



Research paper

# Global change and modern coral reefs: New opportunities to understand shallow-water carbonate depositional processes

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## Abstract

Human activities are impacting coral reefs physically, biologically, and chemically. Nutrifaction, sedimentation, chemical pollution, and overfishing are significant local threats that are occurring worldwide. Ozone depletion and global warming are triggering mass coral-bleaching events; corals under temperature stress lose the ability to synthesize protective sunscreens and become more sensitive to sunlight. Photo-oxidative stress also reduces fitness, rendering reef-building organisms more susceptible to emerging diseases. Increasing concentration of atmospheric CO<sub>2</sub> has already reduced CaCO<sub>3</sub> saturation in surface waters by more than 10%. Doubling of atmospheric CO<sub>2</sub> concentration over pre-industrial concentration in the 21st century may reduce carbonate production in tropical shallow marine environments by as much as 80%.

As shallow-water reefs decline worldwide, opportunities abound for researchers to expand understanding of carbonate depositional systems. Coordinated studies of carbonate geochemistry with photozoan physiology and calcification, particularly in cool subtropical-transition zones between photozoan-reef and heterotrophic carbonate-ramp communities, will contribute to understanding of carbonate sedimentation under environmental change, both in the future and in the geologic record. Cyanobacteria are becoming increasingly prominent on declining reefs, as these microbes can tolerate strong solar radiation, higher temperatures, and abundant nutrients. The responses of reef-dwelling cyanobacteria to environmental parameters associated with global change are prime topics for further research, with both ecological and geological implications.

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## 1. Introduction

In 1981, when Wolfgang Schlager posed the paradox of drowned reefs, no one anticipated that within 20 years human activities would vividly

demonstrate the accuracy of his conclusion—that “Rapid pulses of relative sea-level rise or reduction of benthic growth by deterioration of the environment” provided “the only plausible explanation of drowning” (p. 197). Even as he wrote these words, scientists were observing local decline of coral reefs (e.g., [Kennington, 1978](#); [Smith et al., 1981](#); [Gladfelter, 1982](#)). By the end of the 20th century, coral-reef decline was evident

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worldwide (e.g., Hoegh-Guldberg, 1999; Wilkinson, 2002). While there is mounting evidence that anthropogenic degradation of reef ecosystems began even before the 20th century (e.g., Jackson et al., 2001; Pandolfi et al., 2003), reef researchers at the International Coral Reef Symposium in 2000 concluded that currently living humans may be the last to see living coral reefs (Wilkinson, 2002). Thus, reef and carbonate researchers who have been active over the past 30 years have witnessed firsthand the environmental-deterioration solution to Schlager's (1981) paradox. Moreover, the rapid-pulse mechanism has been documented in the Holocene record (e.g., Blanchon and Shaw, 1995), depicted in fantasy form on the movie screen, and, at the present rate of global warming, is likely to be observed firsthand by carbonate researchers in the foreseeable future.

Although environmental stresses to coral reefs are of both "natural" (i.e., not related to human activities) and anthropogenic origin, human activities consistently amplify the impacts of naturally occurring stresses (Hallock et al., 2004). For example, a hurricane is a natural event whose impact on coastal ecosystems is hugely exacerbated by deforestation, agriculture, and coastal development. Moreover, the impacts of human activities represent not only local-scale environmental degradation that is so widespread as to be of global importance, but also alteration of the Earth's atmospheric and ocean chemistry, with profound implications for climate and the biosphere.

Yet humans are part of the natural world and are certainly not the first biota to have global impact to the detriment of other life forms. Oxygenation of the Earth's oceans and atmosphere, and associated transfer of atmospheric CO<sub>2</sub> to crustal rocks, by Precambrian cyanobacterial photosynthesis is undoubtedly the most profound environmental impact by biota in Earth history. Hopefully human impacts will be relatively modest by comparison. Ironically, cyanobacterial photosynthesis made multicellular life, including humans, possible on Earth; now human activities are altering the Earth's environments in ways that are particularly beneficial to cyanobacteria.

Similarly, mass extinction events, prolonged hiatuses in carbonate deposition (e.g., Newell, 1982), and proliferation of disaster species at event boundaries (e.g., Fisher and Arthur, 1977) have long been recognized in the geologic record. This paper explores

how the ongoing human-induced episode of global change and mass extinction is impacting carbonate deposition. How can scientists utilize ongoing events to better understand the geologic record? What hypotheses can scientists formulate and test as they document the decline of reef-building ecosystems? While local impacts, including loss of fringing reefs to terrigenous sedimentation and loss of species to overfishing, are obvious contributors to reef decline, this paper will focus on the effects of global alteration of chemistry and climate upon tropical shallow-water carbonate factories.

## 2. Alteration of global nutrient cycles

In the 1970s and early 1980s, the misconception was widespread that the high productivity of coral reefs (e.g., Odum and Odum, 1955) was dependent upon rich nutrient supplies (e.g., Longman, 1981). On the other hand, Margalef (1969) was among the first to recognize that coral reefs are dependent not only upon warm ocean waters, but also upon low-nutrient environments. Smith and Kinsey (1976) observed that the very marginal reefs in the eastern tropical Pacific (ETP) were exposed to no greater temperature extremes than the well developed reefs of Australia's Great Barrier Reef, attributing the difference in reef development to nutrients from upwelling in the ETP. Muscatine and Porter (1977) concluded, in reference to reef corals with zooxanthellae, "a cardinal feature of algae-invertebrate symbioses is their ability to survive in nutrient-poor environments" (p. 458). Hallock (1981), using mathematical models, suggested that such symbioses provide the holobiont with literally orders of magnitude energetic advantage over non-symbiotic plants and animals, but *only* in environments where nutrients are scarce. Hallock and Schlager (1986) applied those and other biological principles, along with simple illustrations of how water transparency influences depth distributions of coral communities, to argue that changes in nutrient flux not only influence shallow-water carbonate sedimentation, but can also be used to interpret drowned reefs in the geologic record.

