symbiotic interactions in the processes leading to the development of the geological structures and biological communities of coral reefs make the terms used in studies of other communities problematic when dealing with coral reefs. The "individuals" in population ecology of coral reefs can often be a combination of organisms of different kingdoms. Conversely, the "individual" genetic code may be embodied in numerous scattered colonies, many of which live long after the original colony has died. The concepts of "species," "trophic levels," and "communities" become all the more diffuse when trying to understand the factors that tip the balance in processes of coral-reef systems.

2

Reefs and Reef Limestones in Earth History

Pamela Hallock

To seafarers, a **reef** is a submerged hazard to navigation, usually a ridge of rocks or sand at or near the surface of the water. This is why the Exxon *Valdez* could hit a "reef" in Prince William Sound, Alaska, thousands of miles from the nearest coral reef. Historically, tropical waters were particularly treacherous for mariners because reefs constructed by coral communities may lurk just below the surface in otherwise open seas. In both calm seas and storms, often the first indication that a reef was nearby was when a ship ran aground. The earliest European "settlers" in the Florida Keys made their living salvaging shipwrecks. Today the most visible indication of many Pacific atolls is a rusting freighter.

The characteristic that distinguishes coral, oyster, and other **biogenic reefs** from sand and rock reefs is that biogenic reefs are produced by biological as well as geological processes. Another term for a limestone structure or buildup produced by biological activity is **bioherm**. Ideally, a biogenic reef is a significant, rigid skeletal framework that influences deposition of sediments in its vicinity and that is topographically higher than surrounding sediments. For example, a **coral reef** is a rigid skeletal structure in which stony corals are major framework constituents. Less rigid accumulations of biologically produced sediments are sometimes called reef mounds (James, 1983).

The history of biogenic limestones is a topic of considerable economic importance because many ancient reef provinces are major oil and gas reservoirs today. As a result, the literature on ancient reefs and lesser carbonate buildups is vast. A few of the multitude of useful compilations include Milliman (1974), Wilson (1975), Bathurst (1976), Toomey (1981), Scholle et al. (1983), Crevello et al. (1989), and Riding (1991). In particular, Fagerstrom (1987) details *The Evolution of Reef Communities* by examining modern and ancient reefs in the context of the changing organisms through time and the roles those organisms played in reef communities.

This summary cannot provide the details available in such larger compilations.

Instead it summarizes the significance of biogenic reefs and limestones within the context of Earth history. Limestones are predominantly calcium carbonate ($CaCO_3$), and are therefore intimately related to carbon dioxide (CO_2) concentrations in the atmosphere and oceans. Because many limestones are made up of the shells and skeletons of calcareous plants and animals, a substantial part of the marine fossil record is found in limestones. The relationships between atmospheric CO_2 and reef building are not clear-cut; the mechanisms involved are complex and full of poorly understood feedback mechanisms. Nevertheless, the history of biogenic reefs provides a fascinating glimpse at the major events in Earth history, including why life can exist at all.

2.1. Biogenic Sediments and Bioherms

Calcareous shells and skeletons of a wide variety of protists, plants, and animals become biogenic sediments upon the death of those organisms. The metabolic activities of certain bacteria and microalgae also contribute to the biogeochemical precipitation of calcareous (lime) muds in seawater overlying shallow banks and shelves. Biogenic sediments are most prevalent in marine environments that are separated by distance or physical barrier from the influx of sediments from land. Nearly 50% of the modern ocean floor is covered by foraminiferal ooze, the empty shells of protists that live as plankton in the surface waters of the open ocean. Shells and skeletons of benthic organisms are also important sediment constituents, especially on continental shelves, in some coastal areas, and on oceanic banks and shoals.

Whether these biogenic constituents make up most of the bottom sediments or whether they are only minor contributors depends on several factors. One factor is the rate at which sediments from land are entering the marine environment via runoff from rivers and streams. Another factor is the rate at which shells and skeletons are being produced by the biotic communities living in the marine environment. A third factor is the rate at which sediments, both terrigenous and biogenic, are removed from that environment by transport or dissolution. The biotic community not only produces sediments but also affects rates of dissolution of sediments, as well as rates of physical breakdown and transport of sediments. Thus, composition of the benthic community strongly influences rates of sediment accumulation.

Lees (1975) recognized three classes of shallow-water carbonate sediments, based on their major constituents. He called the simplest group foramol sediments after two of the most important constituents: benthic foraminifera and molluscs, especially fragments of snail and bivalve shells. Lees noted that foramol sediments are characteristic of temperate shelves, but sometimes dominate in tropical areas where reefs do not occur. Other important constituents of foramol sediments are fragments of coralline red algae, sea urchin spines and plates, bryozoa, barnacles, and worm tubes. Lees's second sediment type is called chloralgal, for its dominant constituent, the remains of calcareous green algae such as *Halimeda*. Chloralgal sediments have foramol constituents as secondary components. Chloralgal sediments are prevalent in expansive shallows like Florida Bay and the Bahama Banks, and in deep-euphotic settings including the lagoon behind the Ribbon Reefs of the northern Australian Great Barrier Reef. Lees's final sediment category is chlorozoan, which is the typical sediment around coral reefs. Coral and calcareous algal remains are the dominant constituents. Coralline algae, foraminifera, mollusc, and urchin fragments are secondary components. Bryozoa, barnacle, and worm shell debris are typically scarce in chlorozoan sediments because these organisms thrive best in waters with richer food supplies than do corals.

Foramol, chloralgal, and chlorozoan sediments are produced on shelves, oceanic banks and atolls, and nearshore environments. Whether these sediments accumulate in place or whether they are transported away depends on the strengths of waves and currents and the ability of the benthic community to hold sediments in place. Sediments are accumulated and bound by the presence and growth of organisms. Those that project upward from the sediment, slowing water motion and providing quieter places for sediments to settle, can be termed bafflers; those that live in or directly on the sediment, holding or encrusting it in place, can be referred to as binders (Fagerstrom, 1987).

Binders such as microalgae and bacteria grow and develop mats directly on sediments accumulating where wave and current motion is limited or intermittent. Bacterial filaments provide strength to these mats, which can resist as much as 10 times more wave or current energy than is required to move similar unbound sediments (Grant and Gust, 1987). Stromatolites, which are biogenic reefs constructed by this process, are layered accumulations of sediment and algal-bacterial mats. Ancient stromatolites were the first bioherms in the fossil record. Modern stromatolites are found in Shark's Bay, Australia (Logan et al., 1974), and at several localities on the Bahama Banks (Dill et al., 1986; Reid and Browne, 1991).

In some current-swept environments, specialized sponges live in and on the surface layers of sediment, binding it in place. Sediments may consist of coarse accumulations of *Halimeda* segments. Coralline red algae may colonize the surface of sediment-filled sponges, forming solid substrata upon which other organisms settle and grow. These communities produce sponge-algal mounds along the margins of some western Caribbean banks (Hallock et al., 1988; Hine et al., 1988), which show similarities to fossil sponge-algal reef mounds.

A variety of elongate, upward-projecting plants and animals baffle water motion and trap sediments. On modern shallow shelves, seagrass beds effectively stabilize sediment over vast areas. Seagrass blades slow water flow, allowing suspended sediments to settle out. Sediments are then held in place by extensive seagrass root and rhizome systems, as well as by the holdfasts of algae living within the seagrass bed. Sediment-dwelling macroalgae are also effective bafflers and binders, as are sponges, sea whips, and sea fans. In fossil reefs, a variety of less familiar organisms performed similar roles.

The ultimate bafflers are the biogenic framework constructors (Fagerstrom, 1987), which in modern tropical shallow-water environments are the stony corals. These organisms grow upward or outward in branching, massive, or platy morphologies, secreting substantial quantities of calcium carbonate, while trapping even greater quantities of sediment within the lee of the reef framework. Encrusting coralline algae bind the reef framework and enclose sediments into the massive, wave-resistant structures we recognize as coral reefs.

The three-dimensional topography of the reef provides abundant habitats for the diverse array of species that dwell within the reef structure. All contribute to the reef community in some way—many to the reef structure itself, all to energy flow within the community. Some of these species are encrusters, some are sediment producers, and some are wholly soft bodied and have little direct influence on the reef structure. Many species even contribute to the breakdown of the reef structure by boring into it or scraping away at it as they graze. Such organisms are known collectively as bioeroders (Neumann, 1966) or destroyers (Fagerstrom, 1987).

Bioeroding organisms are a diverse and important component of the reef community (Hutchings, 1986). Organisms that bore or etch their way into the reef include bacteria, fungi, several varieties of sponges, worms, clams, and urchins. Organisms that scrape away limestone as they graze algae include urchins, chitons, and some snails. Many reef fish feed by breaking or scraping off bits of coral or coralline algae. In a healthy, actively accreting reef, bioeroders contribute to the diversity of habitats within the massive reef structure. However, if reef growth slows in response to natural or anthropogenic environmental stresses, the rates of destruction can exceed rates of accretion and the reef may cease to exist (Glynn, 1988; Hallock, 1988).

2.2. Basic Carbonate Chemistry

The major chemical constituent of calcareous sediments and limestones is $CaCO_3$. Organisms secrete $CaCO_3$ either as calcite or aragonite. The obvious difference between these minerals is their crystal structure. Calcite forms rhombohedral crystals whereas aragonite forms orthorhombic crystals. Aragonite is structurally stronger than calcite. But the most important difference is in the chemical stability of the minerals at temperatures and pressures found on land and in the oceans. Aragonite more readily precipitates in warm seawaters that are supersaturated with $CaCO_3$, but it is less stable in cooler seawaters and in freshwater. Through time, most aragonite either dissolves or recrystallizes, so calcite predominates in ancient limestones.

The solubility of $CaCO_3$ is easily misunderstood if this chemical is expected to behave like other familiar solids. For example, table salt and sugar both dissolve faster in hot water than in cold. $CaCO_3$ is more soluble in cold water. The key to this intuitive discrepancy is in the reaction of carbon dioxide with water:

$$CO_2 + H_2O \Leftrightarrow H_2CO_3 \Leftrightarrow H^+ + HCO_3^- \Leftrightarrow 2H^+ + CO_3^{2-} \qquad (2\text{–}1)$$

That is, carbon dioxide and water combine to form carbonic acid, which can then dissociate to hydrogen ions and bicarbonate (HCO_3^-) or carbonate (CO_3^{2-}) ions. The two-headed arrows indicate that the reaction can go in either direction depending on environmental conditions. The dissolved inorganic carbon concentration of a sample of seawater is the sum of the carbon in these four states. In surface seawaters, CO_2 is only a small fraction of the total, often less than 1% (Riebesell et al., 1993).

