CORAL REEFS

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Introduction

Coral reefs are highly diverse ecosystems that provide food, income, and coastal protection for hundreds of millions of coastal dwellers. They are found in a diverse range of geomorphologies, from small coral communities of little or no relief, to calcareous structures hundreds of kilometers across. The most diverse coral reefs occur in the waters around southeast Asia. This is primarily because of extinctions that have occurred in other regions due to the gradual restriction of global oceanic circulation associated with continental drift. However, rates of speciation of coral reef organisms in this region may also have been high within the last 50 million years.

Human activities have caused the degradation of coral reefs to varying degrees in all areas of the world. A major focus of present research is on the resilience of coral reefs to disturbances such as storms, diseases of reef species, bleaching (the expulsion of endosymbiotic photosynthetic zooxanthellae) and harvesting to local extinction. Along many coastlines, a combination of increased eutrophication due to coastal runoff and the extraction of herbivorous fish and invertebrates appears to favor the replacement of corals with macroalgae following disturbances. Another important aspect of resilience is the degree to which a depleted population of a given species on one reef can be replenished from other reefs. Most coral reef organisms undergo periods of free-swimming (pelagic) life ranging from a few hours to a few months. Genetic studies show evidence of broad dispersal of the progeny of some species among reefs, but most of the replenishment of a given population from year to year is believed to be from the same or nearby coral reefs.

Coral reefs are complex biophysical systems that are generally linked to similarly complex socioeconomic systems. Their proper management calls for system-level approaches such as integrated coastal management.

General

Types of Coral Reefs

The term 'coral reef' commonly refers to a marine ecosystem in which a prominent ecological functional role is played by scleractinian corals. A 'structural coral reef' differs from a 'nonstructural coral community' in being associated with a geomorphologically significant calcium carbonate (limestone) structure of meters to hundreds of meters height above the surrounding substrate, deposited by components of a coral reef ecosystem. The term 'coral reef' is often applied to both structural and nonstructural coral ecosystems or their fossil remains, although many scientists, especially geomorphologists, reserve the term for structural coral reefs and their underlying limestone. Both types of ecosystem occur within a wide range of tropical and subtropical marine environments, although structural development tends to be greater in waters of lower silt or mud concentration and oceanic salinity. Many reefs survive well amid open ocean waters with low nutrients, aided by efficient 'combing' of waters for plankton, high levels of nitrogen fixation and fast and thorough nutrient cycling. However, extensive coral reefs also occur in coastal waters of much higher nutrient concentrations.

Scleractinian (stony) corals grow as colonies or solitary polyps on a wide variety of substrates, including fallen trees, metal wreckage, rubber tires and rocks. Rates of settlement are often enhanced by the presence of calcareous encrusting algae. Soft sand, silt and mud tend to inhibit the settlement of stony corals, and so few coral ecosystems occur in modern or ancient deltaic deposits. However, coral can grow very near the mouths of small rivers and steams, and fresh or brackish groundwater often percolates through reef structures or emerges periodically through tunnels and caves. Vertical caves are often called 'blue holes'.

Nonstructural coral communities are common on rocky outcrops in shallow seas in many tropical and subtropical regions. They can range from a few clumps of coral to very substantial communities covering many square kilometers of wave-cut shelves near deeper areas.

Structural coral reefs come in many shapes and sizes, from less than a kilometer to many tens of kilometers in linear dimension. It is helpful to differentiate individual coral reefs from systems of coral reefs, such as the misnamed 'Great Barrier Reef' of Australia, which actually consists of thousands of densely packed coral reefs. Common types of structural coral reefs include fringing reefs, barrier reefs, knoll reefs, pinnacle reefs, platform reefs, ribbon reefs, crescent reefs, and atolls. The term 'patch reef' may refer either to a patch of coral and limestone a few meters across within a structural coral reef (typically in a lagoon or on a reef flat), or to a platform or knoll reef. Thus, the term is best avoided. There is a wide range of structures intermediate between crescent reefs, platform reefs, and atolls in areas such as the Great Barrier Reef System.

A fringing reef is, by definition, always found adjacent to a land mass. Most fringing reefs include a wave-breaking reef crest, one or more meters above the rest of the reef, forming a thin strip offshore (**Figure 1**). Between the crest and the land, there is usually a relatively level area, broken by channels, called a 'reef flat' (**Figure 2**). Fringing reefs differ from barrier reefs, in that the latter are separated from land by a 'navigable' water body (lagoon). It is useful to differentiate a lagoon from a reef flat in terms of depth; a lagoon is at least 2 m deep at mean tide. Fringing reefs often include lagoons, but the separation of a reef crest and slope from land is more complete in a barrier reef (**Figure 3**).

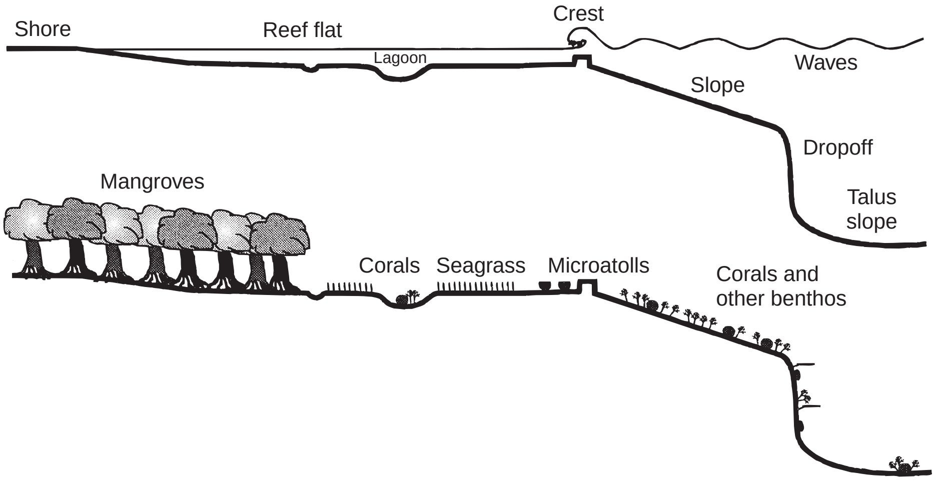


Figure 1 Profiles of a hypothetical fringing reef showing geomorphological and ecological zonation relative to wave action.

