all modern species having descended from a single ancestral form over the last ~5 Ma (Veron 1995; Fukami et al. 2000). However, recent fossil evidence presented by Wallace and Rosen (2006) contradicts this view. Veron and Wallace (1984) divided the genus *Acropora* into 20 'species groups' based on shared skeletal characters and morphological phylogeny. Representatives of at least one-third of these species groups make their first known fossil appearances in English and French deposits from the Eocene (~49–34 Ma), suggesting that the genus has deeper roots than previously recognized and that its modern diversity has developed more slowly over time.

*Acropora* became established in the Western Atlantic and Caribbean region by the Late Eocene but appears to have been absent across most of the Indo-Pacific region until the Late Oligocene (Wallace and Rosen 2006). The genus disappeared from the European region during the mid-Miocene, following the closure of the Tethys seaway between the Indian Ocean and modern-day Mediterranean Sea. This extinction was coincident with rapid global cooling, Antarctic glaciation, and the extinction of all tropical and reefal organisms from the region (Wallace and Rosen 2006). By this time the genus was well-established across the Indo-Pacific, perhaps as offshoots from earlier Western Indian Ocean and European lineages. Since then, it has become a primary contributor to the carbonate budget

of modern reefs and, until recently, was the dominant shallow-water reef builder in the western Atlantic.

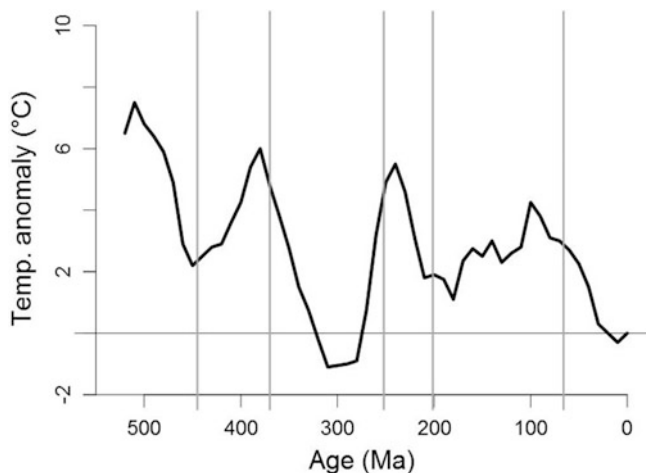
## 9.4 Climate Change and Reef Building in the Past

Individual corals are extremely sensitive to temperatures outside the range to which they are adapted, experiencing bleaching and eventually death at sustained temperatures as little as 1–2 °C above or below normal (reviewed by Jokiel and Coles 1990). For example, when colonies of *Acropora millepora* were reciprocally transplanted between the Central and Southern Great Barrier Reef, corals from the cooler, southern population bleached and died during summer at the northern site, while corals from the warmer, northern population bleached and died during winter at the southern site (Howells et al. 2011). Corals and coral reefs, however, clearly have the capacity to adjust to different thermal regimes. Upper thermal limits for corals span at least 9–10 °C in the modern ocean (Hughes et al. 2003). Given enough time to acclimatize or adapt, corals are capable of surviving and building reefs over an even broader temperature range.

The climate has changed dramatically over the last several hundred million years, and across a variety of temporal and spatial scales. Coral reefs have tolerated many of these changes, and have likely benefitted from some of them, but some have also been adversely affected. Understanding the responses of coral species and coral reefs to climate change in the past before significant human impacts is particularly important today, as the world faces the possibility of large-scale, extremely rapid climate change due to human activities. In this section we will discuss climate change in the past and the responses of corals and reefs to these changes within a modern, physio-ecological framework.

### 9.4.1 Climate Change Over the Phanerozoic

Over the last 542 million years (My) global climate has experienced a general pattern of four quasi-periodic fluctuations between hotter, greenhouse climates and colder, icehouse climates (Royer et al. 2004; Fig. 9.2). The period of these fluctuations has been on the order of 100–200 My. This long-term pattern of warming and cooling is punctuated by numerous shorter-term climate fluctuations, many of which have been quite substantial. A number of factors have contributed to these patterns, but changes in the climatic forcing provided by atmospheric CO<sub>2</sub> appears to be among the most important drivers of climate change over both long and short timescales (Royer et al. 2004; Royer 2006; Came et al. 2007). A critical piece to understand here is that



**Fig. 9.2** Long-term, secular changes in tropical seawater temperature over the Phanerozoic, shown at 10 My resolution. Vertical, grey lines show mass extinctions (Modified from Royer et al. 2004)

atmospheric  $\text{CO}_2$  is not a thermostat, *per se*, and a given atmospheric  $\text{CO}_2$  concentration does not imply a specific global mean temperature. Rather,  $\text{CO}_2$  provides a particular *forcing* on the climate system, and the equilibrium climate response to that forcing also depends on the other drivers and feedbacks within the system. In particular, solar output has slowly increased over the last several billion years (the sun was at about 70 % of current output four billion years ago) and it will continue to increase in the future (Gough 1981). Reconstructed atmospheric  $\text{CO}_2$  concentrations were extremely high on the early Earth, as were some other greenhouse gases, helping to resolve the “Faint Early Sun Paradox” of a relatively warm planet with liquid water under low solar irradiance (Sagan and Mullen 1972; Pavlov et al. 2000; Royer et al. 2004; Ueno et al. 2009). Uncertainty over atmospheric  $\text{CO}_2$  concentration increases substantially the further back we look into the geologic past. Other factors (such as the positions of the continents) also had important effects on the long-term evolution of the climate (see Chap. 6), but variation in atmospheric  $\text{CO}_2$  is a primary driver of climate change.

The coldest climates over the Phanerozoic are represented by glacial maxima during the Pleistocene glaciations (2.6–0.12 Ma; reviewed by IPCC (2013)). During these glacial maxima, global climate cooled to 4–6 °C below the late-twentieth century average. The Pleistocene glaciations were punctuated by interglacial periods of a few thousand years when climate warmed relatively rapidly by several degrees Celsius. Pleistocene interglacials have ranged from slightly cooler than the late-twentieth century mean global temperature to perhaps as much as 2–3 °C warmer than our recent climate during the peak warmth of the Eemian interglacial (~130,000–115,000 years ago).

The Pleistocene was preceded by a general global cooling trend over the previous 50 My from the very warm climates of the Paleocene and early Eocene, with glaciation taking hold in Antarctica by ~30 Ma. This cooling trend was driven by the drawdown of atmospheric  $\text{CO}_2$  and the migration of Antarctica toward the South Pole. Southern migration of Antarctica facilitated its glaciation, increasing the Earth’s albedo and providing a positive feedback that enhanced the cooling trend. A period which was likely as cold or colder than the Pleistocene had occurred during the Late Carboniferous to Early Permian (~360–260 Ma), triggering extensive glaciation. As in the Pleistocene, cooling and glaciation were associated with the draw-down of atmospheric  $\text{CO}_2$ , perhaps due to the expansion of terrestrial forests. Another glacial period occurred during the Late Ordovician to Early Silurian (~450–420 Ma), though this time appears to have been somewhat warmer than during the Pleistocene glaciations, even during the height of the event at the end of the Ordovician (~443 Ma). Another relative cool period occurred during the late Jurassic to early Cretaceous (~160–90 Ma), though this interval was still warmer than the present-day climate.

