EVOLUTION AND FUNCTION OF CORAL REEF ECOSYSTEMS

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Summary

For biologists, a coral reef is a marine community characterized by abundant corals. For geologists, a coral reef is a rigid skeletal structure in which stony corals are major framework constituents, with coralline and calcareous algae, mollusks, foraminifers, and other calcifying organisms contributing to the total reef volume. Zooxanthellate corals are highly specialized symbioses between coral hosts and dinoflagellate algae called zooxanthellae. As a result of this symbiosis, coral reefs thrive in clear, nutrient-poor, shallow waters of tropical oceanic islands and continental shelves. Rapidly

increasing human populations are threatening coral reefs on multiple fronts. Nutrification, sedimentation, chemical pollution, and overfishing are significant and often interrelated local threats of global extent. Increasing concentrations of atmospheric CO_2 threaten to destabilize climate, induce global warming, and alter ocean chemistry. Corals under temperature stress become more sensitive to sunlight, thus, the combination of ozone depletion and global warming is particularly damaging. The fossil record of biogenic reefs and carbonate-producing communities has much to contribute to our understanding of living species and to predictions of how communities may respond to anthropogenically induced environmental change. Reef communities are geologically both productive and fragile, producing thick limestone buildups under favorable conditions, but suffering the most from widespread extinctions under regional or global environmental perturbations.

1. Introduction

In the twenty-first century, studies of coral reefs, carbonate sediments, and limestones will continue to be fundamental to understanding the past, present, and future of marine ecosystems and global climate. The responses of coral reef communities to environmental changes are of interest to governmental agencies, tourism industries, environmental organizations, and the reef-using public, as well as to carbonate sedimentologists and paleontologists. Ever-increasing human populations are profoundly altering global biogeochemical cycles through activities that will soon double the concentration of atmospheric CO_2 over pre-anthropogenic levels and that have already doubled the rate of nitrogen input to terrestrial ecosystems over pre-anthropogenic rates. The major goals of this section are to summarize basic concepts relating to coral reefs and carbonate sedimentation, and to discuss possible consequences of human-influenced global change on reef communities.

For biologists, coral reefs are marine communities characterized by abundant corals. For geologists, those corals must be constructing a biogenic reef, which is a limestone structure or buildup produced by biological as well as geological processes. The predominant organisms that build biogenic reefs include corals, coralline algae, oysters, bryozoans, and serpulid worms. 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. Thus, a coral reef is a rigid skeletal structure in which stony corals are major framework constituents, though not necessarily the dominant contributors to total sediment volume.

The major chemical constituent of carbonate sediments and limestones is calcium carbonate ($CaCO_3$). Organisms secrete $CaCO_3$ either as calcite or aragonite. The mineralogical differences are in crystal structure and solubility 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 more soluble in cooler seawaters and in freshwater. Thus, the energy required to precipitate and maintain an aragonite or calcite shell differs depending upon the carbonate saturation state of the waters in which an organism lives. In addition, aragonite is structurally stronger than calcite, a characteristic of particular importance for organisms with erect growth forms, including branching corals and some large bryozoans.

Energetic and structural aspects of biomineralization were important factors in the adaptation of shelled organisms to their environments.

(See *Paleozoic History.)*

2. Environmental Requirements for Coral Reef Growth

Most people envision coral reefs as tropical islands surrounded by warm, crystal clear seawater, beneath the surface of which lies a profusion of corals and colorful fish. Such pictures are no accident, for they illustrate the basic requirements for reefs (Table 1) that are constructed by zooxanthellate corals (those hosting dinoflagellate algal symbionts) and associated communities.

