Coral habitat in the Hawaiian Islands (NOAA).

CHAPTER 1. CORAL REEF ECOLOGY

Key points

- There are four major reef types (patch, fringing reefs, atolls, barrier).
- Reef-building corals generally require high light, high oxygen, low turbidity, low nutrients, warm seawater temperature (18-30°C), and open ocean salinity (33-36 parts per thousand; ppt).
- Coral reefs depend on currents for dispersal and accumulation of planktonic spores, larvae and juveniles.
- Most corals reproduce annually during spawning events that are synchronized by seasonal seawater temperature changes, lunar cycle, and time of day.
- Stony corals have many growth forms, including massive, branching, plate-like, finger-like, and encrusting; different growth forms may respond to environmental impacts differently.
- Growth rates in corals vary among species, with branching corals growing faster than massive corals.
- Predation, competition, diseases, and storms are the primary reason for coral reef death by natural causes.
- Anthropogenic sources of reef mortality include sedimentation, overfishing, and pollution.
- Coral reefs are tremendously important economic and natural resources, supporting numerous fisheries, recreational, and tourism activities, and protecting shorelines.

Types of reefs, geographic distribution, and environmental influences

There are four major reef types (Figure 1.1):

patch reefs - small, isolated formations

fringing (or apron) reefs - reefs directly bordering shorelines

barrier reefs - former fringing reefs separated from the shoreline by a lagoon

atolls - former fringing reefs encircling submerged volcanic islands

Reef communities are reefs in the earliest developmental stages where structural accretion has either not yet occurred or is being continually interrupted by environmental disturbance. Coral communities also occur in areas where conditions are not conducive to reef development, but where reef coral species can survive. Zones in each reef type (Figure 1.2) are defined by their depth and wave exposure. Coralline algae and occasional encrusting or low-profile corals dominate the reef crest at 0-2 meters (m) deep, the area of highest wave energy. Seaward of and below the reef crest, the fore reef consists of buttresses and channels (spurs and grooves) that dissipate wave forces and allow for offshore transport of reef material. The fore reef zone (~2-10 m deep) generally supports the highest coral diversity and coverage. The outermost and deepest zone is the reef slope, descending from the fore reef to the lower depth limits of coral development (~100 m). Protected from heavy wave action, reef flat and back reef zones are calmer environments that support growth of coral, algae, and seagrass communities. The greatest reef development occurs on the leeward, protected sides of islands or atolls, where there is less erosion from wave action.