The argument that nutrient excess can suppress and even extinguish reef growth has remained counter-intuitive for some researchers (e.g., Rougerie et al., 1992; Szmant, 2002). At the other end of the

spectrum, Risk (1999) considered nutrification to be the single most important contributor to the decline of reefs worldwide. The subtle power of nutrification is that a modest increase in nutrient flux into a benthic environment can result in detectable change in community structure (e.g., Hallock, 2001). Such a change is commonly referred to as a “phase shift” (e.g., McManus et al., 2000; McManus and Polsenberg, 2004). For example, a shift from coral domination to mixed coral-algal domination of a reef community is a predictable result of a modest increase in nutrient flux (e.g., D’Elia and Wiebe, 1990; Hallock et al., 1993). Similarly, a shift from coral domination to domination by filter-feeding, non-symbiotic animals is a predictable result of a substantial increase in nutrient flux (e.g., Smith et al., 1981). Eutrophication, which is more extreme nutrification, occurs when there is sufficient increase in nutrient flux to stimulate plankton blooms, resulting in high biological-oxygen demand and episodic anoxia in the bottoms waters (e.g., Cockey et al., 1996; Szmant and Forrester, 1996).

Anthropogenically induced nutrification is a local to regional threat to coral reefs around the world, because nutrient flux into coastal waters is a direct function of the numbers of humans in the watershed (e.g., Walsh, 1984). Virtually all human activities contribute to nutrification of aquatic systems, from disposal of human wastes to global alteration of nutrient cycles by atmospheric-nitrogen fixation for fertilizer manufacture, by phosphate mining, and by fossil-fuel burning (e.g., Vitousek et al., 1997a,b). Sources of nutrients to a reef system range from local sewage (Griffin et al., 1999) to regional urban and agricultural runoff (Hallock et al., 1993) to atmospheric washout of nitrous oxides (Fanning, 1989) to increased dust fallout associated with desertification, particularly during ENSO events (Shinn et al., 2000; Garrison et al., 2003).

Since 1981, physiological studies of zooxanthellate corals have continued to demonstrate that excess nutrients destabilize the symbiosis (e.g., Falkowski et al., 1993; Steven and Broadbent, 1997) and reduce reproductive capacity of the coral host (e.g., Koop et al., 2001). The detrimental effects of nutrification are reflected in population and community dynamics (e.g., Smith et al., 1981; Koop et al., 2001), thereby impacting reef-building mode and potential (e.g.,

Hallock, 2001). The responses of coral-reef communities to nutrification are straightforward and predictable (Hallock et al., 1993; Hallock, 2001):

- (a) decline in the abundance of reef-building corals,
- (b) increase in abundance of benthic macroalgae,
- (c) nuisance cyanobacterial and algal blooms,
- (d) increase in rates of bioerosion, and
- (e) loss of reef structure, which results in loss of habitat for reef-dwelling organisms.

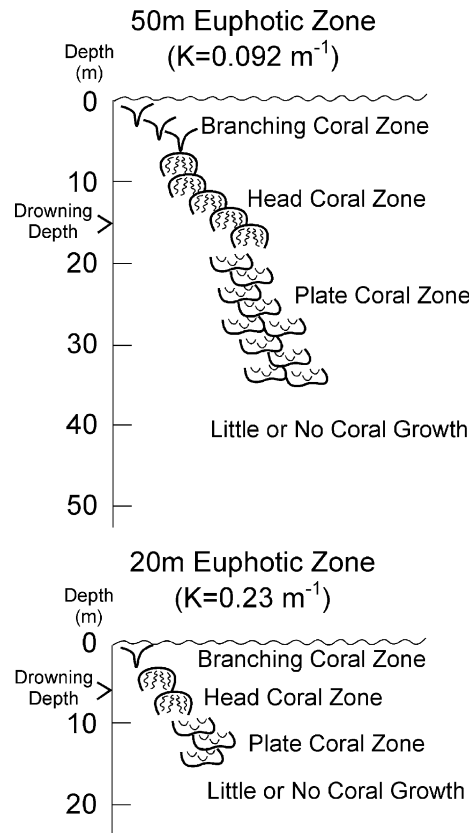


Fig. 1. Cartoons illustrating how water transparency, as indicated by diffuse attenuation coefficient ( $K$ ), influences zonation of zooxanthellate corals. Branching corals such as *Acropora palmata* require at least 60% of surface light, head corals at least 20% and plate corals at least 4%. The upper figure reflects pre-1980s conditions in the Florida Keys (Jaap, 1984); the lower figure reflects median values measured near Key West, Florida, in 1999 by Yentsch et al. (2002), who concluded that insufficient light now penetrates to support significant coral cover. “Drowning depth” shown on each figure is the approximate submergence depth required to physically drown that reef, based only upon light. Modified and updated from Hallock and Schlager (1986).