Between these long-lasting cool periods the planet experienced warmer greenhouse climates. The late Cambrian to early Ordovician (520–480 Ma), Devonian (~400–360 Ma), Permian to early Triassic (290–240 Ma), and late Cretaceous to early Cenozoic (~120–50 Ma) climates were all much warmer than our present-day climate. At their peaks, these periods may have reached global temperatures as much as 10–15 °C higher than the late-twentieth century average. These were all periods of strong, greenhouse gas forcing, and ice was rare or entirely absent globally. Because continental glaciers were minimal, changes in sea level were driven primarily by the expansion and contraction of seawater and of the ocean basins themselves, as there was so little water exchanged between the limited continental ice sheets and the world ocean.

When climate changes, absolute temperature changes tend to be greatest over land and toward the poles and smallest in the ocean and toward the equator. Hence, these major climate fluctuations have resulted in more modest changes in temperature of the tropical oceans. Relative to the last 10 My, the tropical oceans averaged 1–2 °C cooler during the Carboniferous glaciations (Royer et al. 2004), but probably reached even cooler temperatures during the height of glaciation. In contrast, during the Cambrian–Ordovician, Devonian, and Permian–Triassic hothouse intervals, tropical ocean temperatures averaged 6–8 °C warmer than the average over the last 10 My, and perhaps 4–6 °C warmer during the Cretaceous–Cenozoic hothouse. Hence, the long-term average for tropical ocean temperature has varied over a range of about 10 °C during the Phanerozoic, though this

range was certainly a bit larger when considering climatic fluctuations over shorter timescales.

#### 9.4.2 Past Effects of Secular Changes in Climate on Reef Building

Any time-series can be decomposed into periodic as well as secular (i.e., long-term, non-periodic) variation. The coming and going of the seasons represents a periodic change in temperature. Gradual warming or cooling of the climate represents secular change. In this section we consider the effects of longer-term secular changes in climate on reef building—the meandering between hothouse and icehouse climates that Earth has experienced over the Phanerozoic.

Rugose and tabulate coral reefs flourished during the Silurian, under relatively cooler climatic conditions, and also thrived during the Devonian under an intense hothouse regime. These reefs became extremely repressed during the Carboniferous and Permian, under climates that ranged from intense icehouse to intense hothouse conditions. Rugose and tabulate corals succumbed to the end-Permian mass extinction and scleractinian corals replaced their ecological role as primary reef builders in the Middle Triassic. Scleractinian reefs were extremely successful throughout the Triassic, under intense hothouse conditions, but were devastated by the end-Triassic extinction event. They again rose to major prominence as reef builders during the late Jurassic, under a relatively cooler climate (but still warmer than present-day), but floundered during the late Cretaceous and early Cenozoic hot climates. Scleractinians again rose to dominate reef building during the cooling climate of the Neogene, and have been very successful in our recent icehouse climate. These variations in response suggest that temperature alone has not had a consistent control on geologic reef building.

An upper thermal limit for metazoan life is thought to be 45–47 °C (Pörtner 2001). The tropical ocean has rarely if ever reached such a limit during the Phanerozoic, though equatorial ocean temperatures have soared into the upper 30's and perhaps even the lower 40's °C under the most intense hothouse climates (Sun et al. 2012). Lethally high seawater temperatures beyond which reef builders could not adapt may have occurred in semi-enclosed, shallow seas. Nevertheless, it appears unlikely that the climate has been so hot as to widely prevent reef building during the Phanerozoic, given appropriate evolutionary timescales needed for reef builders to adapt. In contrast, in the modern ocean, coral reefs (except for deep, cold-water reefs) give way to non-reefal communities where the seasonal minimum seawater temperature drops below 18 °C for significant periods of time. Adaptation and/or acclimatization are also required to allow builders to tolerate these low thermal limits. Thus, at least for modern reefs, the lower temperature limit of

roughly 18 °C appears to be more akin to a fixed limit. Ancient reefs, such as those built by rugose and tabulate corals, likewise were restricted to tropical and subtropical climates, and a lower temperature limit for shallow-water reef building of somewhere around 18 °C has likely operated for hundreds of millions of years. Unlike the upper thermal limit, which has rarely if ever constrained reef building over long timescales, the lower thermal limit for reef building has frequently limited the expansion of reefs to higher latitudes.

Over long, steady-state conditions where reef organisms have plenty of time to adapt to temperature change, all else being equal, warmer climates should be more favorable to reef building than cooler climates simply because the latitudinal extent and total area open to colonization increases under a warm climate as compared to a cool one. Shallow-water reefs have thrived under hothouse climates, but a warm climate by itself is not sufficient to predict a period of successful reef building. Reefs were less abundant during the Carboniferous icehouse, yet thrived during the late Jurassic cool period and our more recent, Neogene, icehouse climate. More than anything, this pattern demonstrates that reef organisms can indeed adapt to climate change over sufficiently long time scales, and that factors other than just climate are also critical for determining the relative success of reef building organisms.

#### 9.4.3 Coral Reefs Under Rapid Climate Change

The climate can be relatively stable for long periods of time; however, it can also change rapidly, especially after a major perturbation to the carbon cycle. Rapid climate change may exceed the rate at which reef builders are able to migrate, acclimatize, or adapt, leading to the extinction of reef organisms and reduced reef building. Kiessling and Simpson (2011) identified five major reef crises during the Phanerozoic. All five appear to be associated with rapid climate change—one with rapid cooling, and the other four with rapid warming. During the late Devonian the climate cooled rapidly, associated with the drawdown of atmospheric CO<sub>2</sub> due to the expansion of vascular land plants (Algeo and Scheckler 1998). Rapid cooling and the associated drop in sea level may have contributed to the collapse of reef building during this time, though low data resolution makes it difficult to test this hypothesis. The evolution and proliferation of land plants also led to higher terrestrial weathering rates and increased supply of micronutrients to the ocean that possibly resulted in eutrophication (Algeo and Scheckler 1998). Increased oceanic productivity may have contributed to lower reef building at this time through negative effects on calcifiers adapted to oligotrophic conditions and positive effects on bioeroding organisms. The degree to which the latter would have been an important factor

depends on the extent to which the reef-bioeroder community had proliferated. Cooling that began in the mid-Devonian intensified throughout the Carboniferous and into early Permian time, and undoubtedly contributed to a reduction in reef building during this interval. Lower contributions by corals to reef building during the latter Paleozoic, however, were reinforced by changes in ocean chemistry (see below). A minor, coral/sponge-reef crisis occurred during the Middle-Late Permian (~260 Ma), but there is not evidence for rapid climate change at this time (Kiessling and Simpson 2011).

A clearer role for rapid climate change in suppressing reef building comes from the Permian-Triassic extinction event (~251 Ma) that continued through the Early Triassic. The climate warmed very rapidly at the end of the Permian and the Early Triassic was characterized by a great deal of upheaval and climatic instability (Kiessling and Simpson 2011; Sun et al. 2012). As a result, reef building was substantially suppressed during this interval. Once the climate began to stabilize during the Middle Triassic, the first scleractinian reefs rapidly burst onto the scene and were extremely successful throughout the Triassic. Reefs were again devastated by the Triassic-Jurassic extinction events (~200 Ma) and rapid global warming is similarly implicated as tropical taxa were more severely affected than were non-tropical ones (Kiessling and Aberhan 2007). Throughout the earliest Jurassic, reefs and corals were concentrated toward the mid-latitudes, suggesting an escape from heat (Flügel and Kiessling 2002; Lathuilière and Marchal 2009; Kiessling and Simpson 2011).