How much CO_2 can be dissolved in water and which state predominates depends primarily on temperature, pressure, and concentrations of other dissolved materials. Cold water can hold far more CO_2 in solution than warm water; an example is a cold carbonated beverage, which loses CO_2 as it warms. Similarly, water under pressure can hold more CO_2 in solution. Addition of dissolved salts (i.e., increased salinity) decreases the ability of water to dissolve CO_2. Surface waters of the ocean can hold less CO_2 in solution than deeper waters, and tropical waters hold less than temperate or polar waters.

Carbon dioxide and water react with calcium carbonate in the following way:

$$CO_2 + H_2O + CaCO_3 \Leftrightarrow Ca^{2+} + 2HCO_3^- \qquad (2\text{–}2)$$

The more CO_2 that is dissolved in the water, the more readily the water can dissolve $CaCO_3$. Conversely, any process that removes CO_2 from solution promotes the precipitation of $CaCO_3$. Since calcium ion (Ca^{2+}) and bicarbonate ion (HCO_3^-) are both abundant in seawater, modern tropical ocean-surface waters are most conducive to the precipitation of $CaCO_3$, whereas deeper and colder ocean waters are more apt to dissolve $CaCO_3$.

2.3. Limestones and Earth History

Limestones are one of the major reasons that life can exist on Earth. Since limestones are $CaCO_3$, they provide a mechanism for storage of great quantities of CO_2 in the Earth's crustal rocks. Without limestones, the concentration of CO_2 in the Earth's atmosphere would be about 100 times higher, similar to that of Venus, and the surface of the Earth would be nearly as hot as that of Venus (425°C) (Jastrow and Thompson, 1972; Condie 1989).

Carbon dioxide is referred to as a "greenhouse gas" because it absorbs heat energy. Most of the energy reaching a planet's surface from the Sun is visible light. The planet's surface absorbs that radiation, is warmed by it, and reradiates heat (infrared radiation) back into space. Carbon dioxide, when present in the atmosphere, acts as an insulating blanket, trapping part of the infrared radiation the planet would otherwise lose into space.

Venus and Earth are quite similar planets. A major factor in their histories, which culminated in life on Earth but not on Venus, is distance from the Sun. This determines the intensity of solar radiation falling on the planet's surface. Based on distance from the Sun and without considering atmospheric effects, the average surface temperature of primordial Venus is estimated as 60°C, while the Earth as –30°C. But these planets probably had early atmospheres. Volcanic eruptions released water vapor, hydrogen sulfide, methane, ammonia, carbon dioxide, and other gases from these planets' interiors. Approximately 10% of gaseous volcanic emissions was CO_2. So both planets had insulating atmospheres and likely were somewhat warmer than estimates based only on distance.

Carbon dioxide is removed from the atmosphere during weathering of rocks (Berner et al., 1983). Rainwater, in which carbon dioxide is dissolved, falls on rock (represented here by basalt—$CaSiO_3$), slowly weathering it away to dissolved silica, calcium ions, and bicarbonate ions:

$$3H_2O + 2CO_2 + CaSiO_3 \rightarrow H_4SiO_4 + Ca^{2+} + 2HCO_3^- \qquad (2\text{–}3)$$

In lakes or oceans, dissolved silica precipitates to form opal

$$H_4SiO_4 \Leftrightarrow SiO_2 + 2H_2O \qquad (2\text{–}4)$$

and calcium ions and bicarbonate ions react to form calcium carbonate (equation 2–2 read right to left). Through geologic time, the opal crystallizes to quartz and the calcium carbonate accumulations become limestones and marbles.

The solubility of CO_2 is strongly temperature dependent and so is the weathering reaction (equation 2–3), which further explains why Earth supports life while Venus does not. Because Venus is closer to the Sun, the average surface temperature of Venus has been in excess of 60°C since the formation of the planets in the Solar System. At such high temperatures, there was little dissolution of carbon dioxide in liquid water, so weathering of crustal rocks and formation of limestones was minimal. Carbon dioxide rapidly accumulated in the atmosphere of Venus, resulting in runaway greenhouse effect that precluded the development of life. Because the Earth is further from the Sun, less solar radiation reaches the Earth, so average surface temperatures are lower. Even with the pre-Archean atmosphere, daytime temperatures were probably in the 0–25°C range, which is ideal for CO_2 dissolution in liquid water, for weathering of rocks, and for the formation of limestones. As a result, throughout Earth history, CO_2 accumulated in the crustal rocks of Earth, rather than in the atmosphere. At present, only about 0.03% of the atmosphere is CO_2 and the average temperature of the Earth's surface of 14°C (Axelrod, 1992) readily supports life.

2.4. The Atmosphere and the Evolution of Life

During the first 2 billion years of Earth's history, most precipitation of calcium carbonate likely occurred when concentrations of calcium and carbonate ions supersaturated the water. The evolution of life on Earth profoundly altered this relationship (Fig. 2–1), particularly the activities of photosynthetic microorganisms from 2.5 billion years ago to the present (Lovelock, 1988). During the process of photosynthesis, carbon dioxide is directly removed from the air or water to produce organic matter (abbreviated as CH_2O) and oxygen:

$$H_2O + CO_2 \Leftrightarrow CH_2O + O_2 \qquad (2\text{–}5)$$

If the volume of seawater is limited and the rate of photosynthesis is high, rapid uptake of CO_2 promotes calcium carbonate precipitation. For example, on a warm, shallow, subtidal flat where cyanobacterial (blue-green "algal") mats cover the bottom, $CaCO_3$ crystals may form in the water, or within or on the mats (Pentecost, 1991). The result can be the formation of stromatolites. By this mechanism, tremendous volumes of limestones were deposited in shallow-shelf seas from about 2.5 billion to 600 million years ago (Grotzinger, 1989). And during this time, photosynthesis forever changed the Earth's atmosphere to the oxygen-bearing mixture necessary for the evolution and survival of multicellular life forms.

During the 4.7-billion-year lifetime of the Sun, its luminosity has increased roughly 40% as a part of the natural aging process of a star (Gilliland, 1989). If the process of carbon dioxide removal was purely geochemical, the rate of removal would have declined as solar radiation intensified, and the Earth should have become much warmer. But since the evolution of photosynthesis, life forms influenced the concentrations of carbon dioxide and oxygen in the atmosphere. As solar radiation has intensified, photosynthesis rates have likely increased, since photosynthesis is driven by solar radiation. This may account for the overall decline in carbon dioxide concentrations through geologic history of the Earth, to the very low levels of today.

However, the decline in CO_2 concentrations in the atmosphere has been neither uniform nor continuous. Global volcanic activity, which has not been constant through geologic time, adds CO_2 to the atmosphere. Over Earth history (4.5 billion years; see Fig. 2–1), volcanic rates have generally declined as the Earth's interior has progressively cooled. But over the time scales of large-scale plate tectonic processes (10s–100s of million years), volcanic rates have varied, slowing as large continental masses collide, and speeding up as they rift apart. For example, during the Cretaceous period (the Age of the Dinosaurs), 150 to 65 million years ago, the rates of oceanic rifting and subduction were substantially faster than modern rates. Atmospheric CO_2 concentrations as much as 5–10 times higher than present produced "greenhouse world" conditions in which high

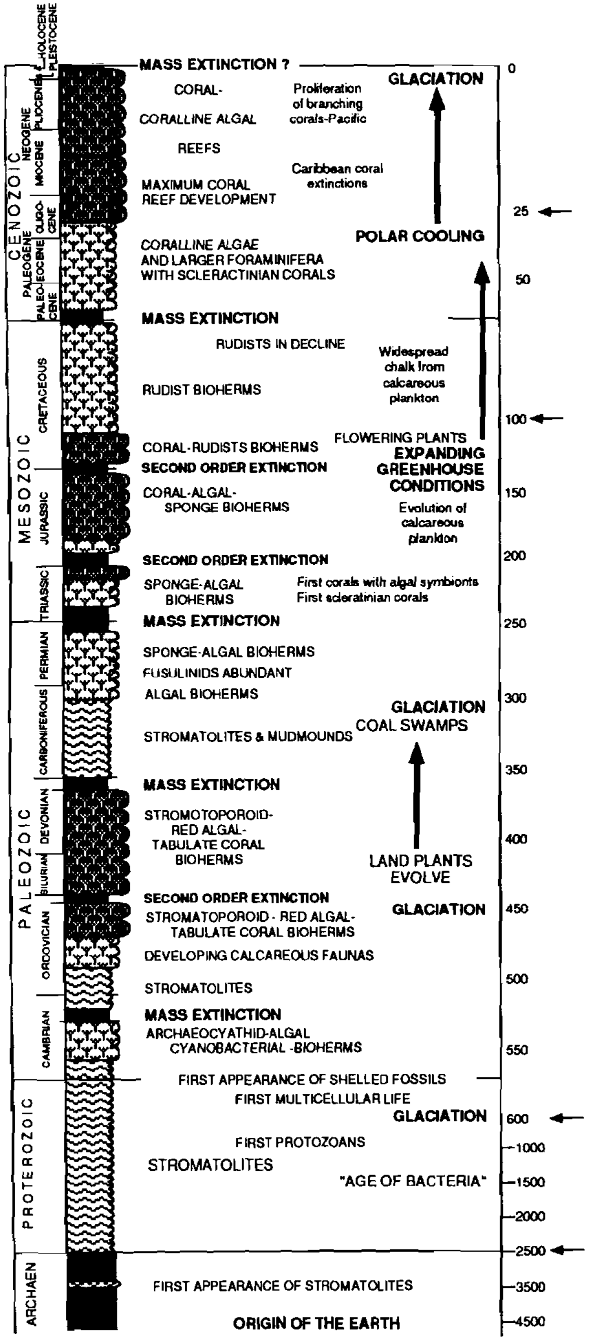


Figure 2–1. The geological time scale illustrating major reef-related events. The arrows along the right side of the figure note scale changes, with the scale greatly expanded over the past 10 'ion years, especially the past 25 million years.

latitudes enjoyed temperate climates and polar regions were ice-free (Worsley et al., 1986). Thus, during intervals such as the Cretaceous, the general long-term decline in atmospheric CO_2 concentrations temporarily reversed.