A profound lesson that ongoing anthropogenic impacts bring to studies of carbonate sedimentation is that the decline of reef-building along an entire reef tract does not require dramatic environmental change. Hallock and Schlager (1986) illustrated a 50 m euphotic zone for the Florida Keys (Fig. 1), which was consistent with historic water-transparency data (Jaap, 1984) and the depth of modern reef development, both representative of a diffuse-attenuation coefficient of approximately  $0.09 \text{ m}^{-1}$ . Yentsch et al. (2002) reported attenuation coefficients from both inshore and offshore measurements made in 1999; fewer than 15% were less than  $0.1 \text{ m}^{-1}$  and more than 40% exceeded  $0.25 \text{ m}^{-1}$ . These researchers concluded that water transparency along the Florida reef tract is now generally too low to support sufficient coral cover for net reef accretion. For example, Palandro et al. (2003) documented change at Carysfort Reef in the Florida Keys between 1984 and 2000; over that time coral cover declined from 33% to 4%, while the category reflecting degraded reef increased comparably.

### 3. Stratospheric-ozone depletion

Reef researchers generally do not consider stratospheric-ozone depletion to be a problem for tropical marine communities because the most extreme ozone depletion occurs at high latitudes, while intensities of ultraviolet radiation (UV, 280–400 nm wavelength) are naturally higher and more seasonally variable at lower latitudes (e.g., Shick et al., 1996). Furthermore, since modern stratospheric-ozone damage is primarily associated with anthropogenically produced chlorofluorocarbons, one might question relevance to the geologic record (e.g., Robock, 2000). The connection lies with bolide impact, supernovae, and explosive volcanism, any of which can temporarily impact the Earth's protective ozone layer (see review by Cockell, 1999). Impact events that generate significant amounts of heat and shock waves can cause direct gas-phase destruction of stratospheric ozone and well as indirect destruction by ionizing atmospheric oxygen and nitrogen, thereby generating ozone-depleting nitrous oxides (Cockell, 1999 and references cited therein). Volcanic eruptions that inject large quantities of chlorine into the stratosphere also trigger ozone

depletion (Johnston, 1980). While the effects of ozone depletion are extremely difficult to distinguish from other detrimental effects of explosive volcanism in the fossil record (Cockell, 1999), Guo et al. (2003) documented mass mortalities in Mesozoic vertebrates, which they attributed to volcanic eruptions that ejected exceptionally high concentrations of halogens.

The mistaken belief that biologically damaging UV wavelengths (principally UV-B, 280–320 nm) do not penetrate significantly into seawater has also contributed to misunderstanding of the potential impact of ozone depletion on reef communities. In fact, UV-B is rapidly absorbed only in waters with significant concentrations of chromophoric dissolved-organic matter (CDOM), much of which originates from breakdown of plant material in coastal wetlands and seagrass meadows (e.g., Bricaud et al., 1981; Kirk, 1996; Anderson et al., 2001). Clear, nutrient-deficient tropical waters typically contain relatively low phytoplankton densities and limited CDOM, allowing significant doses of UV-B to penetrate seawater to tens of meters depth (e.g., Smith and Baker, 1979; Gleason and Wellington, 1993).

Subtropical shallow-water marine communities are arguably among those most vulnerable to increasing intensities of ultraviolet radiation (Hallock, 2001). Anthropogenically induced stratospheric-ozone depletion at subtropical latitudes has progressed to the extent that UV-B intensities formerly only experienced around the summer solstice now are common throughout the summer months (Shick et al., 1996). In addition, major volcanic eruptions such as the El Chichón eruption in Mexico in 1982 and the Mt. Pinatubo eruption in the Philippines in 1991 injected  $\text{SO}_2$  molecules into the stratosphere that provided substrate for chlorofluorocarbons to attack ozone molecules, accelerating stratospheric ozone depletion by 3–4% at subtropical and tropical latitudes (e.g., Randel et al., 1995). While ozone depletion of 3–4% intuitively seems minimal, two amplification factors increase the probability for impact. First, atmospheric researchers estimate that a 1% decrease in stratospheric ozone increases UV-B reaching the Earth's surface by 2% (Shick et al., 1996). Second, CDOM in seawater not only absorbs UV-B, but is broken down in the process. For every 1% increase in UV-B hitting the sea surface, the rate of CDOM breakdown is

increased roughly three fold (Moran and Sheldon, 2000). Moreover, CDOM preferentially absorbs not just UV-B, but all the shorter, higher-energy wavelengths, from blue through UV-B (280–490 nm). Thus, a 3–4% decline in stratospheric ozone results in roughly an 18–24% increase in penetration of higher-energy solar radiation.

The assumption that organisms live near their upper physiological limit for an environmental parameter (e.g., Glynn, 1996) has primarily been applied to temperature. However, a major group of reef-dwelling foraminifers with algal symbionts thrive near their upper physiological limit for solar radiation. These foraminifers are now exhibiting damage from increasing penetration of shorter-wavelength radiation (Williams and Hallock, 2004). In summer 1991, following the Mt. Pinatubo eruption, *Amphistegina* populations in the Florida Keys began to exhibit visible loss of algal endosymbionts. By November, population densities had plummeted to less than 5% pre-event levels and remained low for more than a year. Sampling at Heron Island, Australia, Montego Bay, Jamaica, and elsewhere in 1992 indicated that this previously unknown malady was suddenly widespread. Monitoring of *Amphistegina* populations in the Florida Keys was carried out monthly between 1993 and 1996, and continued quarterly to 1998. Results revealed strong correlation to the solar light cycle, which peaks with the summer solstice in the Florida Keys, and not to the seasonal temperature cycle, which peaks in August or September (Hallock et al., 1995; Talge et al., 1997; Williams et al., 1997).