Coral reefs require subtropical to tropical temperatures year-round. Seasonal temperatures range from occasional winter lows of about 14 °C to summer highs of about 30 °C, with optimum summer temperatures of from 23 °C to 29 °C. Prolonged exposure to temperatures even a degree or two above normal summer temperatures can promote coral bleaching, which is the loss of color caused either by the loss of chlorophyll in the zooxanthellae or expulsion of the zooxanthellae from live coral. Winter cold fronts can also damage or kill corals, though on the southern Great Barrier Reef of Australia and in the Persian Gulf, some species tolerate exposure to temperatures below 10 °C.

Parameter	**Optimum**	**Consequences of stress**
Temperature	23-29 °C	Low: cold shock, bleaching, mortality High: bleaching, mortality
Salinity	33–38‰	Stress, reproductive failure, bleaching, mortality
Water motion	Substantial	Little or no water motion prevents elimination of metabolites Consistent large waves or repeated storms can inhibit coral growth
Terrigenous sediments	Little or none	Sediments increase turbidity (reduce water transparency) and require energy for removal.
Nutrients DIN* SRP**	Low <1 μM <0.2 μM	Phytoplankton blooms, overgrowth of corals by benthic algae. More may destabilize symbiosis between coral and zooxanthellae. More may stimulate growth of nitrogen-fixing cyanobacteria.
Plankton	Low	Higher densities reduce water transparency and stimulate growth of bioeroding organisms.
Water transparency	High	Reduced light reduces photosynthesis and calcification rates. Low transparency is a consequence of sediment or plankton blooms.
UVB	Varies with adaptation	Excess UVB induces photooxidative stress, photoinhibition, and increases susceptibility to

		thermal stress.

*DIN, Dissolved inorganic nitrogen: fixed nitrogen available for uptake by photosynthetic organisms.
**SRP, Soluble reactive phosphorus: phosphate ion or other forms of phosphate available for uptake.

Table 1. Environmental parameters controlling coral reef growth

Corals also require seawater of normal marine salinities, typically from 33 to 37‰. Though many corals can tolerate limited exposure to rainwater or freshwater runoff, reefs are generally not found immediately offshore from even small streams. Research on coral reproduction indicates that lower salinities reduce the viability of coral gametes and larvae. At the other extreme, in the Persian Gulf, some coral species have adapted to salinities in excess of 40‰.

Pictures of coral reefs in crystal clear waters are also no accident. Corals, with their zooxanthellae, require abundant sunlight to grow and calcify. Particles in the water that reduce water transparency, such as sediments or abundant plankton, are detrimental to reef growth. Even the island setting is typical, for while there are (or until recently, were) fringing reefs on continental shorelines around the Caribbean, East Africa, the Middle East, and Southeast Asia, the most spectacular coral reefs thrive in settings removed from significant terrestrial runoff, and thus away from freshwater,sediment, and nutrients. At the same time, coral reefs require a shallow substrate upon which to grow. Thus, islands or shoals on continental shelves and volcanic structures in the open ocean provide ideal substrate in clear, warm, nutrient-poor, and relatively sediment-free waters.

As a result, coral reefs are found throughout the tropical oceans (Figure 1) where suitable shallow-water substrate existed for reef growth to occur as sea level rose over the past 18 000 BP, since the last glaciation. Reefs are poorly developed or sparse on the eastern sides of the Atlantic and Pacific Oceans because regional upwelling produces cool, nutrient-laden currents that suppress reef growth. Studies on the effects of El Niño/Southern Oscillation events over the period from 1980 to 2000 have revealed that bleaching and mortality in response to elevated temperatures during El Niño years further limit reef development in the eastern tropical Pacific. Reef development is also suppressed by runoff from major river systems such as the Amazon and Orinoco Rivers of South America.

See *El Niño/Southern Oscillation*.