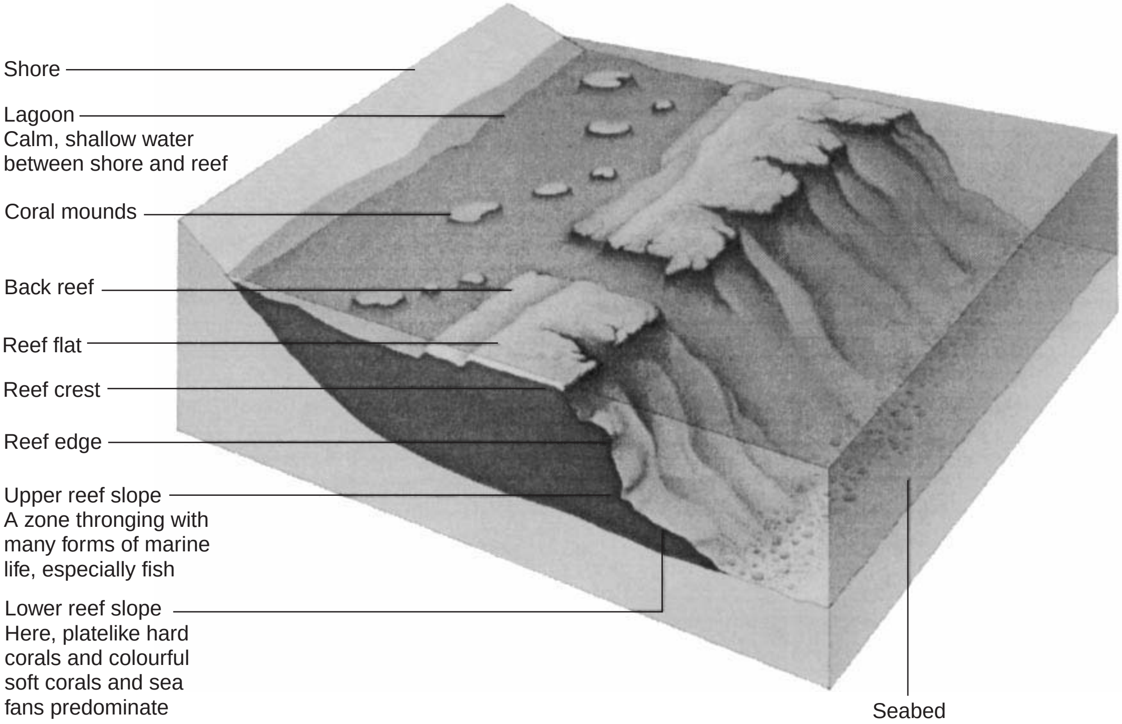


Figure 2 Geomorphology of a typical fringing reef. (Adapted from Holliday, 1989.)

Structural reefs such as knoll, pinnacle, platform, ribbon, or crescent reefs, are arbitrarily labeled based on their shape. Atolls are donut-shaped structures which, although often supporting islands along the outer rim, do not have an island in the central portion (**Figure 4**). The large Apo Reef, east of the Philippine island of Mindoro, is a double atoll, with two lagoons within adjacent triangular

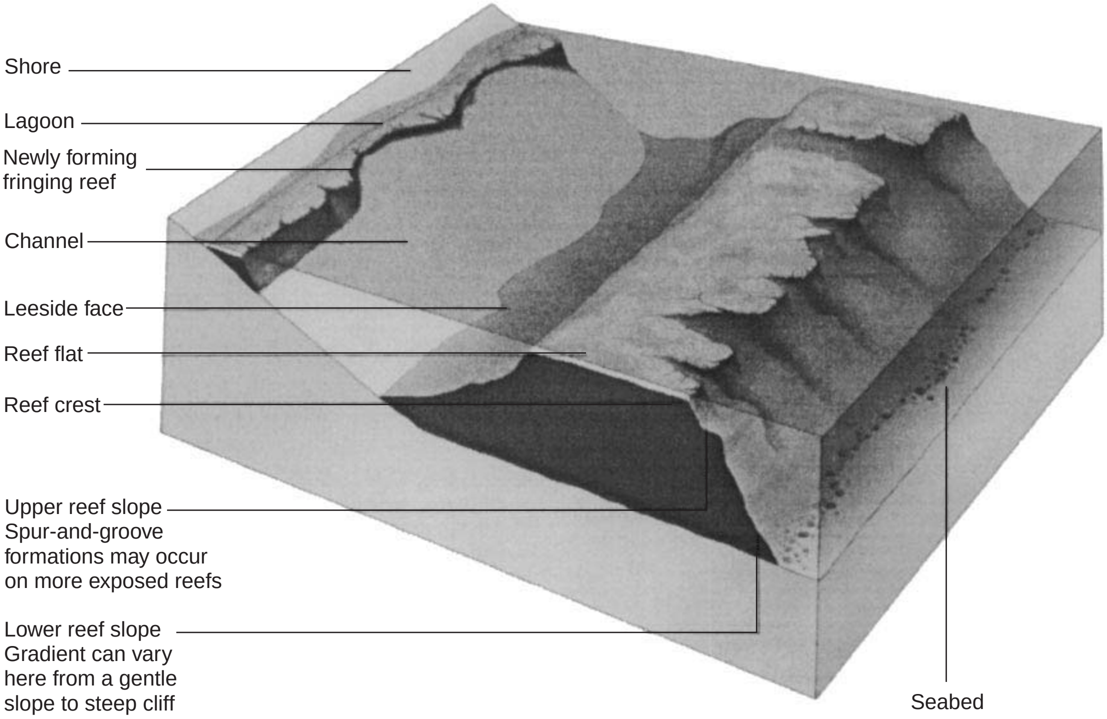


Figure 3 Geomorphology of a typical barrier reef. (Adapted from Holliday, 1989.)