The kinds of damage exhibited by the afflicted foraminifers also were consistent with UV-B damage (Hallock et al., 1995), which typically influences photosynthesis, protein synthesis, DNA structure, and behavior in protists (e.g., Hadar and Worrest, 1991). Reproduction was profoundly impacted; asexual broods produced by these free-living foraminifers frequently included encrusting offspring (Hallock et al., 1995). Had these apparent mutants successfully reproduced and founded a new lineage, the event would have represented a punctuated family-level evolutionary event.

Sublethal effects of biologically damaging UV-B characteristically include increased susceptibility to diseases and predation (e.g., Hadar and Worrest, 1991). Affected foraminifers exhibited frequent infes-

tation by cyanobacteria (Hallock, 2000) and evidence for predation (Hallock and Talge, 1994). Blue and UV radiation both have been shown experimentally to cause bleaching in corals and larger foraminifers (Fitt et al., 2001; Williams and Hallock, 2004), providing insight into the epidemics of previously rare or unknown diseases that are currently ravaging corals and other reef organisms (e.g., Richardson et al., 1997, 1998; Santavy and Peters, 1997).

Thus, the emergence of coral bleaching as a problem over the past two decades is likely compounded by sublethal stress to corals by high-energy, short-wavelength solar radiation (280–490 nm). The first widespread coral mass-bleaching event occurred in 1982–1983 (Williams and Bunckley-Williams, 1990), soon after the El Chichón volcanic eruption (Fig. 2). Corals are known to bleach in response to elevated UV-B (Gleason and Wellington, 1993; Glynn et al., 1993; Reaka-Kudla et al., 1994), as well as to increased blue radiation (Fitt et al., 2001). Physiological studies of *Montastrea* in the Florida Keys in 1999 revealed significant photo-oxidative stress in May, although bleaching did not occur until late summer when sea-surface temperatures reached their peak (Downs et al., 2002).

The damaging effects of increased UV-B radiation associated with volcanism, bolide impacts, or supernovae in the geologic record will continue to be

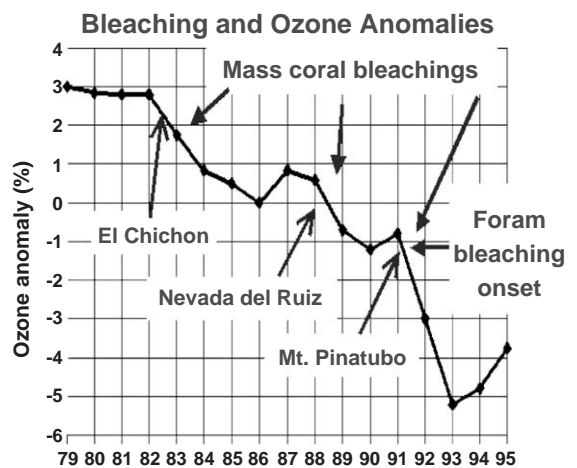


Fig. 2. Ozone anomaly at mid-latitudes in the northern hemisphere compared with coral-reef bleaching events. Modified from Roscoe (2001).



difficult to distinguish from simultaneous effects on climate and marine environments (Cockell, 1999). However, UV-B is a powerful mutagen and may have contributed to rapid diversification events that followed mass extinction events such as the Cretaceous–Paleogene boundary event. Since mutations are mostly harmful, abundant, rapidly growing viral and bacterial populations are the most likely short-term beneficiaries of increasing evolutionary rates. New diseases are becoming increasingly prevalent in modern ecosystems (e.g., Harvell et al., 1999), including coral reefs, possibly the result of changing selective pressures, mutations, and global transport of pathogens (Hallock et al., 2004).

Cyanobacteria, which are typically UV-tolerant microorganisms (He and Hadar, 2002; He et al., 2002), have become increasingly prominent on modern reefs. Black-band and related coral diseases are assemblages of microbes that include cyanobacteria (e.g., Rützler and Santavy, 1983; Richardson et al., 1997; Sutherland et al., 2004). Nuisance “algal” outbreaks are commonly cyanobacterial blooms (e.g., Hallock et al., 1993; Butler et al., 1995; Landsberg, 2002). Cyanobacteria are ubiquitous members of the reef microbiota. Cyanobacterial blooms and outbreaks of pathogenicity in cyanobacterial assemblages appear to be opportunistic events that occur when environmental conditions stress other members of the community. Cyanobacterial communities frequently flourished during and after environmental perturbations in the Paleozoic as well, as recorded in limestones by proliferation of stromatolites and other microbial biogenic carbonates following extinction events (e.g., Copper, 1994).

#### 4. Increasing concentrations of atmospheric CO<sub>2</sub>

The rapidly increasing concentration of atmospheric CO<sub>2</sub>, resulting from fossil-fuel burning and a variety of activities that reduce fixation by photosynthesis, is arguably the single greatest threat to global environments. Global climate change, rapid sea-level rise, and acidification of the oceans are predictable consequences of this perturbation of atmospheric and ocean chemistry. The consequences for shallow-water carbonate depositional environments tend to be both dramatic and predictable.