Additional reef crises occurred during the Early Jurassic (~183 Ma) and the Paleocene-Eocene (~56 Ma). Temperature changes during the latter were among the most rapid in the geologic record (Kiessling and Simpson 2011) and some have proposed this event as an analogue to twenty-first century climate change. Not every variation in the climate was associated with declines in reef building, nor has every period of relatively rapid climate change brought about a reef crisis. The question then becomes, how much climate change can reef builders cope with via migration, acclimatization, and adaptation, and at what point does it exceed these capabilities, leading to a reef crisis?

An instructive example comes from the geologically recent past. During the Eemian interglacial period (~130,000–115,000 years ago) the climate was warmer than during our present interglacial (the Holocene), by perhaps 2–3 °C. This warmth was likely driven by differences in orbital forcing, particularly at high latitudes. Annual mean temperatures at low latitudes appear to have been only slightly warmer than present-day temperatures—perhaps 0.7 °C warmer (McKay et al. 2011)—though seasonality was higher due to changes in orbital forcing (Winter 2003). Sea level was ~6 m higher than today, largely due to the

retreat of the Greenland ice sheet, but coral reefs flourished as they have during the Holocene. Indeed, reefs and tropical coral species spread to higher latitudes than during the present interglacial (Greenstein and Pandolfi 2008). What is perhaps most striking about the Eemian is that not only did coral reefs persist, but coral species distributions changed rapidly. Many tropical and subtropical corals spread further toward the poles than during the Holocene, but some taxa became rare or disappeared in the equatorial zones (Kiessling et al. 2012). Hence, the reef response to the Eemian interglacial was one of continued growth, facilitated by adaptation/acclimatization *in situ* as well as migration to higher latitudes by species that were unable to cope with the warm, equatorial temperatures.

This response was more pronounced in the Northern Hemisphere, consistent with both modeling and proxy data showing higher levels of warming in the Northern as compared to the Southern Hemisphere, but temperatures were higher world-wide during the Eemian (Kiessling et al. 2012). Proxy data from the Western Pacific Warm Pool show seawater temperature during the Holocene of about 29–30 °C, similar to present-day seasonal maxima. In contrast, during the Eemian the same proxy data suggest seawater temperatures >30 °C, and up to 31.5 °C at times (Visser et al. 2003; Leduc et al. 2010; Nikolova et al. 2013). Similarly, proxy data shows Eemian seawater temperatures ~1–1.5 °C higher in the Caribbean (Herbert and Schuffert 2000) and up to 3 °C warmer in the Eastern Equatorial Pacific than present-day temperatures (Lea et al. 2006; Nikolova et al. 2013). These temperature increases occurred over not more than a few centuries, and followed on the heels of warming from the previous glacial period. A temperature increase of 1–3 °C in coral reef waters over the course of a few centuries during the Eemian implies a maximum warming rate on the order of about 0.5 °C per century. This rate of warming was not detrimental to reef building, however, there was rapid reorganization of the coral community structure, especially at low latitudes and may be near the upper limit of what many coral species can cope with. Without a doubt, the rate of warming is important, and perhaps even more so than the absolute magnitude of warming. For example, a 1–2 °C increase in seawater temperature over a single year would likely have greater effects than the same magnitude of warming spread over a few centuries. A longer timescale simply allows more time for corals to migrate, acclimatize, or adapt, leading to a slow, adaptive turnover in the reef community, rather than the abrupt loss of corals and recolonization by the few remaining survivors.

As described earlier, thermal tolerance is related to the long-term regional temperatures to which corals have adapted and acclimatized rather than to any absolute global threshold. On the reefs of the Arabian Gulf, corals tolerate

temperatures of at least 34 °C, but bleach when the temperature reaches 35–36 °C for prolonged periods. This is at least 4–6 °C higher than the bleaching threshold for other corals in the Indian Ocean (~30–31 °C), from which Arabian corals are derived (Riegl et al. 2011). Arabian corals appear to have gained this exceptional thermal tolerance within the last 6000 years, which would imply a minimum rate of adaptation/acclimatization on the order of 1 °C per millennium (i.e., 6 °C increase in 6000 years), or 0.1 °C per century. While the actual rates of increase in thermal tolerance are not well constrained, 6000 years can be regarded as an upper limit on the timescale. Thus, some reef building corals are capable of tolerating a warming rate of least 0.1 °C per century, and 4–6 °C of total warming.

Field observations of contemporary, repeat-bleaching events as well as manipulative experiments help to further define the potential for corals and coral reefs to tolerate rapid climate change. The mass-bleaching event of 1997/1998 struck coral reefs around the world, including the Central Great Barrier Reef (GBR). Here bleaching was extensive, though mortality was relatively modest. Bleaching impacted the GBR again in 2002. In spite of more severe thermal stress (and higher irradiance, which significantly exacerbates thermal stress), the bleaching observed on the Central GBR was less severe in 2002 than expected based on prior observations (Maynard et al. 2008). Indeed, applying the bleaching thresholds observed in 1998 substantially over-predicted actual rates of bleaching in 2002. Similar findings come from Southeast Asia between the 1998 and 2010 bleaching events (Guest et al. 2012). Here rates of mortality were more severe than on the GBR. Not only were corals more thermally tolerant in 2010 as compared to 1998, but genera such as *Acropora* and *Pocillopora* which usually are among the most thermally sensitive also showed the greatest increases in resistance. Overall, these observations suggest an increase in the thermal tolerance of corals on the order of 0.5–1 °C after the single bleaching event. The changes were apparently due to acclimatization of the resident corals, or adaptation within the changing coral populations. Hence, even rapid increases in seawater temperature of <1 °C may be tolerable for some (but not necessarily all) species of coral. Experimental and modeling studies suggest that larger increases in thermal tolerance, on the order of 1–2 °C, are also possible for at least some corals over timescales ranging from weeks to a century. These changes may occur through physiological acclimatization, switching to more thermally tolerant algal symbionts by the host corals, and/or adaptation (Middlebrook et al. 2008; Baskett et al. 2009; Howells et al. 2011; Logan et al. 2013).

The emerging picture from these various lines of evidence is that some coral species can achieve small increases in thermal tolerance (<1 °C) over timescales ranging from weeks to a few years. Larger increases on the order of 1–2 °C

appear to be possible over short timescales for some corals, but most corals likely require decades to centuries (i.e., multiple generations) to achieve these higher tolerances. The timescales required for increases in tolerance >2 °C have not yet been clearly demonstrated. A maximum warming rate on the order of 0.5 °C per century, such as during the Eemian, appears to be near the upper limit of what many corals can tolerate. The oceans are expected to warm by 1–3 °C this century due to anthropogenic climate change (IPCC 2013). This higher warming rate may exceed what many corals can cope with, resulting in major reductions in reef building and ultimately extinctions during the twenty-first century and beyond.

## 9.5 Reefs Under Changing Ocean Chemistry

Changes in seawater carbonate chemistry can significantly impact calcification rates of corals and other reef builders (reviewed by Pandolfi et al. 2011). The carbonate system in seawater involves the interaction of several, dissolved species:  $\text{Ca}^{2+}$ ,  $\text{CO}_{2(\text{aq})}$ ,  $\text{HCO}_3^-$ ,  $\text{CO}_3^{2-}$ ,  $\text{H}^+$  (or its surrogate, pH) as well as solid phases of  $\text{CaCO}_3$  (aragonite vs. calcite). The reader is referred to Chap. 2 for a discussion of carbonate chemistry as it relates to coral calcification. Additional parameters important to the carbonate system include the aragonite or calcite saturation state ( $\Omega_{\text{arag/calc}}$ ) and the magnesium to calcium ratio (Mg/Ca). Dramatic changes over the Phanerozoic have influenced reef building and may provide useful analogs to the immediate future. We review these below.