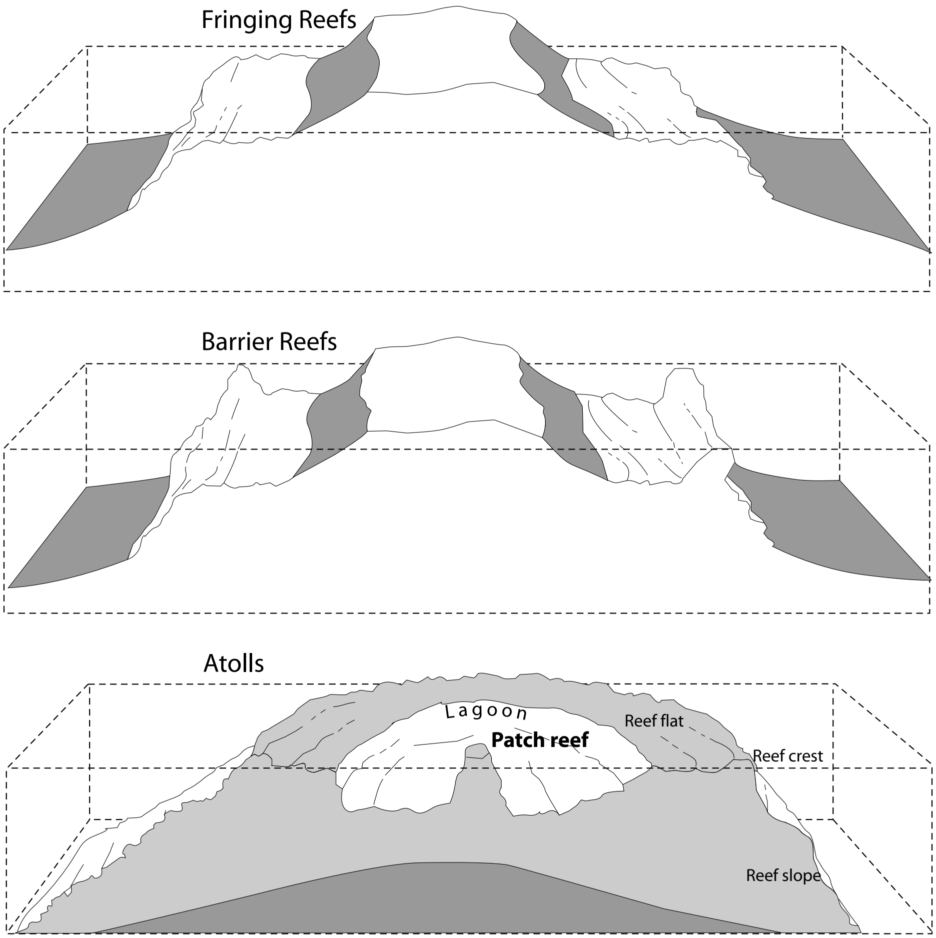

Figure 1.1. Coral reef types, including atoll, fringing, barrier and patch reefs

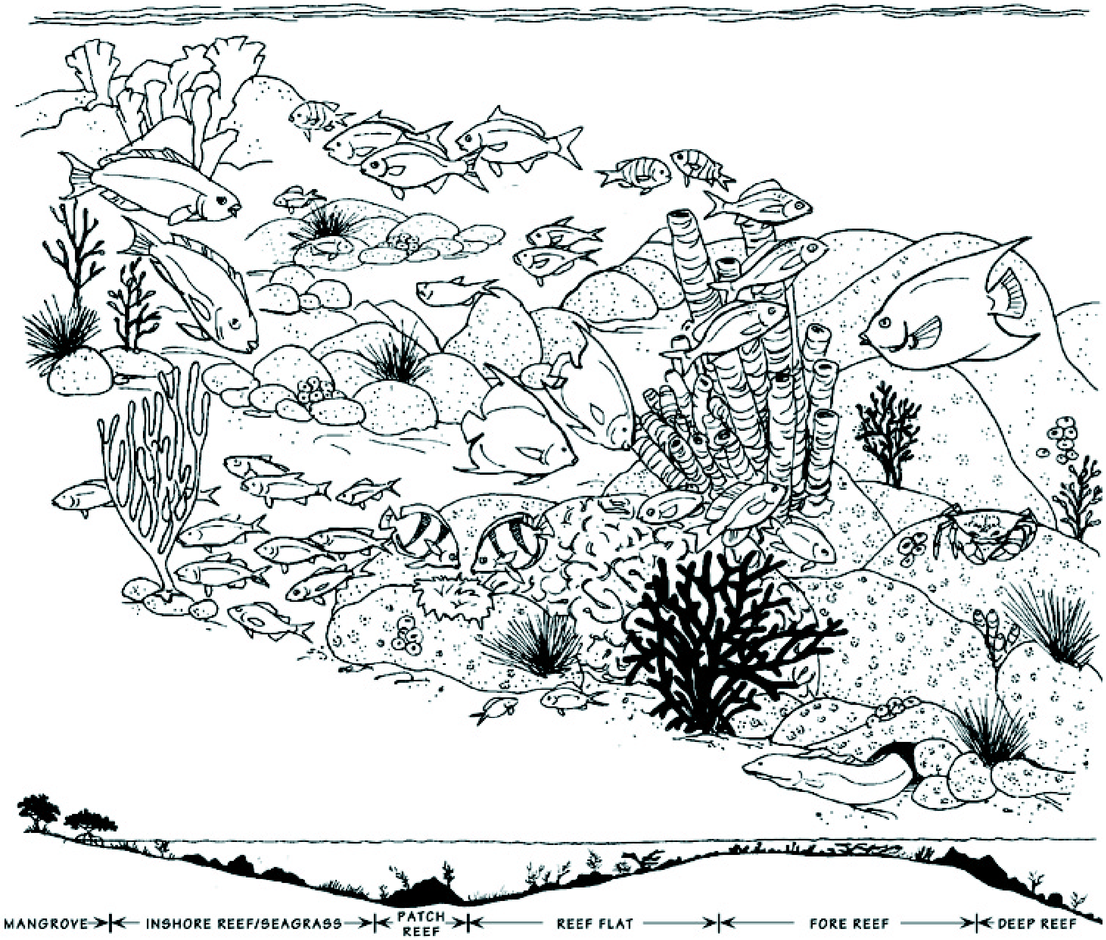

Figure 1.2. Example of a fore reef community and reef zones, including fore reef, reef flat and back reef

Reefs may begin on pre-existing subsea platforms, such as volcanoes or shoal banks, but become coral reefs by continuous buildup of the remains of bottom-dwelling marine animals and plants that grow in shallow tropical and sub-tropical environments. Calcium carbonate from skeletons and sediments accumulate at up to a few centimeters each year, over thousands of years, to form reefs. These reefs provide habitat for some of the most biologically diverse ecosystems on Earth.

Reef-building corals require high light, high oxygen, low turbidity, low nutrients, warm seawater (18-30°C), and open ocean salinity (33-36 ppt). Exceptions generally represent sub-optimal conditions. For example, reef-building corals in Hawai'i have been reported living under very low light conditions more than 150 m deep. Corals may survive short periods of stress during extreme low tides, periodic flooding with fresh water, and suspended sediments by retracting polyps and increasing mucus production. Corals may even recover from stress-induced bleaching by gradually replenishing zooxanthellae in their tissues. The metabolic costs of survival under stressful conditions decrease growth and reproductive potential.

The rotation of the earth and the Coriolis effect generate major ocean currents. These currents move clockwise in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere. Equatorial currents and counter-currents, and dominant northerly and southerly flows mix and disperse larvae across geographic areas within ocean basins. Wind and tide-driven currents exert more local effects on water movement and dispersal.