#### 4.1. Global warming

The recent emergence of coral bleaching as a source of mass mortality on coral reefs has frequently been cited as evidence for global warming (e.g., Glynn, 1996; Hoegh-Guldberg, 1999; Hughes et al., 2003). Bleaching occurs when zooxanthellate corals or other algal mutualisms lose color, either as a result of loss of algal symbionts or because symbionts themselves lose pigment (Glynn, 1996). Although coral bleaching was locally observed occasionally in the 1800s, mass coral-bleaching events were unknown prior to 1982 (e.g., Williams and Bunckley-Williams, 1990; Glynn, 1996). By the 1990s, coral bleaching was reported somewhere nearly every year (e.g., Hoegh-Guldberg, 1999).

The 1997–1998 mass-bleaching event was unprecedented in its extent, intensity, and mortality (Hoegh-Guldberg, 1999; Wilkinson, 2002). In contrast, coral recovery from mass bleaching was the norm following the 1987 mass-bleaching event in the western Atlantic and Caribbean (Lang et al., 1992). Yet even when most corals survive, bleaching impacts coral biomass, calcification, and reproduction (Szmant and Gassman, 1990), and is strongly implicated in the increasing incidences of coral diseases (e.g., Goreau et al., 1998; McField, 1999).

The association between elevated sea-surface temperatures and mass bleaching events is so strong that a website (<http://www.osdpd.noaa.gov/PSB/EPS/SST/climohot.html>) has been established (NOAA/NESDIS, 2003) and has successfully predicted bleaching events (e.g., Carriquiry et al., 2001). Hoegh-Guldberg (1999) reviewed the coral-bleaching literature, examined global climate models, and predicted that summer sea-surface temperatures high enough to induce coral bleaching will become nearly annual events on reefs worldwide over the next several decades. Realistically, coral populations cannot survive annual bleaching. If global-warming models are even close to accurate, bleaching could eliminate shallow-water coral reefs within a few decades.

Nevertheless, if global warming was the only environmental change occurring, at least some coral species should ultimately acclimate or adapt (e.g., Coles and Brown, 2003; Baker et al., 2004; Rowan, 2004). For example, modern corals in the Persian Gulf

tolerate considerably larger fluctuations in temperature than corals living in regions that typically see much smaller seasonal fluctuations (e.g., Coles, 1997; Coles and Brown, 2003). Corals that do adapt may benefit as rising sea level and expanding subtropical climatic zones increase suitable habitat (e.g., Kleypas et al., 2001). Higher temperatures also increase carbonate saturation, enhancing carbonate precipitation (e.g., Kleypas et al., 2001). Thus, despite the strong connection between bleaching and global warming, other consequences of increasing atmospheric CO<sub>2</sub> quite likely will have more serious impacts on carbonate sedimentation.

#### 4.2. *Sea-level rise*

The acceleration of global rise in sea level is another probable consequence of increasing atmospheric CO<sub>2</sub>. If collapse of existing ice sheets triggers a pulse of sea-level rise on the order of a meter per decade, consistent with Blanchon and Shaw's (1995) interpretations of early Holocene catastrophic-rise events, reef communities will be affected, though not necessarily fatally. As seen in the fossil record, during sea-level rise reef communities either back step, keep up, deepen and later catch up, or drown (e.g., Neuman and Macintyre, 1986). In some cases, flooding of lowland areas or increased rainfall will deliver sediments and nutrients to the shelf margin, terminating or precluding reef development. In other cases, the combination of expanding subtropical climatic zones and sea-level rise could provide additional habitat for carbonate deposition (e.g., Hallock, 2001; Kleypas et al., 2001).

#### 4.3. *Acidification of the oceans*

The most serious consequence of increasing atmospheric CO<sub>2</sub> concentrations for coral reefs is the one most commonly overlooked, i.e., alteration of ocean chemistry (Caldeira and Wickett, 2003), particularly reduction in carbonate saturation (e.g., Kleypas et al., 1999, 2001).

The predominant biotic producers of carbonate in Cenozoic tropical shallow-water carbonate factories (Schlager, 2003) are photozoans (James, 1997), i.e., organisms associated with photosynthesis either directly, e.g., calcareous algae, or through photosym-

biotic associations, e.g., zooxanthellate corals and larger foraminifers. Among the photozoan calcifiers, ocean chemistry appears to be a major factor determining which modes of calcification and shell mineralogies are advantageous (Hallock, 1996, 2001; Stanley and Hardie, 1998). Sandberg (1983) noted Phanerozoic oscillations in primary mineralogies of abiotic carbonates, and postulated that tectonically induced changes in atmospheric pCO<sub>2</sub> were responsible for mineralogic changes.

Vandepoel and Schlager (1994) and Stanley and Hardie (1998) observed that the oscillations reported by Sandberg (1983) were paralleled by oscillations in dominant calcite- and aragonite-secreting, reef-building organisms. For example, scleractinian corals evolved calcification of aragonite skeletons and established symbioses with dinoflagellate zooxanthellae during the Triassic (Stanley, 1981, 2003). However, as atmospheric CO<sub>2</sub> and oceanic-calcium concentrations rose in the Cretaceous, the aragonite-secreting corals, while remaining highly diverse, lost dominance in shallow-water habitats to the mixed calcite/aragonite-secreting rudist bivalves (e.g., Gili et al., 1995; Johnson and Kauffman, 2001).