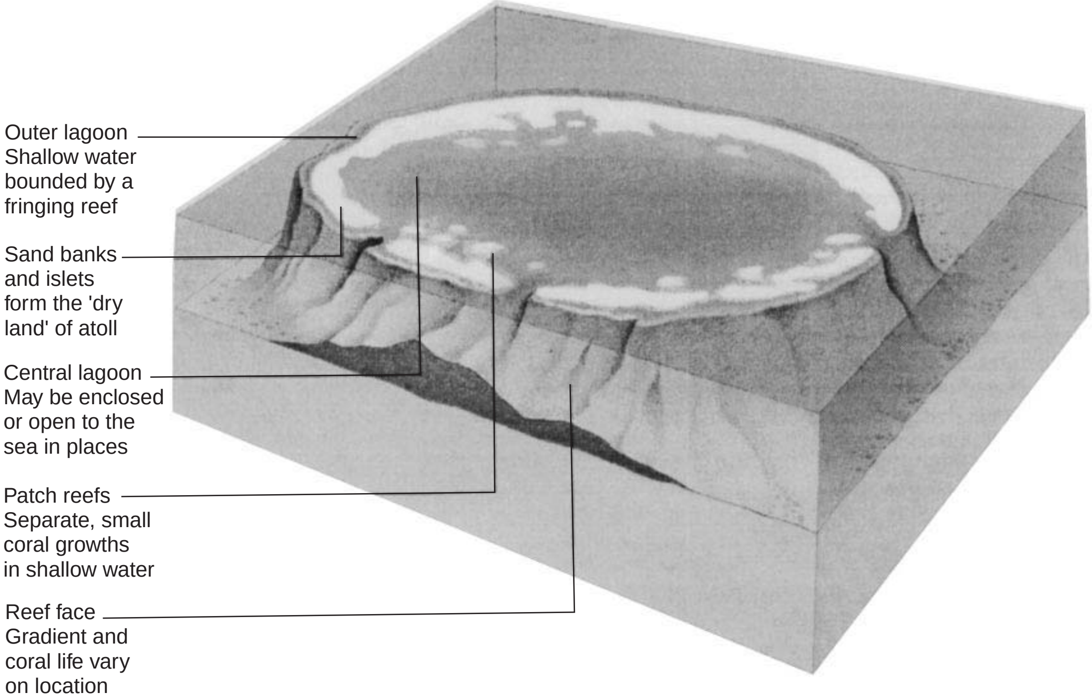


Figure 4 Geomorphology of a typical atoll. (Adapted from Holliday, 1989.)

rims, the whole reef being roughly diamond-shaped. Atolls can be quite large, such as the North Male Atoll, which houses the capital of the Maldives (**Figure 5**).

Although one commonly thinks of structural coral reefs as reaching to the sea surface, most of the coral reefs of the world do not. For example, there is a system of atolls and other reefs to approximately 50 km off the north-west of Palawan Island (Philippines) that closely resembles portions of the Australian Great Barrier Reef. However, very few reefs of the Palawan 'barrier system' come within 10 m of the sea surface. Some estimates of coral reef area are based on reefs at or near the sea surface, partly because the larger examples of such reefs tend to be well-charted, whereas most other coral reefs are poorly known in terms of location and characteristics.

Importance

Coral reefs support the highest known biodiversity of marine life, and constitute the largest biologically generated structures on Earth. Coral reefs are of substantial social, cultural, and economic importance. Coral reef systems in Florida, Hawaii, the Philippines, and Australia each account for more than $1 billion in tourist-related income each year. Coral reefs provide food and livelihoods for several tens of millions of fishers and their families, most of whom live in developing countries on low incomes, and have limited occupational mobility. Coral reefs protect coastal developments and farm lands from erosion. In many countries, particularly among Pacific islands, coral reefs are culturally very important, as they are involved in social structuring and interaction, and in religion. Despite poor taxonomic understanding and increasingly strict controls on bioprospecting, coral reef species are yielding substantial numbers of important drugs and other products.

Figure 5 North Male Atoll of the Maldives. Large atolls often support substantial human population that will be threatened as sealevels rise. (Adapted from Holliday, 1989.)

Zonation

The ecological zonation of most coral reefs depends on physical factors, including depth, exposure to waves and currents, and oxygen limitation. A fringing reef is basically a large slab of limestone jutting out from land. The landward margin may support extensive mangrove forests. A sandy channel may separate these from extensive seagrass beds on a reef flat. Other channels, depressions, and basins may be predominated by sandy bottoms, studded with clumps of coral. Clumps in deeper waters, rising 2 m or more from the bottom and consisting of several species of coral are known as 'bommies.' Some lagoons hold large numbers of 'pillars,' tall shafts of limestone, similarly supporting corals. Throughout the reef flat, there are, typically, low clumps of coral. Macroalgae and seagrass are often kept away from these clumps by the feeding action of the herbivorous fish and sea urchins, particularly active at night and resting during the day in the clumps of coral. Low massive coral colonies may form 'microatolls,' in which central portions of the colony are dead, while the raised outer edge and sides continue to flourish. On some reef flats, branching corals form patches which extend over hectares. Other reef flats and lagoons may be packed with high densities of diverse coral colonies, and have little or no seagrass.

The seaward edge of the reef flat often leads into low branching or massive corals, including microatolls, which become increasingly dense to seaward. A thin band of macroalgae, such as *Turbinaria*, may be present, just before the clumps of coral and hard substrate rise to form a reef crest or 'pavement.' In some areas, the crest may be made of living coral. In areas protected from heavy wave action, the crest may consist of fingerlike *Montipora* or *Porites* forming a band several meters wide, broken periodically by whorl-shaped colonies of leafy corals, all apparently formed to efficiently comb breaking waves for zooplankton. On higher-energy coasts, the corals may be primarily dense growths of wave-adapted *Pocillopora*. Other crests may be covered with various species and growth forms of the brown alga

Sargassum. The edible and commercially important alga *Caulerpa* may also be abundant. Other reef crests may be densely packed with small clumps of articulated calcareous algae such as *Halimeda* and *Amphiroa*. Still others consist of a pavement of calcareous material or sheared-off ancient corals, and are relatively devoid of all macrobenthos except tiny clumps of algal turf or encrusting algae, sometimes forming a white or pink algal crest. The height of a reef crest above the reef flat is often determined by the height of local tides.