A second factor that may have influenced rates of CO_2 decline has been the successive evolution of groups of photosynthetic protists and plants with new and more efficient pigments and enzyme systems. Proliferation of these new organisms may have contributed to declines in atmospheric CO_2 concentrations that triggered global cooling and culminated in "icehouse world" conditions characterized by major episodes of high-latitude glaciation. Prior to the late Proterozoic, which began roughly 1 billion years ago (Fig. 2–1), bacteria were the major photosynthesizers. The evolution of the nucleated cell from the symbiosis of three or four different kinds of bacteria provided the evolutionary breakthrough that later made multicellular life possible (Margulis, 1993). The evolution of green and red algae (Schopf and Oehler, 1976), and of primitive phytoplankton known as acritarchs, may have increased the efficiency of photosynthesis and therefore rates of CO_2 extraction. A major glacial event occurred in the late Proterozoic, ending approximately 600 million years ago. Global cooling associated with this early glacial event would have slowed the rates of extraction of atmospheric CO_2 by the biotic community.

The appearance of multicellular life following that glacial event (Cloud and Glaessner, 1982) has been attributed to rising atmospheric oxygen concentrations. Shelled organisms appeared 570 million years ago (Conway Morris, 1993). Rising atmospheric oxygen concentrations probably also supported primitive land photosynthesizers, including lichens and cyanobacteria (Fischer, 1965). The organic acids and primitive soils produced by these early land plants likely increased rates of rock weathering. Major diversifications and proliferations of marine life were occurring by the Ordovician period, which culminated in a major glacial episode 458 million to 428 million years ago (Frakes and Francis, 1988).

The evolution and diversification of land plants more than 350 million years ago, which led to the accumulation of vast quantities of Carboniferous coals worldwide, removed tremendous quantities of CO_2 from the atmosphere and may have contributed to late Carboniferous glaciation. Another factor was the increasing intensity of rock weathering as soils became better developed.

In the Mesozoic, many new taxa evolved with the potential to alter the distribution of CO_2 and HCO_3^- in the atmosphere, oceans, and sediments. The middle Triassic to early Jurassic saw the evolution and diversifications of several new groups of $CaCO_3$ producers that profoundly changed oceanic sedimentation. Coccolithophorids, which represented a new lineage of phytoplankton, and planktonic foraminifera began producing calcite plates and shells in the surface waters of the open ocean, so that today calcareous sediments cover half the area of the ocean floor. On the shallow shelves, scleractinian corals and a variety of larger foraminifera developed symbioses with microalgae, greatly increasing their potential for carbonate production. CO_2 emission by the rapid volcanism of the Cretaceous more than compensated for carbonate production by these new groups of organisms. However, along with the new calcareous organisms, the proliferation of flowering plants on land and the extremely fast-growing diatoms in aquatic environments during the late Cretaceous and early Paleogene may have played a role in the global cooling that has occurred over the past 50 million years, culminating in the Ice Ages of the past few million years (Volk, 1989).

Atmospheric CO_2 concentrations have varied on much shorter time scales. Concentrations were about 200 ppm during glacial advances and about 280 ppm during interglacials (Delmas, 1992). These differences, their causes, and their significance is at the heart of modern studies of global climate change. Vegetation has such a strong influence on atmospheric CO_2 concentrations that differences between winter and summer can be detected in the Northern Hemisphere (Heinmann et al., 1989).

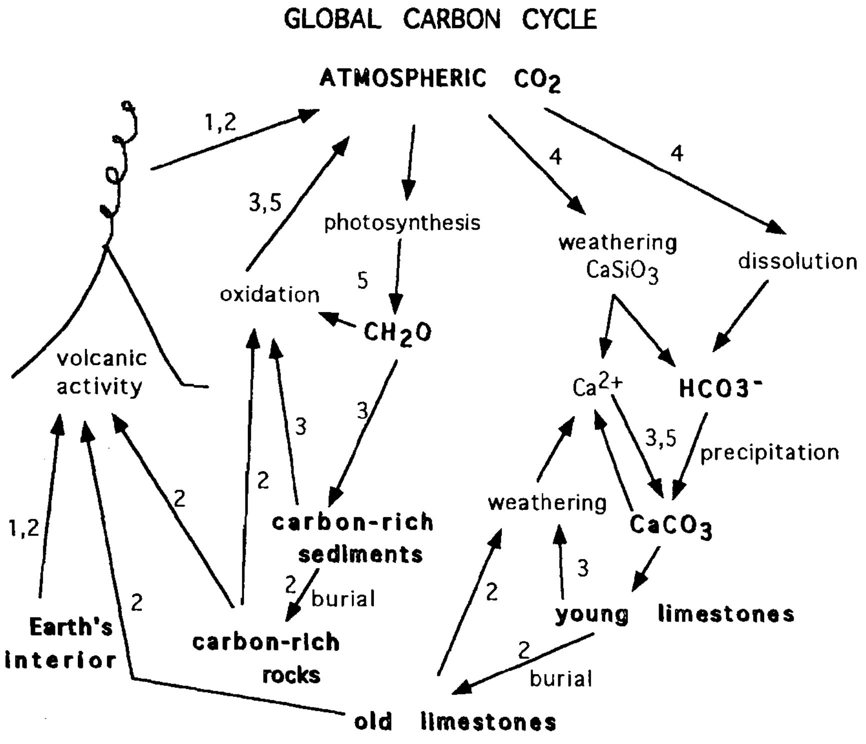
2.5. CO_2 and Time Scales

The weathering of rocks and the accumulation of limestones have different effects on atmospheric CO_2 concentrations, depending on the time scale being considered (Kinsey and Hopley, 1991). On the scale of Earth history, limestones are clearly important reservoirs of CO_2. This process can be summarized by the simplified expression:

$$CO_2 + CaSiO_3 \Rightarrow SiO_2 + CaCO_3 \qquad (2\text{–}6)$$

On time scales relevant to humans, Berger (1982), Opdyke and Walker (1992), and others have argued that production of limestones is a net producer of CO_2, based on the relationship shown in equation 2–2 that for each $CaCO_3$ secreted, one HCO_3^- is converted to CO_2.

The key to understanding this apparent paradox is recognizing that carbon exists in a variety of forms (Fig. 2–2). The ultimate source of carbon is from within the Earth. Volcanic activity delivers carbon to the atmosphere, where it mostly occurs as CO_2, or to the ocean, where it mostly occurs as HCO_3^-. Organic carbon, produced mostly by photosynthesis (equation 2–5), occurs in short-term forms including living organisms and wood, and in water and sediments, and in long-term forms of carbon-rich rocks like coal and oil shales. Carbon stored in $CaCO_3$ can be recycled quickly, such as when aragonitic lime muds from the Bahama Banks are carried by currents into the deep ocean where they dissolve at depths greater than about 3,000 m. $CaCO_3$ in limestones can be recycled during glacial advances when reefs are exposed to the air and eroded; or $CaCO_3$ in limestones can be stored for millions to thousands of millions of years until plate tectonic activity uplifts them from the sea and exposes them to erosion, or until they are melted or metamorphosed by volcanic activity.



1. Rates have slowed through Earth history.
2. Rates controlled by plate tectonics.
3. Rates have changed with sea-level fluctuations.
4. All of these processes influence rates.
5. Biological scale processes.

Figure 2–2. Simplified representation of the global carbon cycle.

Figure 2–2 is a simplified representation of the CO_2 cycle, which is characterized by processes operating on four major time scales:

1. On the scale of Earth history and the evolution of life, CO_2 concentrations have been declining in the atmosphere to compensate for increasing solar output. Carbon has been stored in the Earth's crust as limestones and carbon-rich materials such as coal, oil shale, oil, and gas.
2. On the scale of 10s to 100s of millions of years, CO_2 has varied in response to plate movements and changes in rates of volcanic activity. Limestones and other carbon-rich rocks can be melted or metamor-

phosed by volcanic activity, recycling stored CO_2 back to the atmosphere-ocean pool.

3. On the scale of 10s to 100s of thousands of years, CO_2 in carbon-rich sediments is recycled as shallow-marine sediments are alternately deposited and eroded in response to sea-level rise and fall. During interglacial times when reefs are actively accreting, the global HCO_3^- pool is more rapidly converted to CO_2 and $CaCO_3$, so atmospheric CO_2 concentrations rise. During glacial events, when sea level is low and reef limestones are more actively eroded by atmospheric CO_2 and water, atmospheric CO_2 is decreased and oceanic HCO_3^- is increased.
4. Organisms typically act on biological time scales ranging from hours for bacteria to thousands of years for some long-lived trees.

Humans, however, have recently begun to perturb long-term cycles by extracting fossil fuels, burning them, and releasing huge quantities of CO_2 into the atmosphere. This process shifts carbon from long-term storage in the Earth's crustal rocks to CO_2 in the atmosphere. At the same time, we are cutting and burning forests. This shifts carbon from short-term storage in vegetation to CO_2 in the atmosphere. This process also reduces the rate of CO_2 removal from the atmosphere to short-term storage. By damaging coral reefs, humans have also influenced rates of $CaCO_3$ production. By perturbing both long- and short-term cycles, human activities over the past 100 years have increased CO_2 concentrations in the atmosphere more than reef growth increased CO_2 in the past 15,000 years.

2.6. Atmospheric CO_2 as an Evolutionary Driving Force

A geochemical paradox of declining concentrations of atmospheric CO_2 through time is that $CaCO_3$ has become increasingly easier for organisms to precipitate. The Proterozoic oceans, responding to a more CO_2-rich atmosphere, were more acidic and therefore able to hold in solution relatively high concentrations of Ca^{2+} and HCO_3^-, even in shallow water. $CaCO_3$ precipitation was primarily a "daytime" activity in restricted shallow-shelf areas in response to rapid CO_2 removal for photosynthesis by dense mats of cyanobacteria. At night and possibly seasonally during the day, seawater became undersaturated when photosynthetic rates slowed or stopped.