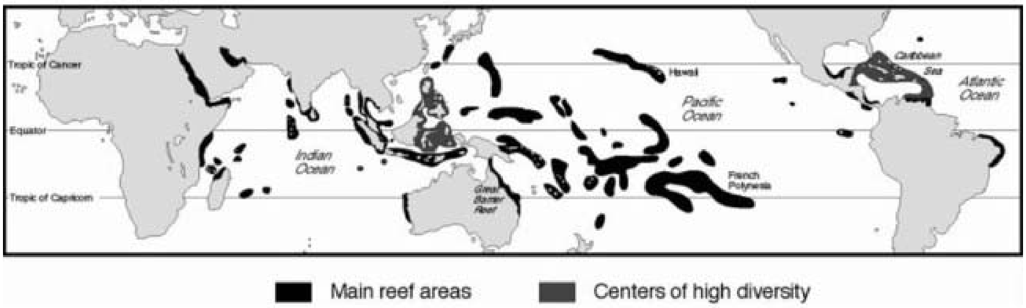

Figure 1. Global distribution of coral reefs
Adapted from Birkeland C., ed. (1996). *Life and Death of Coral Reefs,* 536 pp. New York: Chapman and Hall.

3. Coral Reef Organisms and Their Many Roles

Coral reefs are often compared with rain forests as the most biologically diverse ecosystems on Earth. The comparisons are valid for two important reasons. The first is because the major creators of structure, trees in a rain forest and corals in tropical oceans, provide an almost infinite array of habitats for other plants, animals, and microbes. The second is that both ecosystems thrive in environments in which essential nutrients, including fixed nitrogen, phosphorus, iron and trace nutrients, are exceedingly scarce and therefore complex pathways for nutrient recycling have evolved within the ecosystems.

3.1. The Coral–Zooxanthellae Symbiosis

Coral reefs thrive in nutrient poor waters as the result of a fundamental evolutionary adaptation that apparently evolved approximately 230 Ma during the Triassic period. The development of the symbiosis between scleractinian corals and dinoflagellate algae known as zooxanthellae allowed these corals to be exceptionally competitive in warm, clear waters that are so nutrient deficient as to inhibit the recruitment and growth of most macroalgae and of most sessile animals that lack algal symbionts. In the tropical sunlight, the zooxanthellae must photosynthesize. If the zooxanthellae are deficient in fixed nitrogen, reproduction is inhibited, so they primarily excrete their photosynthetic products, which include simple sugars and glycerol. The host corals utilize this photosynthate to support their metabolic needs, to promote calcification, and to secrete mucus to keep clean of sediments and fend off microbial invasion. Thus, with basic energy needs supplied by the zooxanthellae, any prey the coral captures for food can be utilized to support the growth and reproduction of the corals.

However, the exceptional adaptation to nutrient-poor subtropical and tropical oceanic environments comes with a price. For a variety of reasons, corals are not competitive when nutrient supplies increase. Nutrient input into the water column promotes plankton growth, which reduces water transparency and therefore the light reaching the bottom-dwelling corals. Abundant plankton provides food for other suspension- and filter-feeding animals, such as sponges and bivalves that may compete with corals for space on the reef, or that bioerode the coral structure and therefore can damage or destroy coral colonies. Furthermore, more nutrients promote faster growth of benthic algae, which compete with juvenile corals for space and can even overgrow adult corals in some situations.

(See *Nutrients.)*

Another liability of the coral–zoothanthellae symbiosis is the susceptibility of the coral to light and temperature stress. Insufficient light limits photosynthesis by the zooxanthellae, and growth and calcification by the coral. At the other extreme, all plants, including zooxanthellae, can be damaged by too much light, and the susceptibility to light stress increases with increasing temperature. Corals that are severely light or heat stressed typically undergo bleaching and, if extremely stressed, may die.

Another important concept in understanding the distributions of most animals is that the environmental requirements for successful reproduction and recruitment of young are generally narrower than the requirements for adult survival. This is a particular problem in long-lived organisms or meta-organisms, such as colonies of reef-building coral species. Adult colonies may continue to survive long after the environment has been altered to an extent to prevent juvenile recruitment. Because large colonies continue to visually dominate the community, the lack of recruitment can be easily overlooked until a mortality event such as a storm or intense bleaching results in widespread die-off of the adult corals.