Most reef crests are broken by channels of varying width and depth – exit routes for water piled up behind the reef crest by the breaking waves. These may be studded with corals or smoothed by scouring sand and rock carried along with the exiting water. They are particularly important as breeding grounds for a variety of reef fish.

Beyond the reef crest, on the upper reaches of the 'reef slope,' one often finds small thick clumps of branching *Pocillopora* coral or various species of *Acropora* colonies in similar, wave-resistant growth forms. Encrusting and low lump-like (submassive) colonies may be common. More of the brown algae *Turbinaria* and *Sargassum* may be present. Along a rounded or gentle upper reef slope in the Indo-Pacific, there may be table-shaped *Acropora* colonies of gradually larger size as one proceeds to deeper waters. On many reefs, the reef slope is the most active area of coral growth, because of the oxygen, nutrients, and plankton brought in on the waves and currents. Coral cover may exceed 100%, as colonies overgrow colonies, all competing for light. Soft corals dominate some reef slopes, *Sargassum* others, and on some, the profusion of corals, sponges, algae, and other benthic organisms may prevent the identification of a dominant group. The mean and median stony coral cover (the percentage of the substrate covered with coral) on a reef slope globally are both approximately 40%, with a broad variance.

On most reefs, small channels on the upper slope consolidate into increasingly wider and deeper channels along lower reaches of the slope. Some may be steepened or converted into tunnels by coral growth. The channels may occur fairly regularly at distances of tens of meters, resulting in a 'ridge and rift' or 'spur (or buttress) and groove' structure resembling the toes of giant feet. The bottoms are generally filled with a mix of sand and debris from the reefs, which makes its way downwards, particularly during storms. Sand may drop continuously from escarpments, in flows resembling waterfalls, and spectacular columns of limestone cut away from the reef proper may border deeper rifts.

Many reef slopes lead to a steep 'wall' or 'drop-off,' often beginning about 10–20 m depth. On shelf areas, the drop-off may end at 20–30 m depth, followed by a 'talus' slope of deposited reef materials, often 30°–60°, leading into the more gradual shelf slope. Typically, this shelf will be interrupted by outcrops of limestone and bommies for considerable distances from the reef itself. On reefs jutting into deep waters, the drop-off may extend downwards for hundreds of thousands of meters. Corals and a myriad of other organisms generally cover the slopes, leaving little or no bare substrate.

On some reefs, such as some small fringing reefs along the Sinai, the upper portion consists almost entirely of live massive, platy or occasionally thick branching corals extending from land or from a small reef flat. The corals are joined together tangentially, leaving large spaces of water between. There may be no identifiable reef crest, and the mass simply juts out over a steep dropoff to hundreds of meters depth.

The zonation of atolls and other surface reefs is generally similar. However, as one proceeds across a lagoon basin from the windward to the leeward side of an atoll, one encounters a 'backreef' area (note that the term is also applied by some to the coral-dominated area behind a reef crest). The leeward side of the atoll is subject to less energetic waves and currents. It tends to have less well-defined zonation, less of a distinct crest, and often broader, more gradual slopes.

Storms are very important in determining features of the reef. It is common to find large chunks of limestone on upper slopes, crests and reef flats, representing masses of coral and substrate pulled up from the lower slope and deposited during a storm. Pieces of this jetsam may weight several tonnes each. Smaller pieces of coral and substrate, and masses of sand may pile up during storms, forming islands. Processes of calcification in intertidal areas may glue together pieces of coral and reef substrate thrown up by storms, forming 'beach rock,' which helps to prevent erosion at the edge of low islands. Other islands may be formed on portions of a reef uplifted by tectonic processes. Islands developed by storm action or uplift often have very little relief, but may support human communities. Entire nations, as with the Maldives or some Pacific island nations, may consist of such low islands on atoll reefs.

Geology

Calcification

Carbon dioxide and water combine to form carbonic acid, which can then dissociate into hydrogen ions (H^+) and (HCO_3^-) bicarbonate, or carbonate (CO_3^{2-}) ions as follows:

$$CO_2 + H_2O \Leftrightarrow H^+ + HO_3^- \Leftrightarrow 2H^+ + CO_3^{2-}$$

Colder water can hold more CO_2 in solution than warmer water. Calcium carbonate reacts with CO_2 and water as follows:

$$CO_2 + H_2O + CaCO_3 \Leftrightarrow Ca^{2+} + 2HCO_3^-$$

The dissolution of $CaCO_3$ depends directly on the amount of dissolved CO_2 present in the water. Thus, in colder waters the higher levels of CO_2 inhibit calcification. Structural coral reefs are primarily limited to a circumglobal band stretching from the Line Islands in Hawaii to Perth, Australia, with nonstructural coral communities being increasingly dominant along the fringes. The distribution band varies, such that cold waters (e.g., Peru) narrow the range of coral reefs closer to the equator, and warm currents facilitate higher latitude development (e.g., Bermuda).

Calcification in stony corals is greatly enhanced by the presence of zooxanthellae in the tissues. Zooxanthellae are nonmotile stages of a dinoflagellate algae. They are contained within specialized coral cells, growing on excess nutrients and trace metals from the carnivorous corals, producing sugars for utilization by the host, and using up excess CO_2 to enhance calcification by the coral. Zooxanthellae are found in other reef organisms, including giant clams, and the tiny foraminifera, amoeba-like organisms (Order Sarcodina) with calcareous skeletons that create substantial amounts of the sand on coral reefs and nearby white-sand beaches. Much of the biology and ecology of zooxanthellae is poorly known.