Then, sometime between 600 and 570 million years ago, a critical point was reached in the atmospheric-oceanic chemical system; shells evolved in several different groups of organisms. This indicates that atmospheric CO_2 concentrations must have dropped sufficiently so that low-latitude, shallow-water systems were consistently saturated with $CaCO_3$. Possibly the protective or supportive advantages of a mineralized shell finally exceeded the energetic costs of shell precipitation and maintenance. Biomineralized organisms have since flourished in the seas, secreting predominantly calcium carbonate shells or skeletons.

The succession of carbonate minerals through the geologic record also indicates a geochemical influence (Sandberg, 1983; MacKenzie and Morse, 1992). Though some of the earliest animals secreted calcium phosphate, calcite rapidly became the dominant shell material. Aragonite, which is stronger but less stable than calcite, also appeared as shell material in the early Paleozoic. But aragonitic algae did not produce significant bioherms until the Carboniferous. Aragonitic scleractinian corals did not evolve and construct reefs until the Triassic, only about 230 million years ago. This trend reversed as aragonite producers lost ground to calcite producers during the warm Cretaceous period, when atmospheric CO_2 concentrations rose in response to high rates of volcanic activity. Aragonite-producing corals did not fully regain a dominant position until 40 million years ago, with the global cooling that led to present glacial conditions.

A second implication of the reduction of CO_2 in the atmosphere, and therefore the partial pressure of CO_2 in surface waters of the ocean, is the possibility that shortage of CO_2 can limit photosynthesis (Riebesell et al., 1993). In shallow, warm, brightly illuminated waters, HCO_3^- is abundant and dissolved CO_2 is scarce. By using energy from photosynthesis to actively uptake Ca^{2+} ions from seawater, these organisms can use the calcification process to convert bicarbonate ions (HCO_3^-) to CO_2 needed for photosynthesis (McConnaughey, 1989). Calcareous algae, which may have been the first organisms to utilize calcification this way, first appeared in the Cambrian. The Mesozoic diversifications of more modern calcifying algae, including the coccolithophorids in the plankton, and melobesian green and coralline red algae in the benthos, along with the proliferation of algal symbiosis in foraminifera, corals, and some bivalves, may be further evidence of biotic response to declining CO_2 concentrations in the atmosphere.

There appear to be at least three major mechanisms of calcification in global oceans (Fig. 2–3). The first mechanism, geochemical precipitation of $CaCO_3$ in response to CO_2 uptake by photosynthesis, was particularly effective under relatively high atmospheric pressures of CO_2. The second mechanism, biomineralization by protozoan and animal cells, probably appeared when CO_2 concentrations declined sufficiently that the expenditure of energy for shell construction and maintenance became energetically feasible. The third mechanism, use of calcification to provide CO_2 for photosynthesis, was also likely related to declining atmospheric CO_2 concentrations, when reduced atmospheric concentrations began to limit aquatic photosynthesis in warm, shallow seas.

This third mechanism apparently arose independently in at least three groups of algae (reds, greens, and coccolithophorids) and several additional times when algal symbioses developed in calcified animals and protists. This mechanism has profound and almost paradoxical implications for atmospheric CO_2 concentrations. The very process that makes CO_2 instantaneously available for photosynthesis is responsible for the long-term removal and burial of CO_2 as $CaCO_3$.

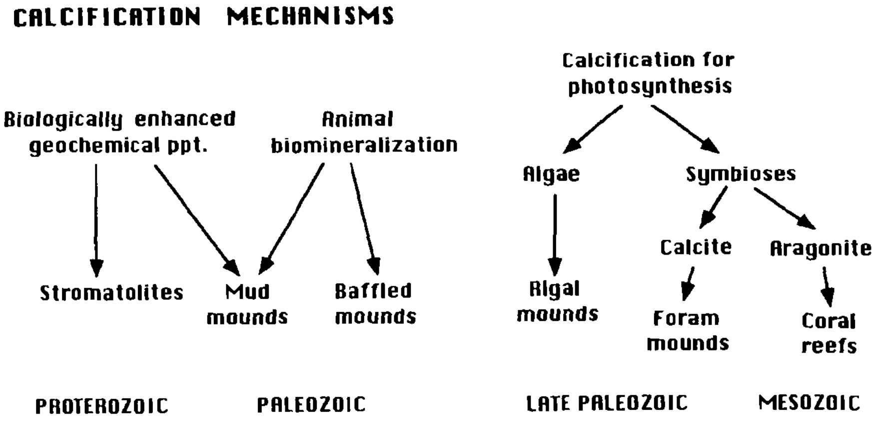


Figure 2–3. Calcification mechanisms and when they became important in the construction of biogenic reefs.

One mechanism that reduces the rate of CO_2 burial by calcification is global cooling. If organisms draw too much CO_2 out of the atmosphere, onset of glaciation lowers sea levels and reduces the habitats of warm-water calcifying organisms, as well as that of terrestrial plants. Lowered sea levels also prevent burial of some limestones, instead exposing them to erosion and returning the CO_2 to the ocean-atmosphere system. Interestingly, as atmospheric CO_2 concentrations have declined, aragonite is easier to precipitate in warm waters, and is more rapidly recycled by freshwater weathering.

2.7. What It Takes to Accumulate $CaCO_3$

Although calcium carbonate sediments have been precipitating and limestones have been forming for at least 3.5 billion years of Earth history, limestones in the rock record represent deposition during relatively small proportions of geologic time. This is because preservation of $CaCO_3$ is as important as production for accumulation and persistence in the rock record. Several factors influence both production and preservation potential. One very important condition is the persistence or repeated submergence of substantial areas of shallow shelf at mid to low latitudes over sufficient time so that limestones can accumulate. A second condition is relatively low input of terrigenous sediments and inorganic nutrients, especially nitrogen and phosphorus. A third condition is the presence of biota that can precipitate or enhance the precipitation of $CaCO_3$.

The persistence or repeated submergence of substantial areas of shallow shelf at mid to low latitudes is controlled by tectonics and climate, which together control sea level. Rates of seafloor spreading influence the average depth of the ocean (Fig. 2–4), pushing water higher onto the continental shelves when spreading rates are high (Kennett, 1982). The relative proportions of continents that are colliding or overlying rifting centers also influence global and local sea level. For example, all of the major continents came together in the late Paleozoic to form the supercontinent of Pangaea (Fig. 2–5). This can be compared to India colliding with Asia to form the Himalayas, only on a much larger scale. As the continents pushed together, sea level relative to the continents was low, so there were few shallow-shelf areas, and most that occurred were being buried in sediments being eroded from the highlands. Through the latest Paleozoic and into the early Mesozoic, Pangaea remained as one supercontinent. Heat from the Earth's interior was building up underneath Pangaea, pushing it up and beginning to break it apart. Sea level remained low and shallow-shelf area was limited. Pangaea at this stage may have been analogous to East Africa today, where eroding highlands plunge into deep rift valleys. As the continents rifted apart and began to move away from each other during the Cretaceous (Fig. 2–5), they slowly subsided and became generally similar to modern Australia. Most of the mountainous areas were island arcs analogous to the Marianas Islands or Japan.

Seafloor spreading rates and climate interact through a variety of feedback mechanisms to influence sea level (Worsley et al., 1986). As the continents

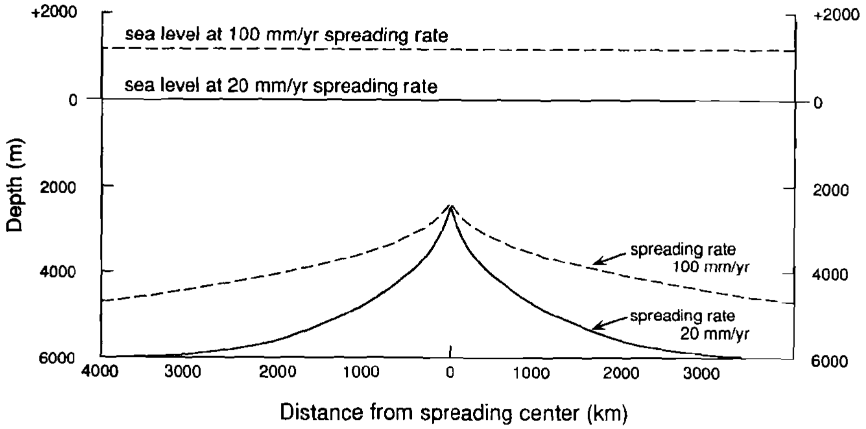
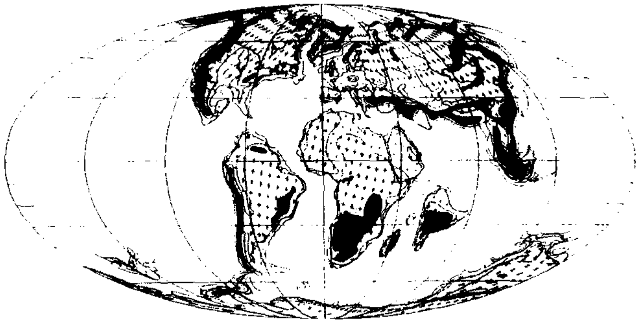
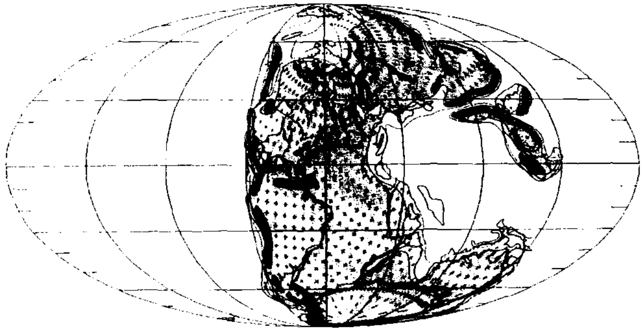


Figure 2–4. The effect of seafloor spreading rate on sea level. Oceanic crust that is newly formed at the mid-ocean ridge crest is hotter and less dense than older crust; oceanic crust cools and subsides with age (Kennett, 1982). The solid profile illustrates oceanic floor formed at 20 mm yr^{-1}, which is a common rate for the present mid-Atlantic ridge. If the spreading rate increased to 100 mm yr^{-1}, within 40 million years the seafloor profile would change to that shown by the dashed line. If the surface area of the ocean basin remained constant, sea level would rise more than 650 m, to the dashed sea-level line. In reality, when sea level rose in Earth history, lower-lying areas of the continents were flooded, spreading ocean waters over much larger areas. Thus, sea-level rises were probably never as much as 650 m; sea level during the Cretaceous was about 300 m higher than today.