### 9.5.1 Calcite and Aragonite Seas

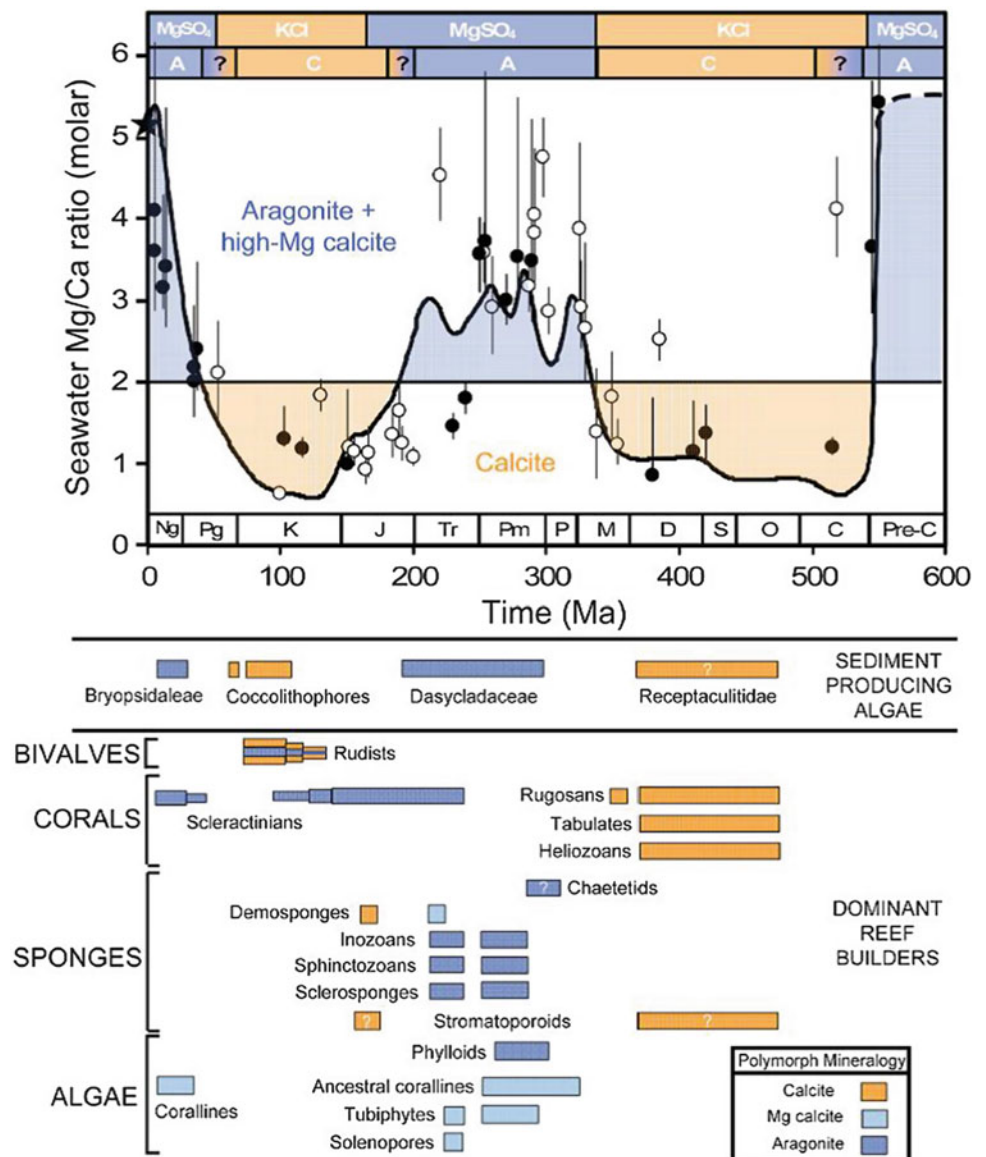
Calcifying organisms primarily produce one of three polymorphs of  $\text{CaCO}_3$ , although some species produce shells and skeletons of mixed composition. These three polymorphs are low-Mg calcite (or simply, calcite), aragonite, and hi-Mg calcite ( $\text{Ca}_x\text{Mg}_{1-x}\text{CO}_3$ ). Low-Mg calcite and hi-Mg calcite differ in the quantity of Mg incorporated into the  $\text{CaCO}_3$  crystal lattice. Low-Mg calcite contains <4 mol % Mg, whereas hi-Mg calcite contains >4 mol% Mg, and usually in the range of 11–20 mol% Mg in modern seawater. Differences in lattice structure and chemical composition among polymorphs lead to differences in solubility and other physical properties of the minerals, with low-Mg calcite being the least soluble, followed by aragonite, and finally with hi-Mg calcite being the most soluble (reviewed by Zeebe and Wolf-Gladrow 2001). Some coralline algae also produce dolomite, which is 50 mol% Mg, and is highly resistant to dissolution (Nash et al. 2013; Diaz-Pulido et al. 2014).

Seawater interacts with basalt in areas of seafloor spreading such that the  $Mg^{2+}$  concentration decreases and the  $Ca^{2+}$  concentration increases. Hence, during periods of rapid seafloor spreading the Mg/Ca ratio decreases whereas during periods of slower seafloor spreading the Mg/Ca ratio increases (Stanley and Hardie 1998). Variations in the rate of seafloor spreading and chemical weathering on land over the Phanerozoic have led to shifts in the seawater Mg/Ca ratio from ~0.9 to 5.2. Under conditions where the Mg/Ca ratio is low (<2), the precipitation of low-Mg calcite is thermodynamically favored over aragonite or hi-Mg calcite. In contrast, at a high Mg/Ca ratio (>2) the precipitation of aragonite and hi-Mg calcite are favored over low-Mg calcite.

As their names imply, calcite seas are characterized by high representation of low-Mg calcite among abiotic precipitates, such as hardgrounds, and to some extent

among calcifying taxa (Fig. 9.3). In contrast, aragonite seas are characterized by higher representation of aragonite and hi-Mg calcite in abiotic precipitates and to some extent among calcifiers. These fluctuations in seawater chemistry are also associated with variation in hypersaline precipitates, with more KCl formed during calcite seas and more  $MgSO_4$  formed during aragonite seas (Stanley and Hardie 1998). During the Phanerozoic there have been two major periods of calcite seas (the Cambrian through the Early Carboniferous and the late Jurassic through the early Neogene) and two periods of aragonite seas (the middle Carboniferous through the late Jurassic and the early Neogene to present). This had a significant impact on the success of particular calcifying species as the seawater chemistry changed. Many carbonate-producing taxa preferentially adopted a skeletal mineralogy that was more favorable within the chemical regime at the

**Fig. 9.3** Changes in the Mg/Ca ratio of sea water and of the major calcifying taxa over the Phanerozoic. Curve shows modeled Mg/Ca ratio in comparison to proxy data from halite inclusions (closed circles) and fossil echinoids (open circles). Top bars show periods of calcite and aragonite seas, and associated KCl or  $MgSO_4$  evaporite deposits. Horizontal line divides aragonite and calcite nucleation fields. Lower bars show relative changes in abundance of dominant calcifiers along with their associated mineralogies (From Ries 2010)



time they were first evolving, though a few taxa deviate from the pattern (Porter 2010). As a result, changes in ocean chemistry can potentially provide important constraints on skeletonization that might reinforce the thermodynamically favored carbonate polymorph.