Paleoecology

Structural coral reefs are forms of ‘biogenic reefs,’ distinct geomorphological structures constructed by living organisms. Biogenic reefs have existed in various forms since approximately 3.5 billion years ago, at which time cyanobacteria began building stromatolites (**Figure 6**). Bioherms, biogenic reefs constructed from limestone produced by shelled animals, became prominent by 570 million years ago. During the mid-Triassic, the Jurassic and early Cretaceous periods (roughly 200–100 million years ago), scleractinian corals had become significant components of coral–algal–sponge bioherms. Some of these corals may have included zooxanthellae. However, by the mid-Cretaceous, rudist bivalves dominated shallow-water reefs, and scleractinian corals were mainly restricted to deeper shelf-slope environments. This may have been due to seawater chemistry or competition with rudists or both. The massive extinction at the end of the Cretaceous, which ended the reign of dinosaurs on land, also led to the extinction of rudists. Many scleractinian corals survived in their deeper habitats, and evolved into most of the modern genera by the Eocene. However, CO_2 concentrations in the atmosphere

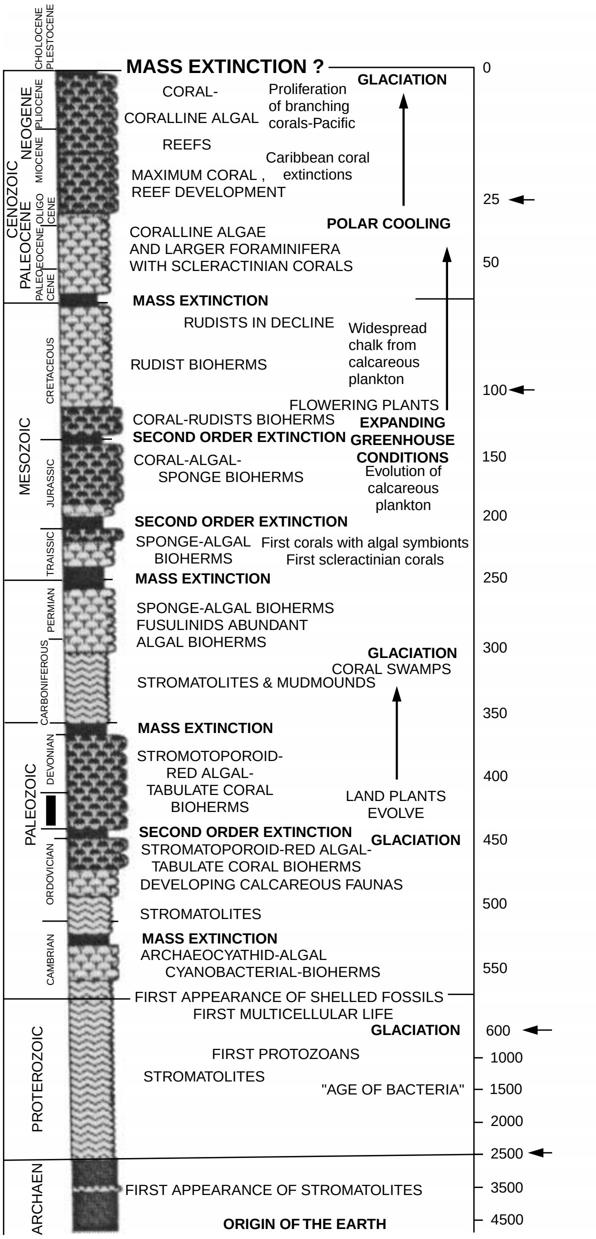
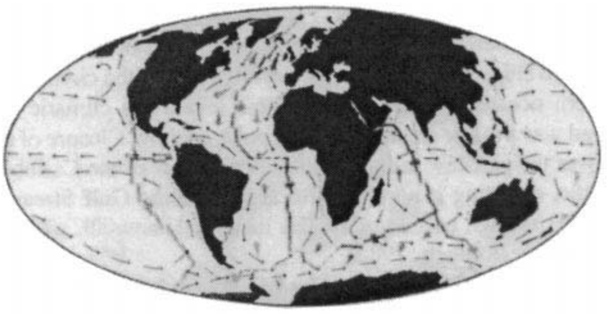


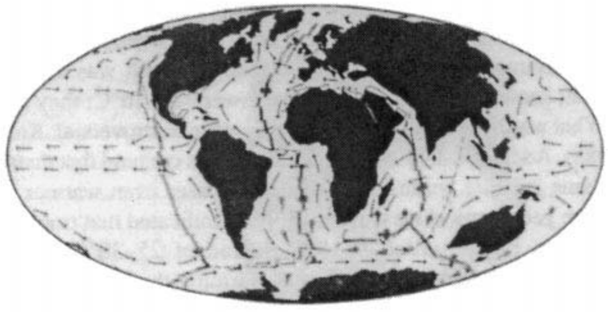
Figure 6 Geological time-scale (in thousand years) highlighting biogenic reef development. Arrows denote changes in scale. (Adapted from Hallock, 1989.)

were high at the time, apparently inhibiting reef development by aragonite-producing corals. Instead, major limestone deposits of the time were formed by calcite-producing organisms such as larger foraminifera (including the limestones from which the Egyptian pyramids were later to be built) and red coralline algae. Calcite is less stable over time than aragonite, but can form in waters of higher CO_2 concentration. Major reef-building by stony corals and their associates did not occur until the middle to late Oligocene. By then, CO_2 concentrations were falling and sea water was warming in tropical areas, whereas at high-latitudes it became cooler. By the late Oligocene, Caribbean coral reefs achieved their greatest development, and by the early Miocene, coral reefs globally had extended to beyond 10° north and south.

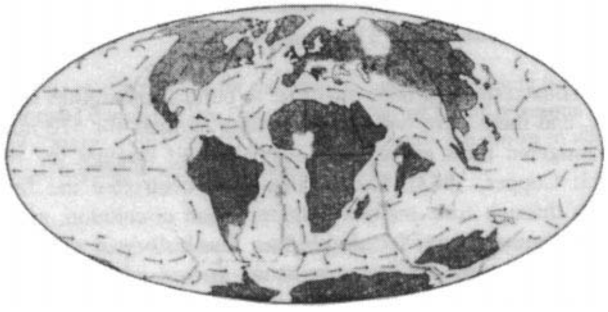
During the late Eocene and early Oligocene, tropical oceans were openly connected, in a system of equatorial waterways known as the Tethys Sea. During this period, most scleractinian corals were cosmopolitan. The upward movements of Africa and India restricted circulation, particularly with the closure of the Qatar arch in the Middle East around the time of the Oligocene–Miocene boundary (**Figure** 7). The Central American passageway became restricted, but did not close until the middle Pliocene. However, nearly half of the Caribbean coral genera became extinct at the Oligocene–Miocene boundary, and many more disappeared during the Miocene. Larger foraminifera suffered similar extinctions. Far less dramatic extinctions occurred in the Indo-Pacific.