LATE CRETACEOUS



TRIASSIC

Figure 2–5. Plate reconstructions for the Triassic (lower), illustrating the supercontinent Pangaea that formed during the late Paleozoic; and for the Late Cretaceous (upper), after the breakup of Pangaea (from Ziegler et al., 1982). Oceans are shown in white and land areas are shaded; highlands are densely shaded.

ground together to form Pangaea, seafloor spreading and overall volcanic rates slowed, further lowering sea level. Slower volcanic rates resulted in slower emissions of volcanic gases, including CO_2. As a result, Earth's climate was cooler. Conversely, as continents moved apart, seafloor spreading rates increased, volcanic rates increased, and CO_2 emissions increased, triggering global warming in the Jurassic and Cretaceous. Relative sea level influences global climate because it alters the reflectivity (albedo) of the Earth; land is more reflective than water and ice is most reflective. The higher the sea level, the more solar energy the Earth can capture and thus the warmer the climate. Warm climates promote even higher sea level, because all polar ice is melted.

The differential heating of the equator relative to the poles drives atmospheric and oceanic circulation. Plate tectonics controls the positions of landmasses relative to the oceans and so further influences ocean circulation and climate by

providing passageways and barriers. For example, the opening of the Drake Passage between Antarctica and South America, which occurred from 40 to 20 million years ago (Fig. 2–6), allowed the development of the circumpolar current in the southern oceans (Kennett, 1982). This led to the climatic isolation of Antarctica and was a major driving force for polar cooling. Closure of the Isthmus of Panama over the past few million years stopped flow of the Caribbean current into the Pacific, diverting it northward to accelerate the Gulf Stream. Delivery of warmer water to high northern latitudes increased snowfall, which may have triggered glaciation (Kennett, 1982).

Global climate is strongly influenced by CO_2 concentrations in the atmosphere, and therein lies another paradox of limestones and coral reefs. Times of global warming, such as the Cretaceous and early Paleogene (Fig. 2–1), are times of widespread limestone deposition, but not of coral-reef development. Geochemical evidence for ancient temperatures indicate that the Earth was so warm during these times that seawaters in the polar regions were 12–16°C; they are less than 1°C today. What was happening in the tropics is more controversial. Kauffman and Johnson (1988), Adams et al. (1990), and many others contend that distributions of fossil organisms indicate warm tropics, in some cases even warmer than today. However, some geochemical measurements have indicated that tropical seas may have been cooler, on the order of 18°C instead of 25–30°C common today (Shackleton, 1984). The explanation is that warming the polar regions required more effective heat transport, and therefore cooling of the tropics.

2.8. History of Biogenic Reefs Through Time

Although cyanobacteria have been available to build stromatolites for nearly 3.5 billion years, and there have been shell-forming animals for 570 million years (Fig. 2–1), biogenic reefs are sporadically scattered through the rock record (James, 1983; Copper, 1988). Factors that have controlled the formation of biogenic reefs through time include climate, ocean circulation, availability of habitat, and existence of reef-forming biotas. The history of reef development and reef-building biotas has not been continuous. Instead, it has been characterized by long periods of persistence of simple reef mound–producing communities, followed by longer episodes of development of complex baffler and reef-building communities, and termination of complex community development, followed by major extinction events (Stanley, 1992; Copper, 1994).

The fossil record is characterized by four kinds of reeflike structures: stromatolites, simple reef mounds, biotically complex reef mounds constructed by baffler/binder communities, and true framework reefs. These categories are more convenient than mutually exclusive. Within reef structures, there may be a colonizing stage by a binder community, a diversification stage by a baffling and binding community, and a climax stage of framework builders, binders, dwellers, and destroyers (Fagerstrom, 1987).

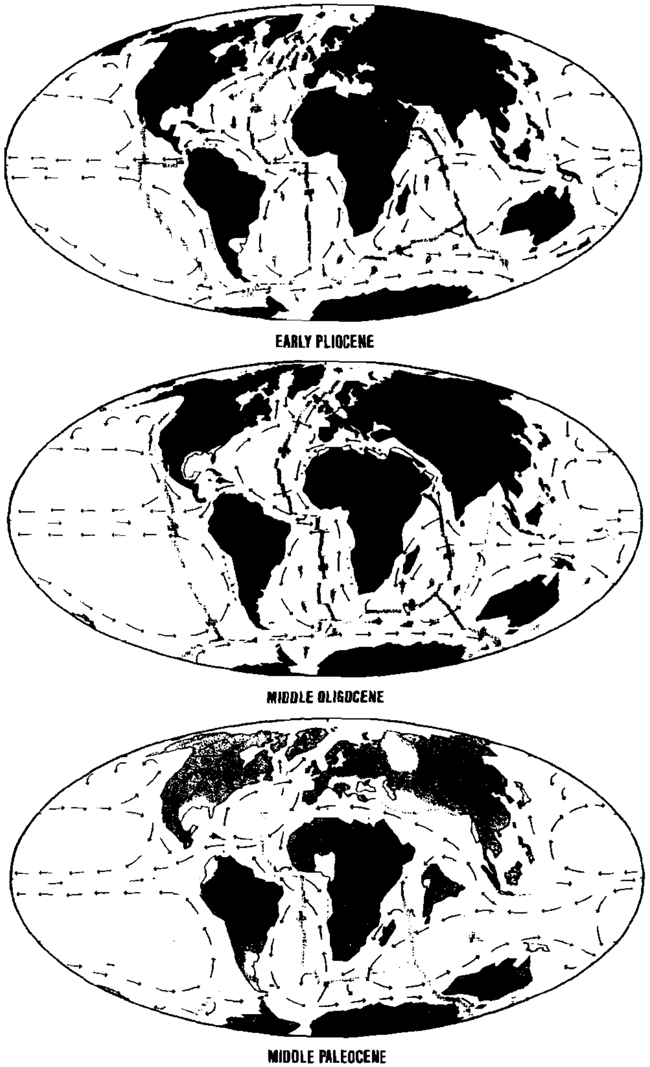


Figure 2–6. Plate reconstructions and inferred circulation patterns of oceanic surface waters (arrows) from Haq and Van Eysinga (1987): middle Paleocene (60 million years ago)—note circumtropical circulation and the lack of south circumpolar circulation; middle Oligocene (30 million years ago)—note that circumtropical circulation diminished as India and the Middle East were approaching Asia, while south circumpolar circulation was complete; and early Pliocene (5 million years ago)—note that the Isthmus of Panama is substantially restricted but not yet fully closed. Oceans are shown in white and land areas are shaded. Oceanic ridge crests are indicated by lighter shading.

From 3.5 to 6 billion years ago, whether stromatolitic reefs developed or not was likely controlled primarily by suitability of the physical and chemical environment. Limestones accumulated where seawater was warm enough and shallow enough for photosynthesis by cyanobacteria to promote $CaCO_3$ precipitation over a substantial area and over sufficient time to be preserved (Grotzinger, 1989). Following the evolution of multicellular life such as worms and trilobites that bulldozed through the algal mats eating and disrupting them, the chances for stromatolite preservation declined (Conway Morris, 1993). However, stromatolites continued to be an important type of bioherm through the early Paleozoic, and some still occur today (Dill et al., 1986).

2.8.1. *Paleozoic Era—Time of Ancient Animal Life*

The first animal communities to act as significant bafflers appeared in the Cambrian period, nearly 560 million years ago. The archaeocyathids or "ancient cups" are thought to have been calcified sponges (Wood et al., 1992); their erect skeletons trapped calcareous muds, which may have been chemically precipitated in response to photosynthesis in cyanobacterial mats and in the plankton. Calcified cyanobacterial/algal mats and encrusters formed a major component of the archaeocyathid reef mounds, which persisted almost 30 million years. Trilobites and sponges were inhabitants of these simple mounds. "Reef tracts" produced by these communities were extensive about 530 million years ago in Siberia, southern Australia, and Antarctica, which lay in low latitudes at that time (Copper, 1994). By the middle Cambrian these primitive reef communities suffered extinctions, so cyanobacterial mats and encrusters once again formed what reef mounds were preserved.

The early Ordovician began the first major diversification of calcified algae and animals capable of producing, trapping, and binding large volumes of calcareous sediments. Sponges and the earliest corals played the major baffler roles, cyanobacteria persisted as binders, while trilobites and primitive snails grazed the algae or ate the algal/bacterial-rich muds. By the middle Ordovician, a variety of calcified animals had evolved. These organisms were more prolific sediment producers, more effective sediment bafflers, and some were even framework constructors. Important contributors included bryozoa; stromatoporoids, which were a kind of sponge; and a calcareous red alga called *Solenopora*. These early reef mounds provided a multitude of niches for trilobites, brachiopods, snails, cephalopods (ancestors of the chambered *Nautilus*), other animals that fossilized, and many soft-bodied organisms that left no fossil record.

By the late Ordovician, tabulate and rugose (horn) corals were becoming important components of the reef community. A typical succession consisted of a colonizer community of stalked crinoids and bryozoa that trapped muds and began to accumulate a structure. Soon this habitat was invaded by sponges, solitary horn corals, small tabulate corals, and massive stromatoporoids, which together constructed larger skeletal structures and trapped calcareous muds and sands. Algae, smaller corals, bryozoa, brachiopods, clams, snails, trilobites, and other arthropods found shelter or food within the reef. Encrusting stromatoporoids bound the skeletal elements together, and typically overgrew and eventually dominated the whole structure. In this climax phase, which may have been very wave resistant like a modern coralline algal ridge, the diversity of species was low (e.g., James, 1983; Copper, 1988).