Coral reefs depend on currents to bring food and nutrients, and to disperse and accumulate planktonic spores, larvae, and juveniles that recruit to and replenish populations and species. Periodic changes in prevailing currents (e.g., during El Niño-Southern Oscillation events) may interrupt normal processes, but may also bring recruits from populations that are normally downstream of a particular reef area.

Reef biodiversity

Thousands of animal and plant species are associated with coral reefs. Scleractinian corals are the dominant structural reef-builders on most reefs. However, many species of algae and other organisms, like snails, oysters, clams, worms, and sponges, produce calcium carbonate skeletons. When these skeletons accumulate in the interstices of the reef, they cement the structure together over time. Relatives of scleractinian corals are the gorgonians—octocorals such as sea fans, sea plumes, sea whips, and leather corals. Referred to collectively as "soft corals," octocorals either lack a skeleton or produce a reduced, flexible skeleton. Sea anemones are other coral relatives, commonly found on reefs in a variety of sizes and habitats. Yet another coral relative are the zoanthids, commonly found atop reef flats or in the intertidal zone.

Coral reefs provide food and shelter to a wide range of fish and invertebrates, including crustaceans (crabs, lobsters, shrimp), echinoderms (sea urchins, sea cucumbers, brittle stars, crinoids), boring, encrusting, and upright sponges, molluscs (bivalves, snails, octopus, nudibranches), and worms belonging to dozens of phyla. Fish range from the smallest gobies to 2 m-long groupers or sharks. Sea turtles shelter in reef overhangs and forage for sponges and other food items; manatees feed in reef-associated seagrass beds.