For example, rugose and tabulate corals evolved in the calcite seas of the Ordovician (Fig. 9.3). They produced low-Mg calcite skeletons and thrived in the calcite seas of the Ordovician, Silurian, and Devonian oceans. However, they declined dramatically as ocean chemistry shifted in the late Devonian and Early Carboniferous. Rugosans and tabulates showed some recovery in the Late Carboniferous, and the late Permian, but they never again achieved the dominance they had during earlier times. The aragonite seas that characterized this interval may have contributed to their reduced roles as reef builders.

However, this relationship was not straightforward. Scleractinian corals, which principally produce aragonite, first began building reefs during the Middle Triassic under aragonite-sea conditions. However, recent evidence suggests that they first evolved skeletons in the calcite seas of the Paleozoic (Stolarski et al. 2011). They were extremely successful during the Triassic, until the Triassic-Jurassic extinction event, generally coincident with a shift toward a calcitic ocean. As the Mg/Ca ratio in seawater fell further into the calcite nucleation field (the chemical parameter space where the precipitation of calcite is thermodynamically favored) during the late Jurassic, however, scleractinians experienced a major resurgence in reef building. Subsequently, scleractinian reefs declined throughout the Cretaceous, during a period when the Mg/Ca was squarely in the calcite nucleation field (~1). At the same time, rudist bivalves, which produced skeletons consisting of a combination of aragonite and low-Mg calcite, were highly successful, as were calcite-producing coccolithophores, and this success was likely facilitated by seawater chemistry which favored their skeletal mineralogies. Scleractinian reefs increased in abundance following the Cretaceous-Paleogene extinction event (though rudists had already declined long before). They were knocked back again by the Paleocene-Eocene Thermal Maximum, a response more to temperature than seawater chemistry (see below). Finally, they expanded dramatically during the early Neogene, coinciding with a shift of the Mg/Ca ratio back into the aragonite nucleation field.

Inconsistent responses of scleractinians to variation in the Mg/Ca ratio show that it alone is not a master control over reef building, though it does appear to influence the relative success of calcifiers during a given interval. In particular, scleractinians were highly successful during the calcite seas of Late Jurassic, but their success dropped off as the Mg/Ca fell even lower during the Cretaceous. Thus, reef accretion can still occur under somewhat unfavorable seawater chemistry, but there are also limits to what organisms can tolerate.

It appears that the threshold for scleractinian reefs was crossed during the Cretaceous, when the Mg/Ca ratio fell to ~1, but not during the Jurassic at a Mg/Ca ratio of ~2. This conclusion contrasts with previous suggestions that corals were out-competed by rudists during the Cretaceous. Instead, the floundering of corals and the flourishing of rudists during Cretaceous time were both likely driven by changes in ocean chemistry and the relative success of each group was probably independent of the other.

Experimental evidence from modern calcifiers (including scleractinian corals) shows that, while they tend to calcify at much higher rates in seawater that favors the precipitation of their CaCO<sub>3</sub> polymorph, they are less tied to their original mineralogy than has generally been assumed (reviewed by Stanley 2006; Ries 2010). Some organisms which produce hi-Mg calcite in modern seawater with a high Mg/Ca ratio will switch to precipitation of low-Mg calcite when the Mg/Ca ratio is lowered experimentally (Stanley 2006; Ries 2010). Likewise, scleractinian corals produce moderate quantities of calcite under experimental conditions as the Mg/Ca ratio dips into the calcite nucleation field (Ries et al. 2006; Higuchi et al. 2014). Hence, skeletal composition is not under absolute control by the organisms—at least when seawater chemistry changes rapidly. Over geologic time, however, most taxa maintain the same skeletal mineralogy in spite of shifts in the Mg/Ca ratio of sea water (Porter 2010). It is not known why calcifiers tend to produce one CaCO<sub>3</sub> polymorph vs. another, but the ability to precipitate the favored polymorph appears to be an important determinant of their calcification rates. Consistent mineralogy within taxa over geologic time may be an evolutionary holdover. That is, the costs of evolving skeletons with a new mineralogy may exceed the costs of calcifying in a less favorable nucleation field, which would explain why switching from one mineralogy to another is rare in the geologic record, when the rate of chemical change is slow relative to reasonable evolutionary responses. Nevertheless, exceptions to the rule do occur (Porter 2010). At least one species of scleractinian coral appears to have switched to calcite as its primary skeletal mineralogy during the calcite seas of the Cretaceous (Stolarski et al. 2007). How this species was able to achieve the switch, and why other species did not follow suit, are unknown.

Regardless of the variability described here, rugose, tabulate, and scleractinian corals as well as other calcifying taxa have generally been more productive when seawater chemistry favored their preferred carbonate mineralogies, but an unfavorable nucleation field is not an insurmountable obstacle (Kiessling et al. 2008). In particular, scleractinians were extremely successful in the late Jurassic despite a relatively low Mg/Ca ratio. Coccolithophores were most successful during the calcite seas of the Cretaceous, but are still prolific today under a geologically high Mg/Ca ratio (5.2). In the



end, the seawater Mg/Ca ratio appears to influence the relative success of calcifying taxa, but is not the master control of either reef-building taxa or the rate of reef building.

### 9.5.2 Ocean Acidification

Ocean acidification (OA) describes the reduction in seawater pH and associated changes in seawater chemistry (i.e., reduced carbonate concentration,  $[\text{CO}_3^{2-}]$ , reduced aragonite and calcite saturation states, ( $\Omega_{\text{arag/calc}}$ , etc.) due to the addition of acid to the ocean). The terminology used with OA can sometimes be confusing. The process of adding an acid to a solution, ultimately reducing that solution's pH, is referred to as *acidification* and makes the solution *more acidic*. However, a solution only becomes *acidic* (as opposed to basic) when the pH drops below neutral (pH  $\sim$ 7). Hence, OA is correctly referred to as acidification, and makes the oceans more acidic, but bulk seawater pH will never drop below neutral, and the oceans will never become "acidic" by accepted chemical standards. Having made this distinction, carbonate minerals will begin to dissolve well above a pH of 7 in normal seawater, and OA makes seawater more corrosive to carbonates.

At local or regional scales, the introduction of mineral acids (e.g., sulfuric acid through volcanic activity) can lead to short-lived OA, but global scale OA is generally only achievable through the release of large amounts of  $\text{CO}_2$ . When  $\text{CO}_2$  dissolves into seawater, it reacts to produce carbonic acid (Caldeira and Wickett 2003; Orr et al. 2005). Over geologic timescales, chemical weathering on land and carbonate dissolution in the ocean can neutralize excess  $\text{CO}_2$ , releasing alkalinity and cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , etc.), and maintain relatively stable  $\Omega_{\text{arag/calc}}$ , though not necessarily stable pH (Archer and Brovkin 2008; Hönisch et al. 2012). Hence, OA is inherently an ephemeral process on geological timescales, restricted to a few tens of thousands of years at most.

OA is occurring today due to human activities, but geological evidence suggests that it has also occurred in the past, causing negative consequences for calcifying taxa and for reef building. The current rate of OA is potentially unprecedented for at least the last 300 Ma of Earth's history, and could push organisms and ecosystems into unknown territory (Hönisch et al. 2012).