Interesting size comparisons can be made between the middle Paleozoic (Ordovician to Devonian) bioherms and modern coral reefs. Individual structures were often similar in size to small patch reefs, connected by expanses of calcareous sands or muds, so the total accumulation of limestones was comparable to a modern reef tract (Fagerstrom, 1987). However, there is no strong evidence for algal symbiosis in the calcifying animals, and calcareous algae are of limited importance. Thus, calcification mechanisms responsible for precipitation of most of the early to middle Paleozoic limestones were probably biologically enhanced geochemical precipitation and biomineralization by animals. Extensive Devonian reef complexes along the northern margin of the Canning Basin, Western Australia, as well as others found in Alberta, Canada; Belgium; and Germany, are comparable in size to, or even larger than, modern western Atlantic reef systems like the Florida Keys reef tract (Stanley, 1992).

In the late Devonian, an extinction event occurred that eliminated most of the reef-building species, setting back reef-building communities to simple stromatolites. Latest Devonian limestones in the Canning Basin are cyanobacterial/algal in origin, with a few sponges providing the little diversity. Early Carboniferous buildups scattered around the world are mud mounds, containing mostly calcareous muds of unknown origin, possibly trapped into buildups by crinoids and bryozoa, the only major skeletal components of the mounds. Rugose corals, chaetitids (an unusual group of calcified sponges), and brachiopods were among the first taxa to reappear to colonize the crinoid-bryozoan mud mounds as carbonate-producing communities evolutionarily began to recover.

Late Carboniferous biotas contain many unusual and taxonomically problematic groups that mostly represent binder and baffler communities. A major change seen in the Carboniferous is the prevalence of calcareous algal species that produced aragonite. The evolution and diversification of the first large, structurally complex foraminifera, the fusulinids, represents the earliest strong evidence for algal symbiosis in an important calcareous sediment producer. These two events may represent the first major proliferation of organisms calcifying to enhance photosynthesis. On a global scale, the continents were coming together to form Pangaea. Glaciation was occurring, indicating reduced atmospheric CO_2 concentrations, which was conducive to aragonite precipitation (Sandberg, 1983) and calcification to enhance photosynthesis.

One of the best known Paleozoic reef complexes in the world is that in western Texas and southeastern New Mexico (e.g., Wilson, 1975), the Permian-age bioherms of the Guadalupe Mountains and Carlsbad Caverns National Parks. These limestones have been intensively studied by petroleum geologists because subsurface limestones in this region have produced tremendous quantities of oil and natural gas. These are well-developed reef mounds in which a variety of sponges and sometimes algae, bryozoa, crinoids, and brachiopods acted as bafflers, trapping muds and coarser sediments produced by the community. Algae and sponges served to bind the trapped sediments. Diverse communities of foraminifera, snails, clams, small corals, brachiopods, cephalopods, and arthropods thrived in these buildups. In the Glass Mountains of western Texas, an unusual group of large, spiny brachiopods clustered to form a kind of reef framework, further developing the sponge-algal baffled structure. Late Permian (Guadalupian) communities are among the first to show a major contribution by encrusting red algae.

2.8.2. *Mesozoic Era—Time of Intermediate Animal Life*

The latest Permian and earliest Triassic witnessed the most extensive extinction event in Earth history and a prolonged episode in which limestones are missing from the rock record. The prolonged absence of limestones indicates widespread unfavorable paleoenvironmental conditions, possibly including geochemical conditions that suppressed carbonate precipitation or inhibited its preservation. When carbonate buildups reappeared in the middle Triassic, they were baffled and bound sediments similar to those of the late Permian, except simpler and with fewer species. Sponge-algal communities gradually resumed production of reef mounds, and included among their subsidiary fauna the first scleractinian (modern stony) corals, with their aragonite skeletons.

By the late Triassic, the scleractinian corals had diversified, and new forms restricted to shallow, brightly illuminated waters appeared that are believed to have hosted zooxanthellae (Stanley, 1981). Corals, sponges, and stromatoporoids produced framework; other sponges and stromatoporoids, as well as bryozoa, serpulid worms, and sponges served as bafflers and binders. Associated fossilized taxa were a diverse group of ammonites, brachiopods, bivalves, snails, echinoderms, foraminifera, and worms.

Following widespread extinctions in the latest Triassic, Jurassic reef-building communities reestablished to a diversity of types comparable to that of modern oceans. Besides coral-stromatoporoid reefs, there were sponge-dominated, sponge-algal, sponge-bivalve, and stromatolitic reef mounds, as well as deep-water coral-sponge mounds. In the late Jurassic, two related trends began that continued and fully developed in the Cretaceous period. Despite a continuing increase in the variety of corals, there was limited coral-reef construction, while large bivalve species proliferated as carbonate producers and sediment trappers. As a result, corals became subsidiary to the bivalves in the Cretaceous.

The major group of bivalves in Cretaceous buildups are the rudistids. Kauffman and Johnson (1988) interpret the rudists as having had algal symbionts to enhance calcification, and suggest that they displaced corals as reef builders during the Cretaceous. European reef researchers contend that there is little evidence for assuming that rudists had algal symbionts, and the prevalence of muddy sediments in most rudist buildups indicates that water transparency may have been poor. For example, Skelton et al. (1992) interpret rudists as having been superbafflers, trapping huge quantities of muds, and actually growing upward supported in muds. Characteristically, thickets and buildups have only one or a few rudist species and few associated organisms. Banktop habitats occupied by many rudists may have been similar to those of modern seagrass beds; the rudist thickets trapped sediments carried in by the currents as well as sediments produced in situ by the breakdown and bioerosion of the rudists themselves. Because of the exceptional high-latitude warming that occurred in the Cretaceous, Kauffman and Johnson (1988) suggested that low-latitude banktop habitats were consistently warm and probably somewhat hypersaline. The more biologically complex bivalves may have been better able to survive these extremes than corals, whose symbiotic relationship is particularly sensitive to temperatures above 30°C (Glynn and D'Croz, 1990).

Furthermore, geochemical factors may have favored rudists over corals. The rudists secreted an outer shell of calcite, with an inner layer and muscle insertion sites of aragonite (Skelton, 1976). Proportions of aragonite to calcite varied in different lineages of rudists. Some secreted shells were 60% aragonite; many were less than 30% (Kauffman and Johnson, 1988). Whatever the proportions, the predominance of rudists over wholly aragonitic corals represents a decline in aragonite production. This may reflect the higher concentrations of CO_2 in the Cretaceous atmosphere that made aragonite more soluble and therefore less energetically advantageous to produce.

2.8.3. *Cretaceous Boundary Extinctions*

A major biotic crisis occurred at the end of the Cretaceous Period. This extinction event is best known for the demise of the dinosaurs. Rudists also became extinct, as did nearly all shallow-water, tropical, carbonate-producing protists and animals. Coccolithophorids and planktonic foraminifera were so abundant in shallow-water plankton during the Cretaceous, and produced such tremendous accumulations of chalks throughout the world, that the Cretaceous actually means "time of chalk terrains." Only a few species of each survived the extinction event.

Fortunately for the scleractinian corals, during the Cretaceous many had retreated to deeper shelf-slope environments, perhaps to escape warm, saline waters or direct competition with rudists (Kauffman and Johnson, 1988). As a result, a few species survived the extinction.

The terminal Cretaceous event was similar to those of the early Cambrian, late Ordovician, late Devonian, and late Permian in that reefs generally vanished a million years or more before the final extinction events (Copper, 1994). Thus, periods of environmental perturbation or climatic deterioration that caused collapse of reef ecosystems must have preceded these major extinction events that geologists use to define significant boundaries in geologic time.

The two major hypotheses for this mass extinction event are a bolide (meteor or comet) impact (Alvarez et al., 1980) or an extensive volcanic episode (Officer and Drake, 1985). Because the bolide impact would have been an instantaneous event, while extensive volcanism would have lasted from 100,000 to a million years or more, scientists with evidence for a more gradual event favor volcanism. While this controversy has been raging in geology since the mid-1980s, strong evidence now indicates a massive impact site on the Yucatán Peninsula in Mexico (Alvarez et al., 1992). However, one can argue that a bolide impact, which occurred during a period of climatic deterioration resulting from volcanism, might have had compounding effects that pushed already stressed ecosystems into collapse.

As for shallow-water, photosynthetic, carbonate-producing, reef organisms, either event would have been equally devastating for some of the same reasons. Either event would have profoundly influenced ocean chemistry in ways detrimental to $CaCO_3$ production. The energy of a meteor passing through the atmosphere would have oxidized nitrogen in the atmosphere, resulting in global acid rain that would have acidified shallow oceanic waters, dissolving $CaCO_3$. Volcanism emits large quantities of hydrogen sulfide (H_2S), which would have oxidized to sulfur dioxide (SO_2) and hydrated to sulfuric acid, resulting in global acid rain. A meteor would have damaged the Earth's protective ozone layer; volcanic emissions are also corrosive to stratospheric ozone. Furthermore, the earthquake caused by a 10-km-diameter bolide hitting the Earth could have eliminated all nutrient-depleted shallow-water environments worldwide, just by stirring the oceans. Deeper oceanic waters, where there is insufficient light for photosynthesis, are substantially richer in inorganic nutrients (dissolved nitrogenous and phosphatic compounds needed by plants to photosynthesize) than photic surface waters. These nutrient-rich waters represent approximately 98% of the total ocean volume. Such a tremendous shock would have generated tsunamis and internal waves, rapidly mixing deeper waters into the shallow waters and stimulating red tidelike blooms of a few, fast-growing species of phytoplankton (disaster species, see Fischer and Arthur, 1977).

Whatever occurred, among the lessons to be learned from the latest Cretaceous and other major extinction events are that the most prolific carbonate-producing organisms are particularly sensitive to environmental perturbations because they thrive within relatively narrow environmental limits. Waters in which they proliferate are warm, but not too warm; clear and well illuminated but with not too much biologically damaging ultraviolet radiation; nutrient depleted; and highly supersaturated with respect to Ca^{2+} and HCO_3^-. Most reef-building organisms live at low latitudes on shelves and banks in the shallowest waters 100 m (330 ft), and thrive at depths less than 20 m (66 ft), in an ocean that averages 3800 m (12,500 ft) in depth. Suitable waters make up less than 1% of the ocean volume under optimum conditions; suitable benthic habitat far less than that. Thus, regional or global events that eliminate habitat for reef-building and reef-dwelling plants and animals can eliminate huge numbers of species and are recorded in the rock record as mass extinction events. Because reef species are often highly specialized to their environment, many specializations are lost in these events, while less specialized, more opportunistic species typically survive.

