CHAPTER TWO

The Ocean Divided

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The formation of the Central American isthmus was the pivotal event 1. in the past 10 million years of earth history. Separation of the two 2. oceans stopped the once strong westward flow of water from the Atlantic into the Pacific and gave birth to the Gulf Stream. The resulting strong poleward transport of tropical Atlantic water warmed the North Atlantic and increased precipitation, thereby providing moisture that intensified northern hemisphere glaciation. This triggering of the Ice 3 Age by a distant change in tropical oceanography is one of the most dramatic examples of the sensitivity of global climate to geographical changes in the relation of continents and oceans.

The new barrier also changed the climate and oceanography on both sides of Central America and divided the once continuous tropical American ocean into two ecologically different realms. The eastern Pacific is highly variable and seasonal, with rich *pelagic* (open-sea) fisheries but poorly developed coral reefs, in contrast to the Caribbean, which has near-shore fisheries concentrated largely around extensive coral reefs. All of these systems are now profoundly threatened by man.

Central America is a maritime land, every nation but Belize and El Salvador being bordered by both oceans, and the ratio of coastline to land is the highest in the continental Americas. The differences in the two oceans are therefore of fundamental economic, social, and political importance and have been so for thousands of years.

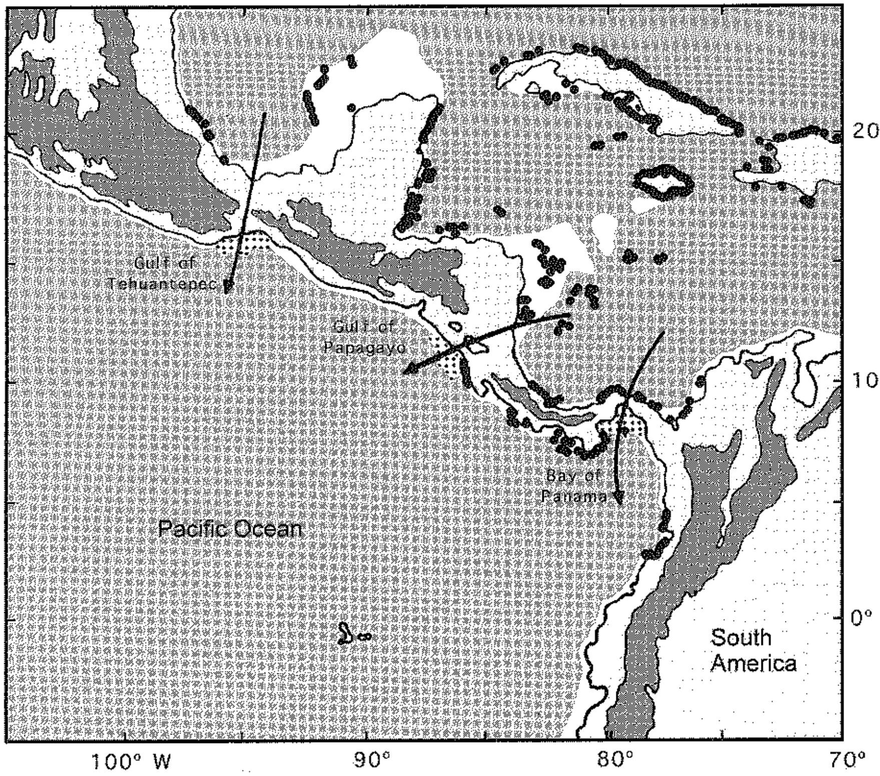
Because of its unique history, Central America is an ideal model for understanding how geographic isolation or connection and environmental change affect life on earth. The dramatic consequences of the connecting of North and South America are well known (see chapter 4). In contrast, the effects of the separation of the Caribbean and eastern Pacific have received much less attention. Fossil species of marine invertebrates from Florida to California are broadly similar until about 5 million years ago but vary afterward. Likewise, chemical analyses of deep-ocean cores from the Caribbean and eastern Pacific demonstrate significant divergence in the temperature and salinity of the sea surface about the time of the final separation of the oceans. Until recently, however, researchers have lacked a precise geological framework in which environmental and biological events might be put in rigorous historical perspective.