3.2. Components of Coral Reef Ecosystems

The diverse array of organisms within a coral reef ecosystem can be discussed or classified in a variety of ways. Traditional systematics, the naming of organisms, is currently in question because modern molecular genetic techniques are creating a revolution in the understanding of relationships at all taxonomic levels. A more useful approach for general discussions of reef ecosystems is to discuss organisms by their mode of life and by the ecologic and geologic roles they play on the reef.

3.2.1. Ecologic Roles

In marine environments, one way to classify organisms is by whether they live in the water column or on the bottom, and by how active they are (Table 2). Plankton drift or weakly swim in the water column, and include multitudes of phytoplankton (microalgae) and zooplankton. Though most plankton are microscopic, there are larger forms such as jellyfish. Holoplankton are true plankton that live throughout their lives in the water column. Meroplankton are organisms that live only part of their life, typically their larval stages, as plankton. Planktic eggs or larvae are the principal dispersal mechanisms for most benthic organisms. Nekton include the strong swimmers such as fish and squid. The benthos include all the organisms that live on the seabed, including attached forms, burrowers, crawlers, and swimmers.

The basic nutritional roles for organisms are autotroph, heterotroph, and, particularly on coral reefs, mixotroph. Autotrophs in reef ecosystems are primarily the photosynthesizers, including phytoplankton in the water column, and cyanobacteria,

microalgae, macroalgae, and sea grasses in the benthos (Table 2). Heterotrophs include bacteria, protists, fungi, and animals that must feed upon organic matter produced by other organisms. Mixotrophs include some microalgae, protists, and plant–animal symbioses, whereby the functional organisms obtain their nutritional requirements from both photosynthesis and uptake of organic matter from the environment. Corals with zooxanthellae are the best known and most important mixotrophs in the reef environment. Larger foraminifers, giant clams, some sponges, and a few ascidians that host symbiotic algae or photosynthetic bacteria are also notable mixotrophs in reef systems.
(See *Plankton*.)

The ecologic roles of heterotrophic organisms depend both on the kind of organic matter they consume and how it is acquired. The basic categories of herbivore (consumers of plants), carnivore (consumers of other animals), and detritivore (consumers of detritus including feces of other organisms, microalgal/bacterial mats, and organic matter in the sediments) apply to many organisms. Also common is feeding by particle size. Examples include most plankton feeders, from sessile sponges to actively swimming fish. Typically the size of the particle of plankton is more important to the consumer than whether the particle is plant, animal, protist, or detritus with bacteria.

Common name (Scientific name)	**Life habit**	**Ecologic roles/ Feeding style**	**Geologic roles (in order of importance)**
Cyanobacteria	Benthic or planktic	Autotrophic	Sediment binders, bioeroders
Green algae (Chlorophyta)	Benthic, attached	Autotrophic	Calcareous forms: sediment producers many forms: sediment binders, dwellers
Red algae (Rhodophyta)	Benthic, attached	Autotrophic	Corallines: encrusters, sediment producers Fleshy forms: bafflers, dwellers
Brown algae (Phaeophyta)	Benthic, attached	Autotrophic	Bafflers, dwellers
Stony corals (Scleractinia)	Benthic, attached	Mixotrophic, plankton feeders	Framework builders, bafflers, sediment producers
Soft corals (Octocorallia)	Benthic, attached	Mixotrophic plankton feeders	Bafflers, binders, minor sediment producers
Larger foraminifers (Foraminifera)	Benthic, free living	Mixotrophic, small particle feeders	Sediment producers
Sponges (Porifera)	Benthic, attached	Heterotrophic, small-plankton feeders	Bioeroders, bafflers, sediment binders
Snails (Gastropoda)	Benthic, free living	Heterotrophic, herbivorous, carnivorous	Sediment producers, bioeroders
Clams (Bivalvia)	Benthic, attached or free living	Heterotrophic, plankton feeders	Sediment producers, bioeroders
Giant clams (*Tridacna*)	Benthic, attached	Mixotrophic, plankton feeders	Sediment producers