Following the terminal-Cretaceous extinctions, which eliminated the rudists, the cool-water carbonate factory dominated, i.e., bryozoans and variable-Mg calcite coralline algae. These producers were joined by calcitic, rotaliid larger foraminifers by the late Paleocene (Adams et al., 1990). Although scleractinian corals survived the terminal Cretaceous extinctions, framework reefs were scarce through the middle Eocene (Perrin, 2002). Boron isotopes indicate elevated and strongly fluctuating pCO<sub>2</sub> concentrations from the Paleocene to mid-Eocene (Pearson and Palmer, 2000). During the late Eocene, atmospheric CO<sub>2</sub> declined to roughly 2–3 times pre-industrial Holocene concentrations (Pearson and Palmer, 2000; DeConto and Pollard, 2003). Although aragonite-secreting corals diversified and produced limited, local framework reefs throughout most of the Paleogene (e.g., Budd et al., 1992; Budd, 2000; Perrin, 2002), shallow-water aragonite factories did not become widespread until the late Oligocene (Frost, 1977; Budd, 2000), when CO<sub>2</sub> concentrations had declined to Neogene levels (Pearson and Palmer, 2000; Zachos et al., 2001). Framework reefs constructed by scleractinian corals reached their acme in

the early to middle Miocene (Frost, 1977; Perrin, 2002), when atmospheric CO<sub>2</sub> concentrations apparently stabilized in the range of pre-industrial concentrations (~200–300 ppm). These Cenozoic events, with predictions for the next 100 years, are summarized in Fig. 3.

Stanley and Hardie (1998) argued that the combination of higher Ca<sup>2+</sup> concentrations and higher Ca<sup>2+</sup>/Mg<sup>2+</sup> ratios in the oceans, rather than higher atmospheric CO<sub>2</sub> concentrations, were the critical factors favoring calcite precipitation over aragonite. Those researchers noted that greenhouse conditions in the Cretaceous and early Paleogene were associated with higher rates of volcanism, including ocean-ridge activity, which was responsible both for higher atmospheric CO<sub>2</sub> concentrations and higher calcium concentrations in the ocean.

To understand temporal trends in reef-building organisms, including predicting future changes as pCO<sub>2</sub> rises, one must also consider biogenic calcification mechanisms (Hallock, 1996, 2001). The simplest mechanism for calcification is biologically enhanced geochemical precipitation, which occurs when biotic activities so supersaturate a microenviron-

ment that calcification occurs. For example, in restricted environments, photosynthesis can remove sufficient CO<sub>2</sub> from seawater that precipitation occurs, usually in the vicinity of the photosynthetic surface (McConnaughey and Whelan, 1997), e.g., a cyanobacterial mat. As Stanley and Hardie (1998) observed, whether calcite or aragonite precipitates is largely a function of Mg/Ca ratio in the seawater.

Most eukaryotic organisms more directly calcify, utilizing ATP (a basic form of biochemical energy) to exchange Ca<sup>2+</sup> and H<sup>+</sup> ions across cell membranes, creating acidic and alkaline surfaces, inducing CaCO<sub>3</sub> precipitation on the latter (McConnaughey and Whelan, 1997; Gattuso et al., 1999). Calcification can be driven by either ATP produced during initial capture of solar energy (Erez, 1983) or ATP produced by respiration of organic molecules. Whether calcite or aragonite precipitates again should be a function of Mg/Ca ratio in the seawater, unless the organism utilizes additional energy to control the mineralogy of the precipitate. Thus, in Cretaceous and Paleogene shallow, tropical seas, where Ca<sup>2+</sup> concentrations typically exceeded 40 meq/l and Mg/Ca ratios exceeded 3 (Stanley and Hardie, 1998), and where

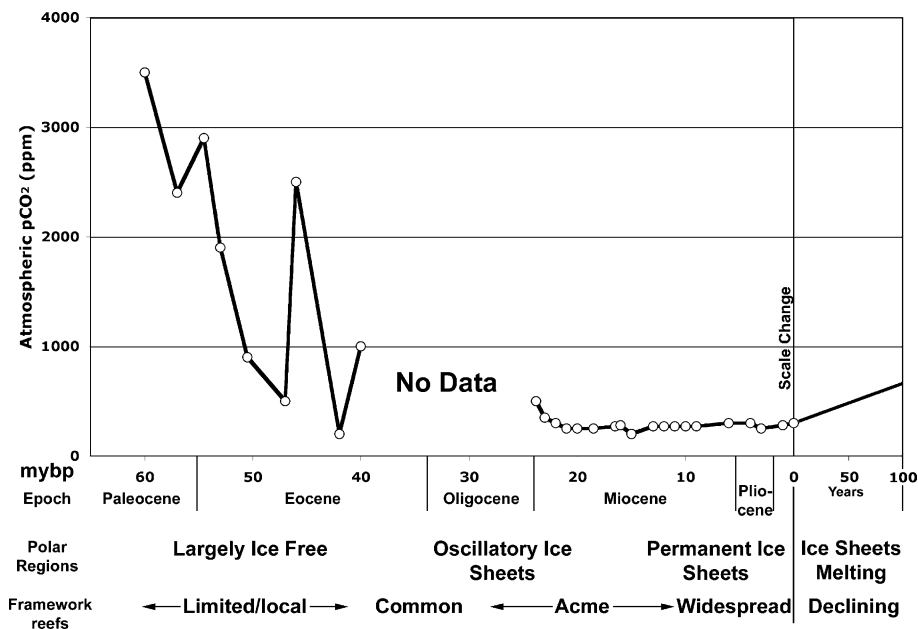


Fig. 3. Trends in atmospheric pCO<sub>2</sub> over the past 60 million years from Pearson and Palmer (2000), with corresponding status of polar ice sheets from Barrett (2003) and status of coral-dominated framework reefs from Perrin (2002). At 0 year, the scale changes and atmospheric pCO<sub>2</sub> for the next 100 years is projected, consistent with Kleypas et al. (2001).