EARLY PLIOCENE



MIDDLE OLIGOCENE



MIDDLE PALEOCENE

Figure 7 Major tectonic movements and inferred patterns of major currents since the Paleocene. Gradually, the circumglobal waterway of the Paleocene, the Tethys Sea, was closed off, resulting in regional extinction of coral reef organisms. This process explains many of the differences in biodiversity now seen among the world's coral reefs. (Adapted from Hallock, 1997.)

Reef Geomorphology

Charles Darwin proposed that atolls were formed by a process involving the sinking of islands (**Figure** 8). He noted that most high islands in the Pacific were the tops of volcanic cones. A rocky, volcanic island would tend to form fringing reefs around its shores. Should the island begin to sink, the highly oxygenated outer edges would be able to maintain themselves at the sea surface, while the less actively growing reef flats would tend to sink, forming lagoons defining barrier reefs. Eventually, a sinking cone would disappear altogether, leaving a lagoon in the midst of an atoll. The feasibility of this explanation was confirmed by the mid-twentieth century when drilling on Enewetak and Bikini reefs yielded signs that the atolls were perched over islands that had gradually subsided over thousands of years.

Modern researchers have identified a variety of explanations for the morphology of various reefs. Variations in relative sea level have had profound influences on most structural coral reefs. Few coral reefs are believed to have exhibited continuous growth prior to 8000 years ago, and most are considerably younger. Coral reefs located on extensive continental shelf areas, such as the Florida reef tract and the vast shelf areas off the Yucatan and peninsular south-east Asia, grow on substrates that were generally far inland during the previous ice age.

The three-dimensional shapes of many coral reefs have been highly influenced by underlying topography, often an ancient reef. Wind, storms, waves,

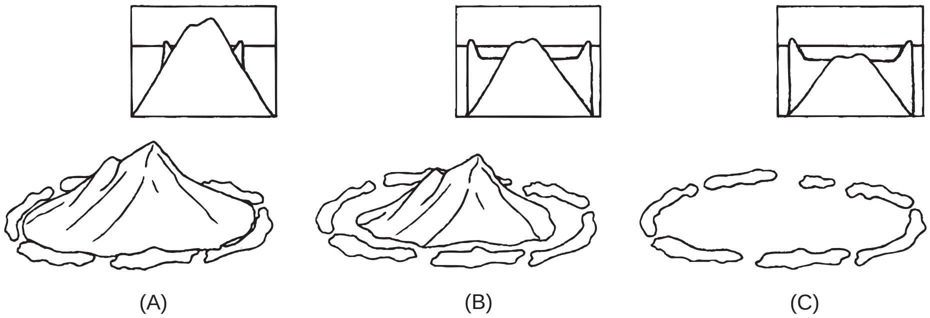


Figure 8 Stages in the development of an atoll as envisioned by Darwin. Fringing reefs surrounding a volcano (A) become barrier reefs as the volcano sinks (B) and finally form a donut-shaped atoll (C) Sinking islands and/or rising sea levels do help to explain the structures of many reefs, but other factors have been more important in the case of other reefs. (Adapted from Slafford-Deitsch, 1991.)

and currents have helped to shape many reefs, resulting in tear-drop shapes with broad, raised, steep edges facing predominant winds and currents. The shapes of some reefs are believed to have been particularly dependent on the erosion of much larger blocks of reef limestone during low stands of sea level. It has been demonstrated in the laboratory that small blocks of limestone subjected to rain-like erosion can form many features now identifiable on coral reefs, including lagoons, rifts and ridges, and channels. Evidence has also been found that the ridge and rift structures and some other features of coral reefs can result from collective ecological growth processes as the biota accommodates effects of waves, channeled water, and scouring by sand and other reef matter as calcifying benthic organisms compete for exposure to sunlight. It has been suggested that the double lagoon structure of the Atoll reef off Mindoro, Philippines, resulted from coral reef growth around the subsurface rim of a volcanic crater. Drilling on some reefs has demonstrated continuous growth for 30 m or more. On other reefs, little or no substantial calcification has occurred, the extreme case being nonstructural coral communities.

The Hawaiian and Line Islands are part of a vast chain of islands formed as a tectonic plate has drifted north and west across the Pacific. Volcanic lava has tended to erupt in a fixed 'hot-spot', forming volcanic islands one after the other. As the islands have drifted north, they have subsided gradually into deeper waters until coral growth has ceased. This process has had a strong influence over the structure of coral reefs along these islands and seamounts. However, at smaller scales, coral reefs along the coasts of the Hawaiian islands also show the effects of heavy storm action, exhibiting mound-like features at the sea surface often dominated by calcareous algae, and sometimes broad platforms which produce the famous surfing waves of the islands.

Role in Oil Exploration

Coral reefs are generally highly porous, filled with holes, tunnels, and caves of all sizes. The most famous 'blue-holes' of the Bahamas are the vertical seaward entrances of huge cave and tunnel systems formed by erosion at low stands of sea level, through which sea water flows beneath the islands as water through a sponge. Much of the porosity of coral reefs results from incomplete filling of spaces between coral heads during the active growth of the reef.

Much of the world's crude oil comes from ancient coral reefs that have been subsequently overlain with terrigenous (land-based) sediments. Dense, horizontally layered sediments have often trapped oil within the mounds of porous coral reef limestone. In some areas, subsequent tectonic activity has produced faults, and much of the oil has been lost. In other areas, however, the ancient reefs have yielded vast amounts of oil.

In some parts of the world, modern coral reefs have grown in areas where ancient reefs once occurred and were subsequently covered by dense sediments that trapped oil. Thus, it is common to find oil drilling platforms on modern reefs. This has frequently raised environmental concerns, centering on the damage done to modern corals by the construction and associated activities, the occasional spillages of drilling muds of various compositions and the leakage of oil.