The Paleocene-Eocene Thermal Maximum (PETM:  $\sim$ 56 M) has been proposed as an analogous event and may provide a window into the future absent aggressive reductions in anthropogenic  $\text{CO}_2$  emissions (Kiessling and Simpson 2011; Hönisch et al. 2012). The rate of acidification during the PETM is not clear, but Wright and Schaller (2013) argue, based on high-resolution proxy data, that the injection of carbon into the atmosphere during the PETM

may have occurred within as little as a year, and surface ocean acidification could have occurred in as little as 13 years. This conclusion is hotly debated (Pearson and Nicholas 2014; Stassen et al. 2014; Wright and Schaller 2014; Zeebe et al. 2014). In contrast, most studies have suggested that the carbon release and resultant OA during the PETM occurred over a timescale of several millennia (e.g., Penman et al. 2014; Zeebe et al. 2014). Hence, depending on the timescale of acidification during the PETM (estimates ranging from  $\sim$ 10 to 10,000 years), the event proceeded at a rate between an order of magnitude faster and two orders of magnitude slower than anthropogenic OA. Additional proxy data and modeling studies are clearly needed to resolve this issue. Nevertheless, the PETM provides our best proxy for possible impacts following rapid  $\text{CO}_2$  release.

The PETM was associated with a 0.25–0.45 pH unit reduction, and an average  $\Omega_{\text{arag}}$  reduction from  $\sim$ 3 to  $\sim$ 1.5 in the surface, mixed layer of the ocean within a period of less than 10,000 years (Zachos et al. 2010; Penman et al. 2014). These changes in seawater chemistry are similar in magnitude to those associated with medium to high  $\text{CO}_2$  emissions from human activity during this century (IPCC 2013). The critical factor would be the timeframe over which these changes occurred. Based on a timescale of a few thousand years, the rate of acidification during the PETM would have been an order of magnitude slower than modern OA due to human activities and any twenty-first century scenario would be more dramatic.

As mentioned previously, the PETM was mild in its effects on coral extinction rates, though it was associated with a mass extinction event among benthic foraminifera (Kiessling and Baron-Szabo 2004; Hönisch et al. 2012). While corals did not experience a major increase in extinction rates during the PETM, reef building was substantially reduced. In fact, the PETM constitutes one of the five major reef crises during the Phanerozoic recognized by Kiessling and Simpson (2011). Therefore, even though changes in coral diversity may have been modest, the impact of OA on reef building was not. Chapter 6 argues that, although related, coral growth and reef building should not be confused. Evidence from the PETM suggests that reef-wide calcification (and, therefore, accretion) may be compromised well in advance of community structure breaking down. That is, reef growth may plummet even when coral cover is high and the ecosystem visually appears to be healthy. This has implications for our ability to understand reef building in the past using taxonomic information alone. Looking to the future, it suggests that lowered calcification and other biological (bioerosion), physical (storms), and chemical factors (acidification) may be as important as coral abundance or diversity in predicting which reefs will keep up with rising sea level and which ones will lag behind.

After the PETM, perhaps the next most similar event to modern OA for which there are also good, geochemical constraints is the last Pleistocene glacial-interglacial transition. During this interval, atmospheric CO<sub>2</sub> increased from ~189 to ~265 μatm, resulting in a ~0.15 decrease in surface ocean pH. This level of pH change is at the low end of the magnitude of anthropogenic OA (0.15 pH units vs. 0.15–0.45 pH units) proposed by the end of the century, depending on anthropogenic CO<sub>2</sub> emissions. However, it is worth noting that this occurred more than an order of magnitude more slowly (~6000 vs. <200 years). Hence, Pleistocene glacial-interglacial transitions are of limited utility in understanding the impacts of rapid OA on reef building. Nevertheless, these transitions were associated with reduced shell weight of foraminifera (Barker and Elderfield 2002) and coccolithophores (Beaufort et al. 2011) even though there was no obvious impacts on reef building (Hönisch et al. 2012). How relevant this is to reef accretion in the immediate future lay in the importance of an order of magnitude faster increase going forward.

The Triassic-Jurassic mass extinction event (~200 Ma) may have also been associated with substantial OA, and could provide another useful proxy for recent events, though the geologic record is much poorer this far back in time. As discussed previously, this extinction event devastated scleractinians and reef building collapsed—another of the five reef crises identified by Kiessling and Simpson (2011) over the Phanerozoic. However, while there is evidence for a rapid increase in atmospheric CO<sub>2</sub> at the time of this mass extinction event, few data are available with the resolution required to unambiguously implicate OA.

Other potential OA events have been identified in the fossil record, including the Permian-Triassic mass extinction event (~252 Ma) and an Early Jurassic ocean anoxia event (Toarcian OAE, ~183 Ma). Both of these correspond to reef crises (Kiessling and Simpson 2011). The Toarcian event led to a modest extinction among corals and calcifying sponges, but had little effect on extinction rates for other organisms. In contrast, the Permian-Triassic event corresponds to the most severe global mass extinction and reef crisis in the fossil record. Two Cretaceous ocean anoxia events (OAE 1a, ~120 Ma; OAE 2, ~93 Ma) may have also involved OA, though the evidence for acidification during these events is not as clear as in those discussed above.

The four reef crises mentioned above all appear to coincide with OA events. In contrast, neither the Late Devonian mass extinction event and reef crisis (~375 Ma) nor the minor coral-sponge extinction event of the Late Permian (~260 Ma) appear to have been associated with a severe drop in pH. Similarly, neither the Late Ordovician (~446–444 Ma) nor the Cretaceous-Paleogene (~66 Ma) mass extinction events appear to be associated with a decline in pH, nor were there global reef crises during these

intervals. Hence, there is not a perfect correspondence among OA events, reef crises, and mass extinction events. Nonetheless, there is compelling geologic evidence for the occurrence of at least four major OA events over the Phanerozoic, and these correspond to four of the five major reef crises over geologic time. The conditions associated with OA are not the only way to hinder reef building, but they appear to be a highly effective mechanism.

### 9.5.3 Ocean Acidification vs. Rapid Climate Change

The geologically rapid release of large amounts of CO<sub>2</sub> to the biosphere results in OA, but also leads to rapid climate change. The four major reef crises in the fossil record that appear to be associated with OA events were also characterized by rapid global warming, making it challenging to decipher which factor (acidification vs. warming) was most responsible for the observed biological and geochemical responses. In fact, rapid warming may have been the more important factor in driving reef decline and elevated extinction rates in at least some of these events. During the Triassic-Jurassic reef crisis, tropical taxa were more severely affected than were non-tropical taxa, and reef building in the earliest Jurassic was concentrated primarily in mid-latitudes and deeper waters (Flügel and Kiessling 2002; Kiessling and Aberhan 2007; Kiessling et al. 2009; Lathuilière and Marchal 2009). Likewise, during the PETM the loss of reefs propagated from tropical to subtropical locations (Scheibner and Speijer 2008). These observations suggest that an escape from heat due to rapid global warming rather than ocean chemistry may have been the more important proximate factor driving the loss of reefs. OA, however, certainly could have reinforced the pattern or acted synergistically with global warming to enhance organisms' sensitivity to heat stress, as has been shown for some contemporary corals and coralline algae (Anthony et al. 2008).

Acidification and rapid warming in combination seem to act as an effective “kill switch” for reef building. Corals are capable of adapting or acclimatizing to a range of temperatures given enough time, as are other reef builders. The extent to which reef builders could adapt or acclimatize to OA conditions is not yet clear, though data showing adaptive responses to OA is beginning to emerge for other calcifiers (Lohbeck et al. 2012; Pespenti et al. 2013; Schlüter et al. 2014; Suckling et al. 2014). OA favors carbonate dissolution rather than accumulation and preservation, however, and even if reef builders are able to tolerate novel environmental conditions during OA/climate change events, OA could still imperil the geologic process of reef building by reducing the calcification rate of reef biota, increasing both bioerosion and dissolution, and decreasing abiotic

cementation (Manzello et al. 2008; Eyre et al. 2014). The latter process may become increasingly important as erosion and breakage due to more intense storm activity remove loose sediment and rubble (Webster et al. 2005).