sunlight could provide abundant energy for photosynthetic production of ATP that created alkaline surfaces for calcification, calcite was the form of  $\text{CaCO}_3$  most easily precipitated and most stable when surface waters equilibrated with high concentrations of atmospheric  $\text{CO}_2$ . In that ocean chemistry, production and maintenance of calcite shells or skeletons would have required less energy expenditure by heterozoans, though the greater strength of aragonite likely offset the higher cost for organisms living where food supply was not the major limiting resource.

Using thermodynamic calculations based on coral-reef growth over the past 8000 years, Kleypas et al. (1999) estimated that coral-reef development occurs where aragonite saturation is at least 4.0. Thus, in Neogene shallow tropical seas, where Mg/Ca ratios exceeded 3 (Stanley and Hardie (1998), aragonite or high Mg calcite were the forms of  $\text{CaCO}_3$  most efficient for both photozoans and heterozoans to precipitate where aragonite saturation was at least 4. Again, since aragonite is structurally stronger than calcite, construction of aragonite skeletons by coral and calcareous algae is clearly advantageous. However,  $\text{Ca}^{2+}$  concentrations are relatively low in Neogene waters (Stanley and Hardie, 1998), so aragonite hypercalcification is restricted to areas where the combination of warm temperatures and normal to slightly elevated salinities increase aragonite saturation (Kleypas et al., 1999, 2001). Because aragonite saturation state is heavily dependent upon  $p\text{CO}_2$ , aragonite saturation is now declining in tropical waters worldwide. Doubling of  $\text{CO}_2$  concentrations over pre-industrial levels in the mid-21st century will reduce aragonite saturation by at least 30% (Kleypas et al., 1999).

Both modeling (e.g., Kleypas et al., 1999) and experimental studies (Langdon et al., 2000, 2003; Marubuni et al., 2001) indicate that rising atmospheric  $\text{CO}_2$  concentrations have already impacted carbonate saturation by at least 10% and by mid-century the magnitude of change will be about 30%. Using thermodynamic calculations, Kleypas et al. (1999) estimated that the average aragonite-saturation state in the tropics has dropped from 4.6 to 4.0 over the past 100 years and projected a drop to  $3.1 \pm 0.2$  by 2065. Reefs with balanced  $\text{CaCO}_3$  budgets, and thus already near their environmental limits for reef accretion, should be most susceptible to declining aragonite saturation (Kleypas et al., 1999). Kleypas et

al. (2001) further concluded that the shift in saturation state projected by 2065 “will shift many reefs from net carbonate accumulation to net carbonate loss” (p. 434).

If the Eocene is a useful model (Fig. 3), calcitic foraminifers and coralline algae may once again predominate shallow-water carbonates, as aragonitic corals and calcareous green algae become less common (Hallock, 2001). Based on Schlager’s (2003) estimates of carbonate productivity by functional groups, the consequence of that change in the shallow-water carbonate factory may be as much as 70–80% decline in carbonate sedimentation rates. However, because both  $\text{Ca}^{2+}$  and  $\text{Ca}^{2+}/\text{Mg}^{2+}$  concentrations are low in modern oceans (Stanley and Hardie, 1998), rising  $p\text{CO}_2$  may be detrimental to calcification rates across mineralogies, not just to aragonite producers. If so, the result may be widespread carbonate-hiatus conditions, similar to major extinction horizons in the fossil record described by Newell (1982), rather than to greenhouse carbonate-factory conditions, at least until carbonate dissolution restores ocean alkalinity to equilibrium with atmospheric conditions.

## 5. Opportunities for carbonate research during global change

Even as coral reefs decline worldwide, opportunities for researchers to understand carbonate-depositional systems continue to expand. Coordinated efforts, in both laboratory and field settings, to study carbonate geochemistry along with population dynamics, physiology, calcification by photozoan organisms, and composition of benthic communities, will produce breakthroughs in both interpretations of the geologic record and prediction of future changes. For example, Marubuni et al. (2003) demonstrated experimentally that reducing the concentration of carbonate ions in seawater reduces calcification rates in selected coral species and can influence microstructure of the resultant corallites.

Modern environments characterized by the transition between photozoan and heterozoan shallow-water carbonate factories likely provide the best analogues for predicting the future of shallow-water carbonates under rising atmospheric  $\text{CO}_2$  and declin-

ing aragonite saturation. Carbonate-depositional environments on the west and southeast Australian shelves (e.g., James et al., 1999; Harriott and Banks, 2002), the west Florida shelf, the south Atlantic shelf of Brazil (e.g., Castro and Pires, 2001; Gherardi and Bosence, 2001), and the Indian Ocean shelf of South Africa (e.g., Riegl and Riegl, 1996; Riegl, 2003) provide natural laboratories to study the photozoan–heterozoan transition and the rates at which aragonite saturation and carbonate-producing biotic communities are changing along those transition zones.