Biology

Biogeography

The highest species diversity on coral reefs occurs in the seas of south-east Asia, often referred to as the

Central Indo-West Pacific region. In the Caribbean or Hawaii, there are 70–80 species of reef-building corals. In south-east Asia, there are more than 70 genera and 400 or more species of reef-building corals (**Figure 9**). The diversities of most other groups of reef-associated species, including fish, tend to be higher in south-east Asia than in other regions.

Diversity begins to drop off gradually to the south below Indonesia, and north above the Philippines. The decline eastward is very dramatic, such that only a few species of corals live in Tahiti and the Galapagos. Westward, the decline is only slight; at least 50 genera of corals live along the coasts of East Africa and the Red Sea. There are only a few species of reef-building corals off the coast of West Africa. Species in south-east Asia tend to have very broad ranges, and endemism is higher in peripheral areas such as the central Pacific.

Much of the global pattern of diversity, particularly at the level of genera and families, can be explained in terms of selective regional extinctions following the gradual breakup of the circumglobal Tethys Sea during the Cenozoic. This is well supported in the fossil records of corals, seagrasses and mangrove trees. Although fish fossils are uncommon, there is a highly diverse assemblage of fossil coral reef fish in Italy, a remnant from the Tethys Sea.

However, there is some reason to believe that rates of speciation have been higher in south-east Asia than elsewhere. The evidence is best known for mollusks, and include unusually high ratios of species to genera and particularly highly evolved armament (such as the spines on many murex shells) in this region. There is a myriad of explanations for this potentially higher speciation rate. Two popular explanations, the Pacific island vicariance hypothesis and the basin isolation hypothesis, both involve changes in sea level. In the former hypothesis, high levels of the sea tend to isolate groups of Pacific islands, facilitating speciation. At low sea levels, the species spread to the heterogeneous refugia habitat of south-east Asia and are gradually lost on the less-heterogeneous Pacific islands due to competition from other species. In the latter hypothesis, low stands of sea level, and, more importantly, periods of mountain building, have isolated particular marine basins within south-east Asia in the past, possibly permitting rapid speciation among whole biotas.

Further understanding of these processes must await increased efforts in taxonomy and systematics. The vast majority of coral reef organisms, particularly in the Indo-West Pacific region, have never been formally identified. The ranges of known organisms are poorly known. Furthermore, recent decades have seen a rapid decline in interest in and support for taxonomy and systematics. It is likely that human impacts will result in vast changes to the distributions and abundances of coral reef species long before existing biogeography and ecology have been well understood.

Coral Reef Ecosystem Health

Resilience and phase shifts Most coral reefs are subjected to periodic disturbances, such as storms. The ability of an ecosystem to maintain constancy in terms of ecological functions and in the abundances and distributions of organisms is ecological resistance. The capacity of an ecosystem to revert to a previous state (or near to it) in terms of these characteristics is ecological resilience. Terms such as ecosystem health, integrity, and stability usually infer degrees of resistance and resilience. Because profound changes often occur to a coral reef following a perturbation such as a storm, there is increasing focus on the resilience of a coral reef.

Many coral reefs have been known to undergo losses of coral cover from greater than 50% to less than 10%, and then to recover to the former level within 4–10 years. Naturally, in reefs in which colonies may have been decades or centuries old, the age structure of the corals present have often been disrupted. This, in turn, may affect resilience to future perturbations, as certain corals are believed to exhibit higher fecundities in older colonies.

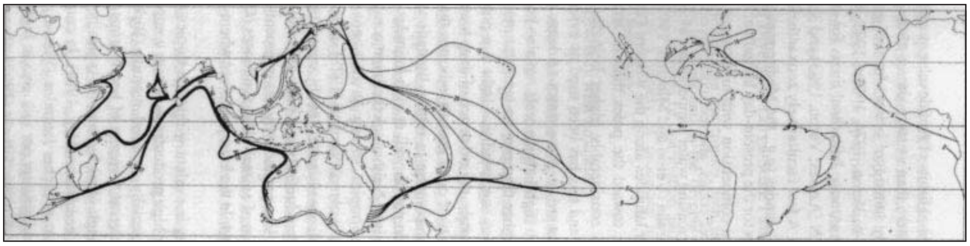


Figure 9 Patterns of generic diversity is scleractinian corals. Contours were estimated from generic patterns and existing data on species distributions. (from Veron 1993; reprinted with permission of the author.)

Some coral reefs do not seem to return to high levels of coral cover after a perturbation, especially if they have been subsequently overgrown by fleshy macroalgae. Human intervention, in the form of increased eutrophication and the removal of herbivorous fish and invertebrates, are suspected to favor the growth of macroalgae following perturbations. Reefs around Jamaica have shown little recovery in more than a decade following coral damage by a hurricane, and both forms of intervention are suspected of being causes of this loss of resilience. Widespread losses of resilience are a concern throughout most coral reef areas.

Reef interconnectivity

Most coral reef organisms undergo pelagic life stages before settling into a reef community. Most corals live as planulae for a few hours to a few days before setting, although longer periods have been recorded. The average benthic invertebrate spends roughly two weeks in waterborne stages, but some survive for months. The average coral reef fish appears to require nearly a month before settling, and many require two months.

The pelagic stages are by no means passive, and although the sizes are very small, the organisms may be adapted to swim into currents and eddies that facilitate their retention or return to particular reefs or groups of reefs. Their success in doing so is believed to depend on factors such as reef geomorphology and the nature and predictability of local oceanography. Analyses indicate that some fish populations regularly exchange genetic material over thousands of kilometers. Although most coral-reef populations are believed to be replenished each year from local progeny, a severely depleted reef may be restocked to some degree from other reefs. This process is crucial to the problem of resilience, and is an active area of controversy and research. The results of this work may have profound implications for the design of marine protected areas, for international agreements on the coordination of management schemes, and for the regulation of harvesting on coral reefs. Furthermore, climate change is likely to alter local oceanographic processes, and has important implications for reef management as such disruptions occur.