Associated habitats: seagrasses and mangroves

Seagrass beds are often found in sandy patches in back reef and reef flat environments. Their root systems stabilize sediments and their high primary productivity supports detritus-based food webs important to omnivorous reef organisms. Closer to shore, mangroves protect nursery areas for juvenile reef fish, crustaceans, and molluscs. They also serve as filtration systems for coastal runoff and protect shorelines from erosion. In Hawai'i, however, mangroves were introduced in the early 1900s and have spread rapidly among the main islands. Many people feel that in Hawai'i they are a weedy pest species because they have altered and now dominate many coastal areas.

Coral physiology

An individual coral, or polyp, is a sac-shaped organism with a central mouth surrounded by a ring of tentacles. Like their cnidarian relatives—sea anemones, jellyfish, and hydroids—corals have a simple body plan consisting of only two tissue layers: ectoderm and gastroderm. In corals, the ectoderm secretes a calcium carbonate cup (corallite) into which the polyp may retract. Polyp sizes vary from <1 mm to many centimeters in diameter. Although some coral species consist only of single polyps, most corals form colonies consisting of thousands of interconnected polyps. All polyps in a colony are genetically identical (clones) because they all budded from the original founding individual.

Corals may be carnivorous, capturing small prey that become trapped on their mucus-covered surfaces or entangled by specialized stinging cells on the tentacles. They absorb dissolved organic materials from surrounding waters, and also produce their own food. Tiny, single-celled algae called zooxanthellae live within the coral cells and generate energy-rich compounds through photosynthesis. This "food" is translocated to the coral host, providing the majority of its energy and carbon requirements. The key to the ecological success of reef-building corals, this symbiotic relationship requires adequate, but not excessive sunlight for the algae to be productive through photosynthesis.

Corals are sedentary marine animals with no specialized organs or sensory systems. Instead, corals use passive diffusion through their thin living tissues to obtain oxygen and expel waste products. They produce mucus for protection and to clear fine debris from tissue surfaces. A diffuse nerve network connects polyps within a colony and allows response to physical and chemical stimuli.

Coral reproduction

Corals reproduce sexually and asexually using a wide repertoire of strategies. For example, gametes (eggs and sperm) are produced within the mesenteries that partition the coral polyp. A coral may be either male or female (gonochoric), or hermaphroditic, with a mixture of male and female polyps within a colony or with male and female gonads within a single polyp. In further evidence of their reproductive flexibility, some polyps or entire colonies may change sex from year to year.

Gametes may be released (broadcast) into the surrounding seawater to fertilize or, in some instances, eggs are retained and fertilized in the polyp where they are brooded until they have developed into larvae called planulae. Coral eggs may contain maternally inherited zooxanthellae at the time of their release, or they may acquire them from the environment before or soon after settlement. Planulae swim weakly using cilia (hair-like motor appendages). Ocean currents transport planulae for several days, weeks, or even months before settlement. This planktonic dispersal of larvae may seed reefs far from the parent colonies.

Most corals reproduce annually during spawning events that are synchronized by seawater temperature changes, lunar cycle, and time of day. Mass spawning events in which most corals

Table 1.1. Spawning mode and occurrence in some common corals are shown below(G=gonochoric, H=hermaphroditic, S=broadcast spawner, B=brooder)

Hawaii	Sex	Mode	Month	Lunar Phase	Time
Porites compressa	**G**	**S**	**Jun-Aug**	**full**	**2300**
Porites lobata	**G**	**S**	**Jul-Aug**	**_**	**varies**
Fungia scutaria	**G**	**S**	**Jul-Sep**	**full**	**1700**
Pocillopora meandrina	**H**	**S**	**Apr-Jun**	**full**	**0730**
Pocillopora damicornis	**H**	**B**	**monthly**	**varies**	**varies**
Montipora dilitata	**H**	**S**	**Jun-Aug**	**full**	**2200**
Montipora capitata	**H**	**S**	**Jun-Jul**	**new**	**2100**