Perhaps the best natural laboratory to study of the role of seawater chemistry on the shallow-water carbonate factory is the West Australian shelf. The relatively small human population of West Australia has limited anthropogenic impacts on the shelf as a whole. Along a desert coastline bounded by a cool-subtropical ocean, the effects of warming and evaporation on the carbonate factory provide a nearly complete spectrum of modern shallow-water carbonate facies (Table 1) (James et al., 1999). The open-shelf communities are dominated by bryozoans, coralline algae, molluscs, and larger benthic foraminifers, with sparse scleractinian corals and leathery rather than calcareous *Halimeda*. The forereefs at Ningaloo (Collins et al., 2003) and the Houtmann Abrolhos Islands (Hatcher, 1985, 1991) are dominated by coralline algae. Coral reefs thrive leeward of Pleistocene barriers, where hot dry winds warm the seawater and elevate salinity (Collins et al., 1993, 1996). In the most restricted bays, notably Shark Bay,

microbial communities construct exquisitely developed stromatolites reminiscent of the Proterozoic (e.g., Riding, 2000; Reid et al., 2003). Similar gradients also have been described in the late Miocene record of the western Mediterranean by Braga and Aguirre (2001) and Pomar (2001), and in the Miocene carbonate platforms of the Marion plateau off north-east Australia (Shipboard Scientific Party, 2002).

Coral reefs today are threatened by the consequences of sedimentation, overfishing, new diseases, increasing ultraviolet radiation, and global warming, as well as nutrification and acidification of the oceans. Many fringing reefs have already been lost to terrigenous sedimentation or nutrification. Even reefs relatively remote from direct human impact are suffering the consequences of regional and global perturbations. Given the variety of modern environmental perturbations, the intensity of some of these perturbations, and particularly the very high rates at which environmental conditions are changing, predicting the future as a mass extinction event is an instructive exercise.

In the fossil record, complex reef-building metazoan communities were typically catastrophically impacted during mass-extinction events (e.g., Stanley, 1992, 2001; Copper, 1994). Moreover, because shallow-water reefs produce complex structures that support high-diversity communities, the decline of reef-building metazoans has far-reaching consequences for global biodiversity. Even if modern corals do not suffer widespread extinctions, species dependent upon the

Table 1

Range of environments, calcareous biotas and mineralogies found on the west Australian shelf (data from Collins et al., 1996; James et al., 1999; and others)

Parameter	Mid-shelf/ramp	Inner shelf/ramp	Reef margin	Backreef	Shark Bay
Depth	50–100 m	<50 m	<50 m	<20 m	<25 m
Temperatures					
Winter	~17–22	~17–22	~17–22	<17–22	<20
Summer	~18–24	~22–26	~23–26	~23–>26	~25–>30
Salinity	35–36	35–36	35–36	35–36	Hypersaline
Calcareous biota	Coralline algae, bryozoa, molluscs, LBF <sup>a</sup>	Coralline algae, bryozoa, molluscs, LBF <sup>a</sup>	Coralline algae	Branching coral	Cyanobacteria, molluscs
Common facies	Skeletal grainstones	Skeletal grainstones	Algal boundstones	Coral framestones	Stromatolites, bivalve coquinas
Predominant mineralogy					
Photozoan	Calcite	Calcite	Mg calcite	Aragonite	Aragonite
Heterozoan	Mixed <sup>b</sup>	Mixed <sup>b</sup>	Mixed <sup>b</sup>	Aragonite	Aragonite

<sup>a</sup> LBF=larger benthic foraminifers.

<sup>b</sup> Mixed=some taxa produce aragonite, some calcite.

structural complexity of reefs undoubtedly will (e.g., Munday, 2004). Once these communities are lost, the fossil record indicates that tens of million years are required for metazoan reef-building communities to re-diversify in suitable environments (Copper, 1994).

Cyanobacteria were not only the first constructors of biotic-carbonate buildups (e.g., Grotzinger, 1989; Grotzinger and Knoll, 1999), but have continued to be ubiquitous inhabitants of carbonate depositional environments through the Phanerozoic. When metazoan reef-building communities experienced mass extinctions in the Paleozoic, stromatolites, and other cyanobacterial structures commonly increased in prevalence as carbonate contributors in shallow-water, tropical marine communities (Stanley, 1992, 2001; Copper, 1994). In modern environments, cyanobacteria flourish on anthropogenic nutrients (Doutereolo et al., 2004), which are often enriched in phosphate relative to nitrogen. Cyanobacteria capable of nitrogen fixation can bloom in response to excess phosphate (e.g., Vitousek et al., 2002). Cyanobacteria thrive in very shallow-water or marginal-aquatic environments, where they are naturally exposed to high intensities of UV-B, as well as significant fluctuations in temperature and salinity (e.g., He and Hadar, 2002; He et al., 2002). The environmental impacts of rising CO<sub>2</sub> concentrations and increased intensities of UV-B appear to be favoring the proliferation of cyanobacteria as compared with more complex and stenotopic eucaryotic organisms. Temperatures that cause mass bleaching and even death in corals (e.g., Glynn, 1996; Hoegh-Guldberg, 1999) can stimulate cyanobacterial growth (e.g., Briand et al., 2004; Murrel and Loes, 2004). However, declining carbonate saturation of surface waters should continue to restrict stromatolite formation to environments where carbonate saturation is elevated by local or regional processes. The responses of reef-dwelling cyanobacteria to environmental parameters associated with global change are prime topics for further research, with both ecological and geological implications.

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