Coral Reef Management

Disturbances

Various types of perturbations have affected coral reefs with increasing frequency within recent decades. Some of these are clearly directly related to human activities, whereas others are suspected to be the indirect results of human interventions.

The majority of coral reefs are located in developing countries. In many of these, crowded low-income human populations increasingly overfish, often reducing herbivorous fish and invertebrates, thereby decreasing reef resilience. In a process known as Malthusian overfishing, social norms break down and fishers turn to destructive fishing methods such as the use of poisons and explosives to capture fish.

Organic pollution from coastal habitations and agricultural fertilizing activities are common along coastlines. Runoff from deforested hillsides, mining operations, and coastal construction often contains materials that favor macroalgal growth, and silt and mud that restrict light to zooxanthellae, abrade reef benthos or bury portions of coral reefs entirely.

Increasingly common outbreaks of the coral-eating crown-of-thorns starfish, *Acanthaster planci*, may be related to reductions in predators, such as lethrinid fishes. During 1997–98, a worldwide epidemic of coral bleaching occurred, in which the zooxanthellae of many colonies were expelled and high rates of coral mortality resulted. The cause was unusually warm patches of sea water associated with a strong El Niño event, which some believe to be related to increasing levels of atmospheric CO_2 and global warming. A more controversial suggestion is that the increasing CO_2 levels will cause acidification of the oceans sufficient to result in the net erosion of some coral reefs, especially at high latitudes. Although there have recently been major epidemics of diseases killing corals and associated organisms in western Atlantic reefs, only certain coral diseases appear to be directly linked to stress from human activities.

Assessments

Efforts are underway to gather empirical information on coral reefs via the quantification of benthic organisms and fish by divers. These efforts are being supplemented by the use of remotely sensed data from satellites, space shuttles, aircraft, ships, manned and unmanned underwater vehicles. The usefulness of these approaches ranges from identifying or mapping reefs, to quantifying bleaching and disease. A global database, ReefBase, has been developed by the International Center for Living Aquatic Resources Management (ICLARM) to gather together existing information about the world's reefs and to make it widely available via CD-ROM and the Internet.

Integrated Coastal Management

Management is a process of modifying human behavior. Biophysical scientists can provide advice and predictions concerning factors such as levels of fishing pressure, siltation, and pollution. However, the management decisions must account for social, cultural, political, and economic considerations. Furthermore, almost all management interventions will have both positive and negative effects on various aspects of the ecosystem and the societies that impact it and depend upon it. For example, diverting fishers into forestry may lead to increased deforestation, siltation, and further reef degradation.

It is increasingly recognized that effective management is achieved only through approaches that integrate biophysical considerations with socioeconomic and related factors. Balanced stakeholder involvement is generally a prerequisite for compliance with management decisions. The field of integrated coastal management is rapidly evolving, as is the set of scientific paradigms on which it is based. To a large degree, the future of the world's coral reefs is directly linked to this evolution.

See also

Air–Sea Transfer: N_2O, NO, CH_4, CO. Autonomous Underwater Vehicles (AUVs). Beaches, Physical Processes affecting. Carbon Cycle. Carbon Dioxide (CO_2) Cycle. Cenozoic Climate – Oxygen Isotope Evidence. Cenozoic Oceans – Carbon Cycle Models. Coral Reef Fishes. Diversity of Marine Species. El Niño Southern Oscillation (ENSO). Eutrophication. Fish Feeding and Foraging. Geomorphology. History of Ocean Sciences. Lagoons. Macrobenthos. Mangroves. Manned Submersibles, Shallow Water. Nitrogen Cycle. Past Climate From Corals. Pelagic Biogeography. Remotely Operated Vehicles (ROVs). Rocky Shores. Sandy Beaches, Biology of. Satellite Oceanography, History and Introductory Concepts. Satellite Remote Sensing of Sea Surface Temperatures. Sea Level Change. Sea Level Variations Over Geologic Time. Ships. Storm Surges.

Further Reading

Birkeland C (ed.) (1997) *Life and Death of Coral Reefs*. New York: Chapman and Hall.

Bryant D, Burke L, McManus J and Spalding M (1998) *Reefs at Risk: a Map-based Indicator of the Threats to the World's Coral Reefs*. Washington, DC: World Resources Institute.

Davidson OG (1998) *The Enchanted Braid: Coming to Terms with Nature on the Coral Reef*. New York: John Wiley.

Holliday L (1989) *Coral Reefs: a Global View by a Diver and Aquarist*. London: Salamander Press.

McManus JW, Ablan MCA, Vergara SG *et al.* (1997) *ReefBase Aquanaut Survey Manual*. Manila, Philippines: International Center for Living Aquatic Resources Management.

McManus JW and Vergara SG (eds) (1998) *ReefBase: a Global Database of Coral Reefs and Their Resources*. Version 3.0 (Manual and CD-ROM). Manila, Philippines: International Center for Living Aquatic Resource Management.

Polunin NVC and Roberts C (eds) (1996) *Reef Fisheries*. New York: Chapman and Hall.

Sale PF (ed.) (1991) *The Ecology of Fishes on Coral Reefs*. New York: Academic Press.

Stafford-Deitsch J (1993) *Reef: a Safari Through the Coral World*. San Francisco: Sierra Club Books.

Veron JEN (1993) *A Biogeographic Database of Hermatypic Corals. Species of the Central Indo-Pacific, Genera of the World*. Monograph Series 10. Townsville, Australia: Australian Institute of Marine Science.

CORAL REEF AND OTHER TROPICAL FISHERIES

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Introduction

Until recently studying and reporting on tropical fisheries tended to be done in the context of development aid projects initiated with the perception that the transfer of technology, management approaches, and scientific models to tropical countries would assist them in a way that would help to raise the standard of living and the food supply. Many of these aims have been achieved, although not necessarily through such North/South transfer but rather through local growth of the preexisting fisheries, and through access rights granted to distant water fleets of developed countries to operate in the waters of developing countries. These developments have turned tropical and reef fisheries from the marginal activities they were in the 1960s and 1970s to key players in international fisheries. Catches in tropical