Florida	Sex	Mode	Month	Lunar Phase	Time
Porites porites	**G/H**	**B**	**Nov-Feb**	**_**	**_**
Montastrea annularis	**H**	**S**	**Aug-Sep**	**_**	**2200**
Montastrea cavernosa	**H**	**S**	**Aug-Sep**	**_**	**2100**
Montastrea faveolata	**H**	**S**	**Aug-Sep**	**_**	**2000**
Acropora palmata	**H**	**S**	**Aug**	**_**	**2300**

release gametes over a few nights occur in many reefs (e.g., Flower Garden Banks, Tortugas, the Great Barrier Reef), while in other regions, different coral species spawn at different seasons, moon phases, or times. Because eggs are generally lipid-rich and positively buoyant, whole slicks of gametes are often seen at the surface during and after spawning events.

Corals commonly reproduce both asexually and sexually. Fragments of colonies broken by wave action or buds produced by individual polyps may re-cement and survive independently on the reef. Thus, numerous colonies on a reef may represent clones of single individuals. Branching growth forms are more prone to fragmentation than are encrusting or massive species. There are often significant geographical differences in how well a species can reproduce from fragments, and these may be exacerbated by other environmental factors like water quality.

Growth and longevity

Corals grow at different rates depending on the morphology of the colony and the environmental conditions. Branching species with linear extension rates of up to 20 cm/year grow faster than massive colonies (~1 cm/year); species with dense skeletons grow slower than more fragile species. Colonies living in areas where high wave energy abrades and breaks coral show more compact or encrusting growth forms than their relatives living in calmer locations.

Some species of corals (e.g., *Pocillopora meandrina*, many *Acropora spp.*) grow to a specific size (~50 cm, 10-15 years for *P. meandrina*) and die. Other corals (e.g., massive *Porites* and *Montastrea*) appear to be able to survive and grow indefinitely. Colonies of *Porites evermanni* near Kealakekua on the island of Hawai'i are over 20 m in diameter and were large when Captain Cook sailed into the Hawaiian Islands more than 200 years ago. Thus, colonies of some coral species may be potentially immortal. However, the longevity of individual polyps in massive *Porites* is on the order of 5-7 years as determined by growth tracks in skeletal sections.

Species diversity

The degree of coral biodiversity varies geographically, ecologically, historically, and geologically. The number of coral species on Florida and Hawaiian reefs is similar at 45 and 52 species, respectively. However, there are more than 70 reef-building coral species in the Caribbean; counting deepwater and non-reef-builders brings this number to well over 100. In the main Hawaiian Islands, there are an additional 29 non-reef building deepwater species, and at least 10 other species are found in the Northwest Hawaiian Islands that do not occur on main island reefs.

Soft corals, sea whips, and sea fans (octocorals), and massive colonies of star coral (*Montastrea spp.*) and brain coral (*Colpophyllia natans*) dominate reefs in Florida and the Caribbean. Before bleaching and disease outbreaks of the 1980s-1990s, thickets of elkhorn (*Acropora palmata*) and staghorn (*A. cervicornis*) corals were common shallow-reef species but have now been largely replaced in some areas by lettuce coral, *Agaricia spp.* Massive *Porites* (*P. lobata* and *P. evermanni*), branching *Porites* (*P. compressa*), encrusting (*Montipora spp.)*, and cauliflower and lace coral (*Pocillopora meandrina* and *P. damicornis*) dominate Hawaiian reefs.

Geographic variability

Very different assemblages of dominant organisms characterize Atlantic/Caribbean and Pacific reefs. Associated habitats are quite different as well: while seagrass beds and mangroves are common and important components of Atlantic/Caribbean coastal ecosystems, they are generally much less abundant on Pacific islands. For example, Hawai'i has a single species of seagrass that, while important as a sediment stabilizer and as an important food item for sea turtles, is a very small plant with blades less than 2 cm long. In contrast, seagrasses in Florida and elsewhere have large morphology and diverse community structure with three primary species.