2.8.4. *Cenozoic—Time of Recent Animal Life*

Earliest Paleocene shallow-water limestones are dominated by bryozoans, coralline algae, and miliolid foraminifera (Hallock et al., 1991; Copper, 1994). The latter group live in warm, shallow-water environments, especially thriving on fleshy algae and seagrass.

Despite the mass extinction event, the high atmospheric CO_2 levels and greenhouse climate, which had developed during the Cretaceous, continued for another 20 million years. Recovery of diverse coral assemblages occurred much faster than reef-building potential. All the major circumtropical frame-building genera of scleractinian corals had evolved by the latest Eocene (Frost, 1977). Thus, the Eocene, like the Cretaceous, was a time of diverse coral assemblages and widespread occurrences of "reef-associated" biotas, but limited coral-reef production. Frost suggests that the capacity to construct massive wave-resistant reef structures developed long before such structures were widely produced.

Consistent with higher atmospheric CO_2 concentrations, prolific calcification by calcite-secreting larger foraminifera (e.g., Plaziat and Perrin, 1992) and coralline red algae appears to have recovered faster than comparable aragonite production by corals and calcareous green algae. The best known larger foraminiferal limestones are the Eocene nummulitic limestones of Egypt, from which the Pyramids were built. Larger foraminifera-rich, shallow-water limestones are widespread in mid to low latitudes. Fossils of larger foraminifera of this age can be found in Oregon, southern England, and other localities as high as 51°N latitude (Adams et al., 1990). Their complex shells, by analogy with modern larger foraminifera, are believed to have been highly adapted to house algal symbionts. Shallow-water limestones dominated by coralline algal nodules were also common (Bryan, 1991).

High-latitude cooling began in the middle Eocene, culminating with the Eocene–Oligocene boundary events, which appears to have been one of the coolest times of the past 200 million years (Shackleton, 1984). This boundary is characterized by extinctions of larger and planktic foraminifera (Hallock et al., 1991) and an interval of shallow-water coralline algae and miliolid limestones (Adams et al., 1986).

Following this setback, coral communities flourished circumtropically in the middle and late Oligocene. The sudden expansion in reef-building capacity may have resulted from falling atmospheric CO_2 concentrations and rising tropical sea-surface temperatures that accompanied high-latitude cooling (Shackleton, 1984). In the Caribbean, coral reefs reached their acme of development in the late Oligocene (Frost, 1977). By the early Miocene, reefs and reef-associated biotas worldwide extended their distributions more than 10° north and south into higher latitudes (Adams et al., 1990).

At least one factor accounting for the widespread distribution of tropical biotas in the Eocene and Oligocene was circumtropical oceanic circulation (Fig. 2–6). While western Pacific reef biotas have consistently been more diverse, most late Eocene and Oligocene coral in the Caribbean region were cosmopolitan taxa. With the breakup of circumtropical circulation, Atlantic biotas became increasingly isolated. Atlantic reef-associated biotas have lost so many taxa that many groups now have only a fraction of the species found in the Pacific. Roughly half of the coral genera were lost from Caribbean faunas at the end of the Oligocene, and many more became extinct during the Miocene (Frost, 1977; Edinger and Risk, 1994). There were also extinctions of Indo-Pacific corals, but far fewer. Larger foraminifera suffered similar losses in the Caribbean.

Progressive blockage of circumtropical circulation (Fig. 2–6) may account for some of these extinctions (Edinger and Risk, 1994). The trade-wind-driven, east-west–flowing circumtropical current passed through two oceanic gateways (Berggren, 1982): the Eastern Tethys through what is now the Middle East and the Central American seaway. The Eastern Tethys closed around the Oligocene-Miocene boundary with the development of the Qatar arch (Berggren, 1982). Although the central American landmass was developing and reducing exchange of Caribbean and Pacific waters, the isthmus of Panama did not close until the middle Pliocene (Keigwin, 1982a).

Because the Atlantic has higher evaporation rates compared with rainfall rates than the Pacific, sea level in the Pacific is actually slightly higher than the Atlantic. As a consequence, when the Central America seaway was open, water had to flow from the eastern Pacific into the Caribbean (Luyendyk et al., 1972). However, the easterly trade winds forced surface waters to flow westward from the Caribbean to the eastern Pacific. As long as the Central American passageway was wide and deep, two-way flow could be accommodated by westward surface flow and eastward subsurface flow, probably at depths in excess of 50–100 m or more (Maier-Reimer et al., 1990). However, as the passageway constricted, flow was constricted and surface flow probably reversed during calm weather. Nutrient-laden eastern tropical Pacific waters were more frequently and consistently introduced into Caribbean surface waters.

Edinger and Risk (1994) observed that shelf-edge and slope-dwelling coral genera were nearly eliminated in the Atlantic in the early Miocene. The corals that survived were mostly banktop species capable of tolerating higher nutrients and higher sedimentation rates that would have accompanied higher bioerosion rates (e.g., Hallock, 1988a). Larger foraminifera show the same trends. Slope-dwelling taxa were nearly eliminated, while shallower-dwelling taxa of banktops and restricted environments thrived and are actually more diverse in the Caribbean than in the Indo-Pacific today (Hallock and Peebles, 1993). Other banktop biota, including octocorals and calcareous algae, became more important components of Caribbean biotas than on comparable Pacific reefs.

Since the middle Miocene, there has been progressive high-latitude cooling, compression of tropical habitats, and increasing temperature gradients between high and low latitudes (Shackleton, 1984). Northern Hemisphere climatic deterioration began approximately 2.7 million years ago and culminated in the Pleistocene Ice Ages during the past million years (Kennett, 1982). The overall cooling and fluctuating climate has strongly influenced tropical reef-associated biotas in a variety of ways. Some taxa have become extinct. Others, like the fast-growing *Acropora* and *Montipora,* have diversified and now account for 25% of the Indo-Pacific coral species (Veron and Kelley, 1988). Regional isolation of populations in sufficiently different environmental conditions can promote speciation (Mayr, 1971). Reconnection of regions then can mix similar but reproductively distinct species. Successive isolation and mixing, which accompanies fluctuations in sea level, has long been recognized as a potential mechanism driving evolutionary diversifications (Hallam, 1985).

2.9. Modern Reefs

Another paradox of limestones and climate is that the Neogene represents a time of active reef building and coral evolution, despite high-latitude climatic deterioration that produced as many as 21 glacial advances and retreats (Delmas, 1992). Sea-level fluctuations of up to 140 m (450 ft), caused by repeated accumulation and melting of Northern Hemisphere continental glaciers, accompanied cyclic reduction and expansion in the areas of warm, tropical seas. The solution to this paradox may be that tropical climatic, geochemical, and topographic conditions during interglacials are close to optimum for reef building. Atmospheric CO_2 concentrations are relatively low (though not as low as during glacial advances) and subtropical/tropical sea-surface temperatures are optimal. Both factors promote aragonite calcification by corals and calcareous green algae, which in turn enhances their rates of photosynthesis and biological productivity.

Periods of rising sea level are also particularly favorable for reef building because there is space for accumulation of substantial thicknesses of reef limestone, which have the best chance for preservation in the rock record. Except for active tectonic areas, most shallow shelves are slowly subsiding at rates of a few centimeters per 1,000 years (Schlager, 1981). The most actively accreting portion of a reef system can grow upward at rates of at least 4 m/1000 years, and under exceptional conditions perhaps as much as 20 m/1,000 years. But they can only grow at those fast rates when growing in water depths of less than 20 m, where there is plenty of sunlight for photosynthesis. The only way they can grow upward at high rates for more than about 5,000 years, and produce more than 20–30 m thicknesses of limestone, is if the shelf subsides or sea level rises. Thus, during interglacial sea-level rise episodes, the margins of continental shelves, limestone banks, and volcanic islands provided ideal locations for thick sequences of reef-associated limestones to accumulate.

Fluctuating sea level strongly influences the morphologies of reefs. If the rate of sea-level rise at any time is too rapid, upward growth of coral reefs simply cannot keep pace, and one of three things happens (Neumann and Macintyre, 1985). That is, during the primary glacial melting event 10,000–12,000 years ago, sea level rose at least 20 m. Very few reefs could keep pace with that rise, so most backstepped (Fig. 2–7), if there was a higher substratum to which to backstep. Others did not fully keep pace during rapid melting events, but caught up when rates of sea-level rise slowed, while some simply failed to catch up and became submerged banks.

On most bank- or shelf-margin reefs, the most rapidly accreting part of the reef system is the zone of living coral that faces toward the prevailing wind and current. Sands and muds in the backreef and lagoon may accumulate much more slowly, providing the profile of the barrier reef or atoll with a deep lagoon (Fig. 2–7C). In such a situation, the reef margin may keep up or catch up, but the rest of the bank will continue to fill, possibly until sea level begins to fall with the next glacial advance. In cases such as Little Bahama Bank, the whole bank is near sea level, and the main direction available for accretion is lateral (Fig. 2–7B). When sea level falls, the most recently deposited limestones are exposed to erosion and the reef-building organisms are forced to relocate downslope (Fig. 2–7A).

Where a reef begins to grow is often dependent on the topography of the seabed (Longman, 1981). Slight topographic highs, particularly if the substratum is rock or coarse shell debris, favor recruitment and growth of colonizing reef builders. The length of time the reef has been growing under stable or slowly rising sea level is reflected by how much reef growth has modified the underlying topography (Fig. 2–8). Even in cases where reef development seems independent of underlying topography (Fig. 2–8C), original colonization probably occurred on minor topographic highs.

Modern reefs and reef shorelines are characterized by two major events: the last interglacial episode 120,000 years ago and the initiation of growth of modern reef structures less than 9,000 years ago (Davies, 1988; Shinn, 1988). During the last interglacial, sea level was at least 6 m higher than today and the limestone was formed that makes up many of the islands associated with reef tracts today. During the last glacial episode, which lasted more than 80,000 years, sea level fell to 130 m below the present level. Continental shelves were dry land; reef growth was limited to steep island or continental slopes. Why present reef growth began almost worldwide about 6,000–9,000 years ago is a fascinating mystery.