Reduced preservation of reef carbonates under OA may be especially important to deep-water coral reefs, such as those built by *Lophelia pertusa*, because they naturally occur closer to the chemical conditions which favor carbonate dissolution. In laboratory experiments, calcification by *Lophelia* appeared to be quite resistant to OA (Maier et al. 2011, 2013), yet *Lophelia* reefs tend to disappear where natural processes make seawater too acidic. OA may substantially reduce deep-water reef building, even if the corals themselves are able to tolerate the new conditions (Turley et al. 2007; Davies et al. 2008). The combined impacts of OA and rapid climate change have led to the global collapse of reef building in the geologic past, and a future collapse of reef building is a real possibility under anthropogenic OA and climate change today.

#### 9.5.4 The Long Tail of CO<sub>2</sub>

Following the geologically rapid release of large amounts of CO<sub>2</sub>, tens of thousands of years are required for climate and ocean chemistry to return to levels roughly similar to those prior to the event. This response is driven in part by the quasi-exponential decay in atmospheric CO<sub>2</sub> concentration, leading to a long right tail in the anomaly distribution and a slow decrease in the future. Under anthropogenic OA and climate change, global mean temperature will remain near the peak level of warming even 1000 years after anthropogenic CO<sub>2</sub> emissions cease, and more than half of the peak level of warming may remain after 10,000 years (Archer and Brovkin 2008; Solomon et al. 2009; Meissner et al. 2012).

The time needed for elevated temperatures to return to initial levels is on the order of 20,000–100,000 years, depending on the ultimate size of the CO<sub>2</sub> perturbation and feedbacks within the Earth system (Archer and Brovkin 2008; Meissner et al. 2012). Hansen et al. (2013) note that geologic precedent points to a higher long-term climate sensitivity and potentially much greater warming of the climate over millennial timescales. Hence, rather than a decay in the level of warming after 10,000 years, the Earth system may continue to warm, leading to almost twice the rise in temperature expected from the medium-term equilibrium climate response. The recovery of seawater chemistry is likewise a slow process, requiring tens of thousands of years, but will occur somewhat more rapidly than the recovery of climate (Archer and Brovkin 2008; Meissner et al. 2012).

These are extremely slow processes on human timescales, but such long periods are supported by both modeling and

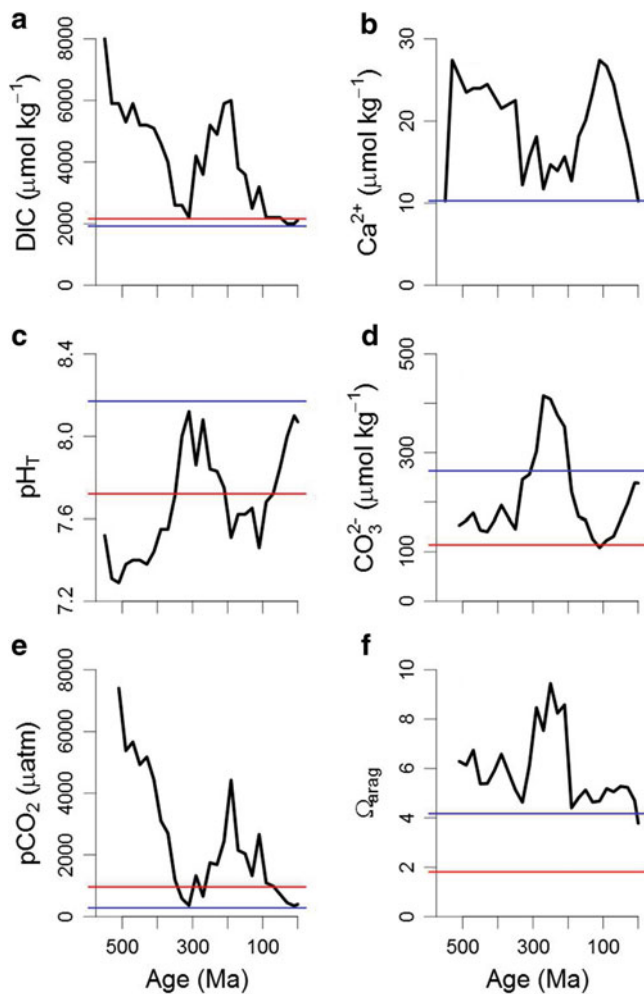
geologic precedent. About 100,000 years was required for oceanic processes, such as carbonate deposition, to return to normal following the PETM, for example (Zachos et al. 2005). Thus, over timescales relevant to human society, climate change and OA are both “irreversible” (*sensu* Solomon et al. 2009), but they are not unstoppable. The magnitude of the perturbations from anthropogenic CO<sub>2</sub> to the Earth system and to reef building depends heavily on the quantity of CO<sub>2</sub> released by human activities over coming decades. The most severe impacts of OA and climate change can be avoided if human-induced CO<sub>2</sub> emissions are rapidly curtailed.

#### 9.5.5 Reef Building Under Persistent, Low pH

Proxy data and modeling studies show that seawater pH and carbonate ion concentration [CO<sub>3</sub><sup>2-</sup>] were much lower and pCO<sub>2</sub> was much higher during most of the Phanerozoic as compared to the modern ocean. Given the negative impacts of OA on reef building, the success of reefs throughout much of geologic time at first seems counterintuitive. This paradox can be solved by recognizing that reef building does not depend simply on seawater pH, [CO<sub>3</sub><sup>2-</sup>], or pCO<sub>2</sub> *per se*, but that these parameters are part of a more complex set of chemical drivers of reef building.

Over geologically short timescales, [Ca<sup>2+</sup>] is essentially constant in sea water, but varies over long timescales due to changes in the rate of chemical weathering and seafloor spreading, as discussed above. Over the Phanerozoic, seawater [Ca<sup>2+</sup>] has varied from a minimum of ~10.3 mM in modern sea water to a maximum of perhaps ~30–40 mM during the Cretaceous (Hardie 1996; Lowenstein et al. 2001; Demicco et al. 2003; 2005). Carbonate ion concentration depends on seawater pH and carbonate alkalinity (at a given temperature, pressure, and salinity), which are themselves determined by the interaction of rates of chemical weathering, CaCO<sub>3</sub> production, and preservation. During much of the Phanerozoic, variation in oceanic [CO<sub>3</sub><sup>2-</sup>] (as well as pH) and [Ca<sup>2+</sup>] have tended to be opposite in phase (Ridgwell 2005). The overall effect of these changes has been relatively stable  $\Omega_{\text{arag/calc}}$  when averaged over long timescales, though the individual parameters of the carbonate system have varied dramatically over geologic time (Ridgwell 2005; Fig. 9.4). This long-term stability does not include short-term perturbations to the carbonate system, such as those associated with an OA event.