Another important distinction between Florida and Pacific island reefs is in their continental vs. oceanic derivation. While seagrass beds and reef communities extend in relatively shallow water for many kilometers from Florida shorelines, Pacific island reef slopes drop steeply from nearshore to hundreds of meters down in fairly short linear distances. One result of this is a much higher level of species uniqueness seen on Pacific Island reefs. Hawai'i has among the highest endemism rates for coral reef organisms in the world with roughly 25% of all the animals seen on Hawaiian reefs being unique to Hawai'i.

Mortality, disease, and physical impacts

Corals can die from any number of causes. Predators include both fish and invertebrate feeders. On Atlantic and Caribbean reefs, parrotfish, damselfish, coral-eating snails, and fireworms are primary coral predators. In the Pacific, parrotfish, blennies, damselfish, butterflyfish, and puffers are major fish predators on corals; the Crown-of-Thorns seastar (*Acanthaster planci*) occasionally undergoes sudden population expansions that can inflict significant damage to corals. Competition for space with algae, sponges, and other sedentary, benthic organisms may result in partial or complete coral mortality. Regional losses of significant herbivorous grazers like the urchin *Diadema* are thought to significantly impact competition for coral settlement and recruitment.

Diseases that affect corals include relatively recent and devastating outbreaks of White (WBD) and Black Band Disease (BBD) and others (aspergillosis, "white pox," "white plague," "yellow band"), particularly in Florida and the Caribbean. WBD affects only acroporid corals, while BBD has been reported from six scleractinian species; "white plague Type II" has been reported from 17 coral species in the Florida Keys. WBD and BBD are generally infrequent and sporadic on reefs at one point in time, with some corals affected while adjacent colonies are not, but cumulative tissue loss of up to several millimeters per day may kill many relatively slow-growing coral species.

While the source of most coral diseases is largely unknown, some progress has been made. The major component of BBD is *Phormidium corallyticum*, a photosynthetic cyanobacterium. Here, coral tissue is killed by lack of oxygen and exposure to hydrogen sulfide produced by the bacterium and associated microorganisms. BBD is more common on reefs subject to sedimentation, high nutrients, and elevated seawater temperatures. Aspergillosis, a disease that causes tissue death and disintegration of the axial skeleton of sea fans, is caused by an organism similar to the terrestrial fungus, *Aspergillus sydowi*, which some researchers believe may arise from spores and iron enrichment borne by dust transported via the jet stream from Saharan Africa.

Storms and high wave energy abrade, break, and bury shallow-water colonies as well as those downslope. Storm-associated sediment runoff and freshwater flooding may also smother or kill corals, particularly those in shallow and nearshore waters. Most corals live within a few degrees of their upper temperature tolerance range. Recent instances of elevated seawater temperatures have killed large number of corals, sometimes more than 100 m deep. Such mortality is preceded by a rapid loss of the pigmented symbiotic zooxanthellae from the corals, a stress response known as coral bleaching.

Human uses

Coral reefs are tremendously important economic resources, supporting numerous recreational activities, tourism, fisheries, and protecting shorelines. In Hawai'i, reef-related tourism activities bring an estimated $800 million annually, and employ over 7,000 people. Tourism-related services contribute $1.2 billion to the Florida Keys economy every year. Legal decisions aimed at recovering costs for damage to reef areas have valued reef areas at as much as $2,833 per square meter, based solely on costs of restoration and lost tourism revenues.

Recreational and commercial fishing annually bring many more millions of dollars to Hawai'i, Florida, and other islands or regions with viable reef resources. Subsistence and commercial food harvest from reefs include fish, octopus, lobster, and crab. The U.S. Coral Reef Task Force estimates that the annual value of reef-dependent commercial and recreational U.S. fisheries is over $200 million. A large, growing aquarium trade also depends on reef species; based on collection reports, over 420,000 aquarium fish were exported from Hawai'i alone in 1995.