Sea urchins (Echinoidea)	Benthic, free living	Heterotrophic, grazing herbivores	Bioeroders, sediment producers
Fish	Nektic, free living	Heterotrophic	Bioeroders, dwellers

Table 2. Ecological and geological roles of important coral reef organisms

3.2.2. Geologic Roles

Equally important to the reef communities are the geologic roles that many organisms play within the reef ecosystem. These roles, which include sediment production, framework construction, encrustation, sediment binding and baffling, and bioerosion, are not mutually exclusive in many cases (Figure 2).

The most basic role is sediment production by calcification. The calcareous shells and skeletons of a wide variety of protists, plants, and animals become biogenic sediments upon the death of those organisms. Sediments are typically classified by size as gravels, sands, or muds. The size of the shell or skeleton and the nature of the organic matrix determines the sediment size to which an organism contributes. For example, coral fragments, snail shells, sea urchin spines, and the segments of the calcareous green alga, *Halimeda*, commonly make up the coarsest sediments. Sand-sized sediments include fragments of larger shells and skeletons, as well as the whole and fragmented shells of foraminifers. The organic matrices of snail and bivalve shells and of the skeletons of calcareous green algae readily disintegrate, freeing the aragonite needles from which the shells and skeletons are made. These aragonite needles are important components of the calcareous muds on reefs and in associated lagoons and tidal flats. The metabolic activities of certain bacteria and microalgae also contribute to the biogeochemical precipitation of ooliths and of calcareous muds. The latter process may cause whitings in seawater overlying shallow banks and shelves.

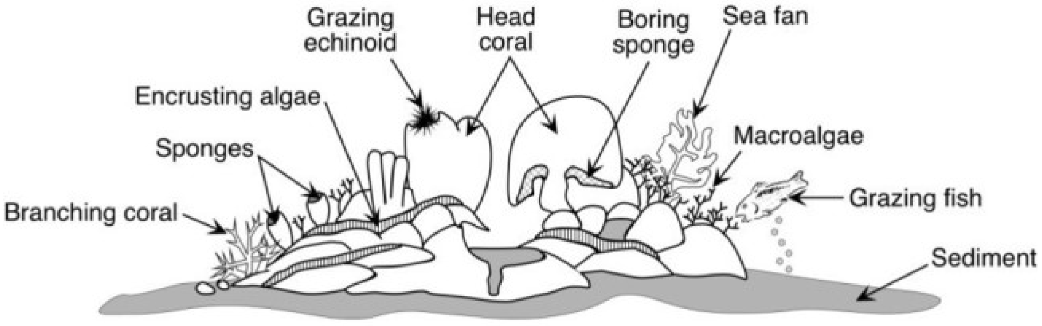

Figure 2. Cartoon depicting geologic roles of some reef organisms
Adapted from Scholle P.A., Bebout D.G., and Moore C.H., eds. (1983). *Carbonate Depositional Systems, Memoir 33,* 708 pp. Tulsa: American Association of Petroleum Geologists.

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 deep-ocean floor is covered by foraminiferal ooze, which is composed primarily of the empty shells of protists that live as plankton in the surface waters of the open ocean. Shells and skeletons of benthic organisms may also be important sediment constituents, especially on continental shelves, in some coastal areas, and on oceanic banks and shoals.

Whether biogenic constituents make up most of the bottom sediments or whether they are only minor contributors depends upon 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 is not only a source of sediments, it 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.

Whether biogenic sediments accumulate in place or are transported away depends both upon the strengths of waves and currents and upon 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 upwards from the sediment, slowing water motion and providing quieter places for sediments to settle, can be termed bafflers. Organisms that live in or directly on the sediment, holding or encrusting it in place, can be referred to as binders.