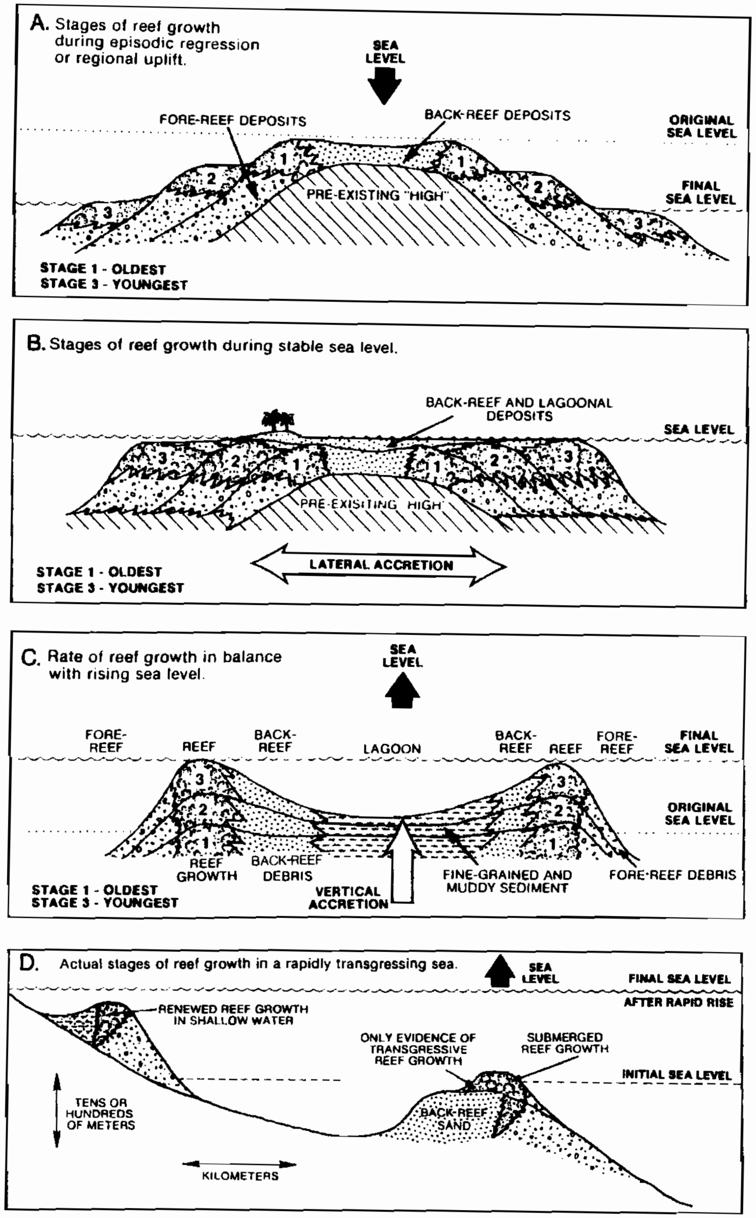


Figure 2–7. Responses of sea level to **(A)** sea-level fall or tectonic uplift; **(B)** stable sea level; **(C)** rising sea level or tectonic subsidence with the reef keeping up; and **(D)** rising sea level with the submerged reef failing to keep up and backstepping (from Longman, 1981).

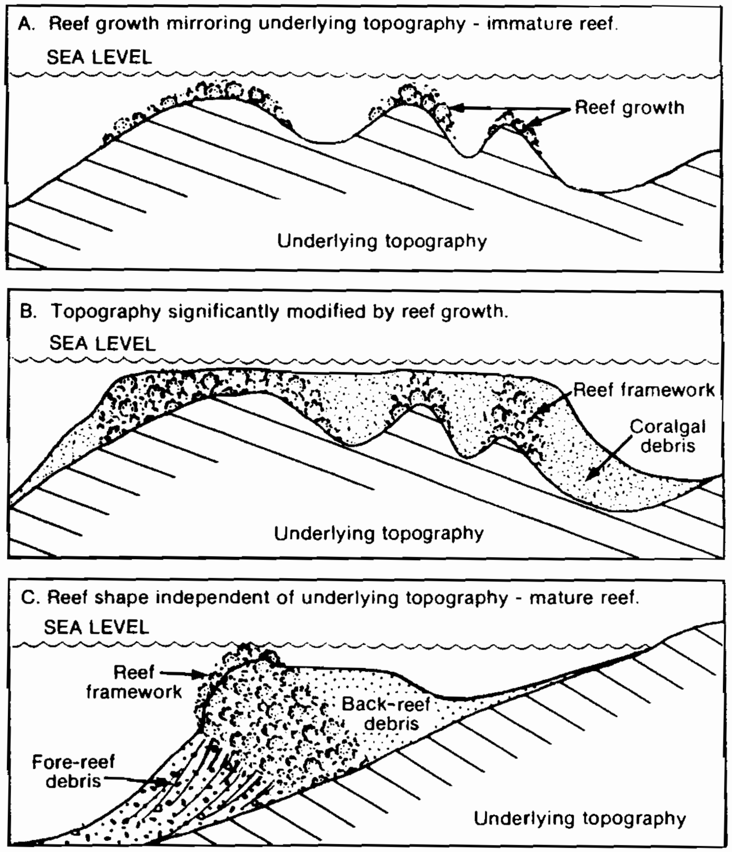


Figure 2–8. Relationships between reef growth and underlying topography: **(A)** colonizing reef-growth mirrors underlying topography; **(B)** reef represents an antecedent topographic high, but features of the underlying topography are modified by reef growth; **(C)** reef shape is independent of the underlying topography (from Longman, 1981).

Did climate or ocean geochemistry play a role? Or did sea-level rise simply slow sufficiently that reef development could keep pace from that time until the present?

Rising sea level does not always promote reef growth (Neumann and Macintyre, 1985). Approximately 4,000 years ago, sea level was about 3 m below the present level (Shinn, 1988). In southern Florida, Florida Bay was still swampland, instead of the vast restricted lagoon it is today. As sea level rose and Florida Bay developed, tides flushed water inconducive to reef growth from Florida Bay onto the reef tract; cold water alternated seasonally with warm, salty water. As a result, today Florida's reefs are best developed where protected from Florida Bay by elongate islands in the upper and lower keys. Middle key reefs, which began to develop about 6,600 years ago, have mostly failed to keep up over the past 4,000 years.

2.10. Conclusion

The history of reefs is a fascinating and ongoing study, full of paradoxes and unexpected feedback mechanisms. One of the most difficult concepts to understand is that limestones are both storehouses and sources of CO_2, depending on the time scale being considered. Through geologic time, limestones have tied up CO_2 and are therefore responsible for a livable planet. Yet on the shorter time scales of oceanic circulation and Ice Ages, interglacial reef building may move as much as 80 ppm of HCO_3^- from the bicarbonate pool in the oceans to CO_2 in the atmosphere. Relatively rapid erosion of young, predominantly aragonitic-coral limestones and sediments occurs when sea level falls. During a glacial advance, atmospheric CO_2 shifts back to HCO_3^- in the oceans. On human time scales, reefs are probably irrelevant to the CO_2 story. Fossil fuels, like ancient limestones, represent long-term storage of CO_2 in the Earth's crust. Human activities, including the burning of fossil fuels, have added more CO_2 to the atmosphere in 100 years than reef building did in 15,000 years.

The major lesson to be learned from the history of reefs is that they are constructed by complex and specialized biological communities. Because these systems are highly specialized to a limited range of environmental conditions, they are extremely sensitive to local, regional, and global environmental perturbations. Environmental crises, culminating in global mass extinction events, have repeatedly caused the extinctions of whole communities of reef-building organisms and the myriad of organisms that depended on the reef structures for habitat. Subsequent recovery of reef-building communities requires millions of years.

It can be argued that humans are simply part of nature; that exploding human populations are naturally generating another episode of mass extinction from which the Earth will recover in 20 or 30 million years. But from a human perspective there is a difference between a mass extinction event caused by a meteor impact and the ongoing one caused by human activities. Human intelligence has reduced biological limitations on both the growth rate of human populations and the environmental damage that any individual human can cause. Is it too much to hope that human intelligence can be utilized to bring an end to the current human-generated mass extinction event before the most specialized communities, like reefs and rain forests, are lost to future human generations? After all, many so-called "primitive" human cultures, including Micronesian and Polynesian inhabitants of atolls and coral pinnacles, thrived in resource-limited habitats. Can "modern" humans develop a sustainable global society based on recognition of globally limited resources? Or do humans represent the latest in the series of "disaster" species that proliferate globally at mass extinction events?

3

Reefs as Dynamic Systems

Dennis K. Hubbard

Rising concerns over the decline of "reef health" have caused scientists to critically reevaluate what we do and do not know about reefs. In the 1960s, and again in the 1980s, a sudden outbreak of *Acanthaster planci* devastated large sections of the northern Great Barrier Reef in Australia (Endean, 1973; Moran, 1986). In 1983, the long-spined sea urchin *Diadema antillarum* underwent an unprecedented population crash throughout the Caribbean. In the 1970s and 1980s, the most important shallow-water coral in the Caribbean and western Atlantic, *Acropora palmata,* was nearly irradicated over large areas by an unknown pathogen simply known as "white band disease" (Gladfelter, 1982). Most recently, the identification of widespread bleaching of Caribbean corals has led to congressional hearings on the state of the world's coral reefs. These sudden events over the past decade have highlighted the complexity of factors involved as well as our fundamental inability to separate human-induced change from the effects of natural cycles, the duration of which may exceed the history of modern reef science.

As discussed in Chapter 2, reefs have evolved throughout geologic time, largely in response to natural changes on the planet that have either placed the existing community at risk or have favored one that was significantly different—the process of natural selection. An underlying tenet of geology is that the present is the key to the past; the best way to understand how ancient organisms or systems functioned is to examine their modern counterparts—uniformitarianism. While this approach is fraught with peril, it has repeatedly provided valuable insights into the workings of ancient biological systems.

This chapter turns the uniformitarian approach around by using past history to place recent changes into a larger spatial and temporal context. Despite the difficulties in this exercise, the examination of reefs from a geological perspective offers two advantages. First, geological studies encompass a larger spatial scale than is addressed by most biological investigations. A more holistic approach