For further reading

Antonius, A. 1985. Coral diseases in the Indo-Pacific: a first record. *Marine Ecology 6*:197-218.

Babcock, R. and A. Heyward. 1986. Larval development of certain gamete-spawning scleractinian corals. *Coral Reefs 5*:111-116.

Barnes, R. and E. Ruppert. 1994. *Invertebrate Zoology*. New York: Saunders College Publishing. 1089 pp.

Birkeland, C. 1997. *Life and Death of Coral Reefs*. Norwell, Massachusetts: Kluwer Academic Publishers. 536 pp.

Clark, A. and D. Gulko. 1999. Hawai'i's State of the Reefs, 1998. Honolulu: State of Hawaii Department of Land and Natural Resources.

Darke, W. and D. Barnes. 1993. Growth trajectories of corallites and ages of polyps in massive colonies of reef-building corals of the genus *Porites*. *Marine Biology 117*: 321- 6.

Davies, P.S. 1984. The role of zooxanthellae in the nutritive energy requirements of *Pocillopora eydouxi*. *Coral Reefs 2*:181-186.

Dubinsky, Z. 1990. *Ecosystems of the World: Coral Reefs*. New York: Elsevier. 525 pp.

Edmunds, P. 1991. Extent and effect of black band disease on a Caribbean reef. Coral Reefs 10:161-165.

Glynn, P. 1991. Coral reef bleaching in the 1980's and possible connections with global warming. *Trends in Ecological Evolution 6*:175-179.

Grigg, R. 1988. Paleoceanography of coral reefs in the Hawaiian-Emperor chain. *Science 240*:1737-1743.

Gulko, D. 1998. *Hawaiian Coral Reef Ecology*. Honolulu: Mutual Publishing. 245 pp.

Hayes, R. and N. Goreau. 1998. The significance of emerging diseases in the tropical coral reef ecosystem. *Revista de Biología Tropical 46*:173-185.

Humann, P. 1993. *Reef Coral Identification: Florida-Caribbean-Bahamas*. Jacksonville: New World Publications. 239 pp.

Jokiel, P. 1980. Solar ultraviolet radiation and coral reef epifauna. *Science 207*:1069-1071.

Jokiel, P., C. Hunter, S. Taguchi, and L. Watarai. 1993. Ecological impact of a freshwater reef "kill" in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs* 12:177-185.

Kuta, K. and L. Richardson. 1996. Abundance and distribution of black band disease in the northern Florida keys. *Coral Reefs 15*:219-223.

Maragos, J. 1977. Order Scleractinia. Reef and Shore Fauna of Hawaii: Section I. Protozoa-Ctenophora. In: Devaney, D. and L.G. Eldredge (eds.), *Reef and Shore Fauna of Hawaii*, B.P. Bishop Museum Press, Honolulu. pp. 158-241.

Peters, E. 1993. Diseases of other invertebrate phyla: Porifera, Cnidaria, Ctenophora, Annelida, Echinodermata. Pathology of Marine and Estuarine Organisms. Couch and Fournie (eds.), *Diseases of other invertebrate phyla: Porifera, Cnidaria, Ctenophora, Annelida, Echinodermata*. Pathology of Marine and Estuarine Organisms, CRC Press, Boca Raton, Florida.

Richardson, L., W. Goldberg, R. Carlton, and J. Halas. 1998. Coral disease outbreak in the Florida Keys: Plague Type II. *Revista de Biología Tropical 46*:187-198.

Richmond, R. and C. Hunter. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific and the Red Sea. *Marine Ecology Progress Series 60*:185-203.

Santavy, D. and E. Peters. 1997. Microbial pests: coral diseases in the Western Atlantic. *Proceedings 8th International Coral Reef Symposium 1*:607-612.

Mangrove forest in the Florida Keys National Marine Sanctuary (NOAA OR&R)