The rate of reef building depends on the net outcome of the opposing processes of carbonate production and carbonate erosion/dissolution. Post-depositional carbonate preservation depends heavily on seawater  $\Omega_{\text{arag/calc}}$  (Eyre et al. 2014), though other factors such as nutrient availability also affect reduced preservation via bioerosion. The relative



**Fig. 9.4** Secular variation in seawater carbonate chemistry over the Phanerozoic. *Black curves* are best estimates of (a) dissolved inorganic carbon, (b) calcium concentration, (c) pH, (d) carbonate concentration, (e) carbon dioxide partial pressure, and (f) aragonite saturation state for the tropical, surface ocean derived from modeling and constrained by geochemical data. Values shown as 20 My averages; error estimates omitted for clarity. Horizontal lines in each plot show modern values for the preindustrial (*blue*) and the end-of-the-century conditions under business-as-usual CO<sub>2</sub> emissions (*red*). Preindustrial and end-of-the-century lines are overlapping in (b) (Modified from Ridgwell 2005)

stability of oceanic  $\Omega_{\text{arag/calc}}$  over long timescales suggests that major changes in reef building generally were not driven by thermodynamically controlled changes in carbonate preservation. This is in contrast to ephemeral OA events, where reduced carbonate preservation and increased dissolution were important factors in the observed reductions in reef-building capacity. Instead, major changes in reef accretion over long timescales were likely driven more by variability in carbonate production, the relative success of reef-building taxa, and the importance of bioerosion, cementation, and encrustation of loose detritus within a given interval.

Much research to date has considered the effects of OA or changes in carbonate chemistry on calcifiers in the context of

changing  $\Omega_{\text{arag/calc}}$ , but physiological data show that such an approach is an oversimplification of the true chemical drivers of organismal calcification (see Chap. 2). While average oceanic  $\Omega_{\text{arag/calc}}$  has been relatively stable over much of geologic time, the other components of the carbonate system have not, and changes in these other parameters may help to explain variation in reef building. Regardless, the apparent paradox of reef building under steady-state low pH, low  $[\text{CO}_3^{2-}]$ , and high  $\text{pCO}_2$  is solved by the compensating effects of higher seawater  $[\text{Ca}^{2+}]$  and carbonate alkalinity on carbonate production and preservation. However, these mechanisms only apply under steady-state conditions, where chemical weathering compensates for high atmospheric CO<sub>2</sub>, and are probably not directly informative of the impacts of OA on reef building on shorter, human timescales.

## 9.6 Coral Reefs in a Brave New Ocean

Human activities today are assaulting coral reefs on multiple fronts. Over the last few decades these pressures have resulted in the loss of at least half the coral cover across the wider Caribbean and Indo-Pacific, though the decline has been highly variable in space and time (Gardner et al. 2003; Bruno and Selig 2007; Jackson et al. 2014). Rates of reef building have likely been reduced by at least these magnitudes, if not more due to reduced growth rates of the surviving corals and community shifts toward less productive species (De'ath et al. 2009; Perry et al. 2013, 2015). The bright spot in this gloomy picture is that relatively healthy reefs still exist, and many reefs which have lost substantial portions of their coral cover could still recover over the decadal timescales relevant to human society. Indeed, without chronic, local, human stressors, some reefs can recover from catastrophic disturbance in as little as 12–20 years (Gilmour et al. 2013; Bahr et al. 2015). The fate of coral reefs over the next 10,000–100,000 years depends heavily on human decisions within the next few decades. With aggressive societal action, many reefs can be put on the path to recovery before the end of this century; without it, many reefs will continue on a downward spiral, culminating in their collapse.

The only scenarios which could save a significant portion of the world's coral reefs are ones where society substantially reduces emissions of greenhouse gases (particularly CO<sub>2</sub>) and improves local reef management (i.e., reductions in sedimentation, pollution, overfishing, eutrophication, etc.) within the next few decades (Kennedy et al. 2013). Without both global reductions in CO<sub>2</sub> emissions and effective local management, coral reefs will become increasingly degraded as bleaching events, acidification impacts, outbreaks of disease, infestations of Crown-of-Thorns starfish, more

powerful storms, sedimentation, pollution, and a host of other stressors kill corals and erode the reef structures they have built. Under increasing stress, reef building will collapse in most places before the end of the century, present-day coral reefs will drown below the rising sea, and reefs will remain rare long into the future, as the geologic history of reef building clearly illustrates. The tools needed to prevent such a decline already exist, but they must be implemented quickly if society wishes to prevent the global collapse of coral reefs.

## 9.7 Conclusions

The geologic history of reef building is one of immense change. Reefs were not always built by corals, and both the dominant taxa and geologic processes of reef building have waxed and waned over time (see Chap. 8). Cyanobacteria and other algal assemblages built the first reefs billions of years ago, but their stromatolites and thrombolites became rare as animal life began to influence what had previously been a microbial world. Some early metazoans and their progenitors began to build mineralized shells and skeletons long ago, becoming obvious by the latter Ediacaran, but first became widespread during the Early Cambrian. Rugose and tabulate corals as well as hypercalcifying sponges came to dominate reef building throughout much of the Paleozoic. These coral-sponge reefs were especially successful during the Ordovician, Silurian, and Devonian, and much less dominant during the Carboniferous and Permian. Changes in the relative success of these calcitic reef builders may be explained in part by changes in the Mg/Ca ratio of seawater, which led to calcite seas during the earlier part of the Paleozoic, but aragonite seas during the latter portion. Rugose and tabulate corals succumbed to the Permian-Triassic mass extinction event.

Scleractinian corals appear to have originated and began calcifying in the calcite seas of the Paleozoic but did not build reefs until the Mesozoic. Their reefs burst onto the scene during the Middle Triassic and scleractinians dominated reef building until the Triassic-Jurassic mass extinction event, which devastated them. They again rose to prominence during the Late Jurassic to Early Cretaceous, but experienced a much-reduced role as reef builders during much of the Cretaceous, perhaps driven in part by a decline of the seawater Mg/Ca ratio deep into the calcite nucleation field. In contrast, calcitic taxa such as some rudist bivalves and planktonic coccolithophores experienced a great deal of success in the calcite seas of the Cretaceous. Rudists went extinct by the end of the Cretaceous and scleractinians survived the Cretaceous-Paleogene mass extinction event. Scleractinian reef building remained at relatively modest

levels until the end of the Paleogene, when the seawater Mg/Ca ratio rapidly rose into the aragonite nucleation field.

Slow, secular changes in climate have influenced the latitudinal extent of reefs over time, with reefs expanding toward the poles under warmer climates and retreating toward the equator during cooler periods. Prevailing climate alone, however, is not a good predictor of the relative success of reef building over time. All else being equal, warmer climates expand the potentially habitable area for tropical reef builders, but other factors can override favorable climatic conditions. Similarly, slow, secular changes in seawater pH and CO<sub>2</sub> concentration have been balanced by the release of alkalinity and calcium to the ocean over geologic timescales, maintaining suitable carbonate chemistry for reef building across a range of pH and CO<sub>2</sub> levels.

In contrast to slow, secular, changes in climate and ocean chemistry, the geologically rapid release of CO<sub>2</sub> to the biosphere leads to rapid climate change and OA. It is not entirely clear which of these factors, or their combination has the most severe effects on reef building, but episodes of rapid climate change and OA are associated with reef crises in the geologic past that may be realistic models for the near future. The fate of coral reefs during this century and beyond depends heavily on decisions regarding global CO<sub>2</sub> emissions and local reef management over the next few decades. Optimistically, CO<sub>2</sub> emissions and local human impacts can be reduced sufficiently to allow coral reefs to begin to recover from the assaults of recent decades. Less optimistically, human actions will lead to the next major coral reef crisis, leaving an indelible mark on the geologic history of reef building.

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