Binders such as microalgae and bacteria grow and develop mats directly upon sediments 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. Stromatolites, which are biogenic reef components constructed by this process, are layered accumulations of biogeochemically precipitated carbonate sediment and algal–bacterial mats. Ancient stromatolites were the first bioherms in the fossil record. Modern stromatolites are found in Shark's Bay, Western Australia, and on the Bahama Banks.

(See *Proterozoic History, Stromatolites.*)

In some current-swept environments, specialized sponges live in and on the surface layers of sediment, binding them in place. Sediments may consist of coarse accumulations of segments of the calcareous green alga *Halimeda*. Coralline red algae may colonize the surface of sediment-filled sponges, forming solid substrate upon which other organisms settle and grow. These communities produce sponge–algal mounds along the margins of some western Caribbean banks, and are similar 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, sea-grass beds effectively stabilize sediment over vast areas. Sea-grass blades slow water flow, allowing suspended sediments to settle out. Sediments are held in place by extensive sea-grass root and rhizome systems, as well as by the holdfasts of algae living within the sea-grass 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 also the major biogenic framework constructors, the stony corals. These organisms grow upwards or outwards in branching, massive, or platy morphologies. Corals secrete substantial quantities of calcium carbonate while trapping even greater quantities of sediment within and in 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 and around the reef structure. All contribute ecologically to the reef community and many contribute to the reef structure. Some species are encrusters. Many organisms have shells or spicules that contribute to sediment production upon the death of the individual. Some organisms are wholly soft bodied and have little direct influence on the reef structure. Many species contribute to the breakdown of the reef structure by boring into it, scraping away at it as they graze, or even biting off bits of the reef. Such organisms are known collectively as bioeroders.

Bioeroding organisms are a diverse and important component of the reef community. Organisms that bore or etch their way into the reef include bacteria, fungi, several varieties of sponges, worms, clams, and sea urchins. Organisms that scrape away limestone as they graze algae include sea urchins, chitons, and some snails. Many reef fish feed by breaking or scraping off and ingesting bits of coral or coralline algae, and defecating the sediment particles. 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 by physical and biological erosion can exceed rates of accretion, and the reef may cease to exist.

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Biographical Sketch

Pamela Hallock Muller is a Professor in the College of Marine Science at the University of South Florida in St. Petersburg, Florida, USA, where she teaches and mentors students in the geological and biological oceanography programs. She and her students study modern coral reefs and larger foraminifera to gain insight not only into environments of the past and present, but also into the potential effects of human activities on the future of Earth's ecosystems. She has published extensively on the effects of nutrient supply on reef ecosystems and calcifying organisms. Current projects include bleaching in reef-dwelling foraminifera as an indicator of increasing ultraviolet radiation associated with global ozone depletion, and development of an index of biological integrity applicable to coastal environments worldwide. She has published more than 75 scholarly papers in scientific journals and books.

Dr. Hallock earned a BA in zoology in 1969 from the University of Montana in Missoula, an MS in 1972 and PhD in 1977 in oceanography from the University of Hawaii in Honolulu. She did postdoctoral work at the University of Copenhagen, Denmark, and Kiel University, Germany; then began her academic career as an assistant professor of earth sciences at the University of Texas of the Permian Basin in Odessa, Texas, in 1978. She moved to the University of South Florida in 1983.

She is a Fellow of the Geological Society of America; a member and past President of the Board of Directors of Cushman Foundation for Foraminiferal Research; and a past Paleontology Councilor of the Society for Sedimentary Geology (SEPM). She received the 1994 W. Storrs Cole Research Award from the Geological Society of America and the 1999 Outstanding Educator Award from the Association for Women Geoscientists. She has served on the editorial boards of Geology, Journal of Foraminiferal Research, and Marine Micropaleontology.