In this chapter we compare similarities and differences in marine environments and marine life of the two tropical American oceans that border Central America and how they came to be. In addition to being of intrinsic scientific interest, the results help to explain differences in the vulnerability of the two oceans to human disturbance.

Two Different Oceans

The coastal geography of the two sides of Central America reflects their dissimilar geological origins (see chapter 1). The Caribbean coast is broadly sinuous and forms the western boundary of a semi-isolated sea; maximum distances between Central America and the Greater Antilles are only a few hundred to one thousand kilometers (fig. 2–1). The shelf is narrow along Panama and Costa Rica but widens broadly to more than 200 kilometers off the Nicaraguan and Yucatán peninsulas, whose offshore banks extend with only narrow breaks all the way to Cuba and Jamaica. In contrast, the eastern Pacific coast is comparatively straight and wide open to the Pacific, with the nearest substantial land being located more than 10,000 kilometers to the west. The continental shelf is narrow and closely bounded by the Middle America Trench, which brings deep-ocean conditions within 50 kilometers of the land everywhere except the Bay of Panama (see fig. 2–1).

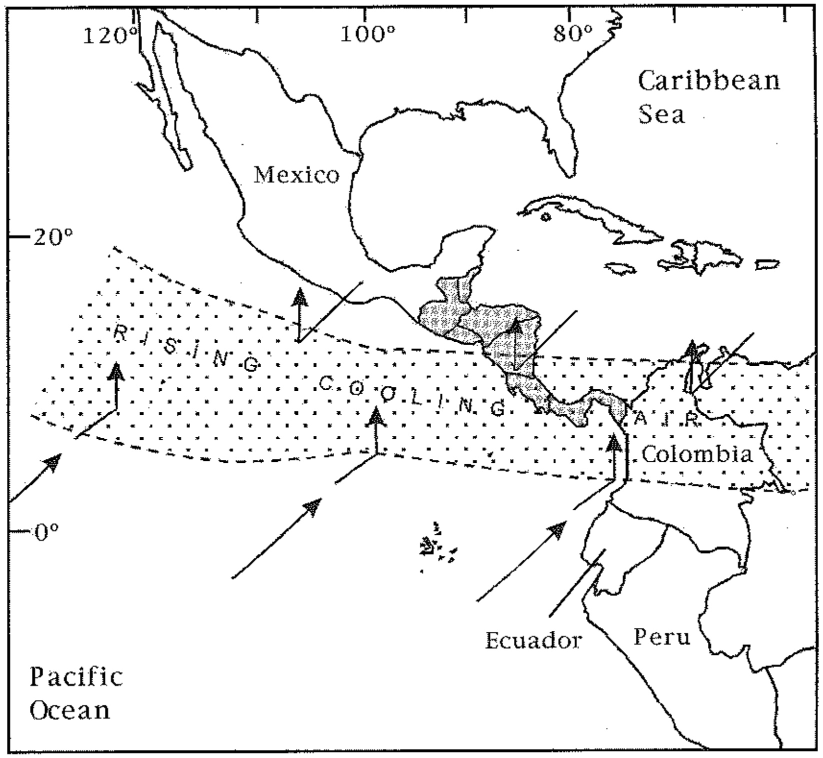
Central America lies in the path of the trade winds, which blow strongly from the northeast to southwest all year. The seasonal climate of the region is determined by the interaction of the trade winds with a large, low-pressure air mass called the Intertropical Convergence Zone. This convergence zone moves northward to sit over Central America from approximately May to December each year (fig. 2–2), interrupting the flow of the trade winds and bringing variably intense rainfall,



2–1. Geography, topography, and distribution of coral reefs and upwelling zones along the coasts of Central America. The Caribbean coast is part of the extensive western Caribbean system of coral reefs (black dots), mangroves, and sea grasses that blankets the coastline throughout most of the region. Arrows indicate passes in the mountains where trade winds blow across the isthmus and cause upwelling, shown by the stipple pattern. White areas are continental shelf between 0 and 200 meters depth; dark gray areas are land above 2000 meters.

which is everywhere greater along the Caribbean slope of the continental divide. In contrast, during the dry season from December to May (fig. 2–3) the Intertropical Convergence Zone lies well south of Central America, so the trade winds blow across the isthmus and precipitation is much less.

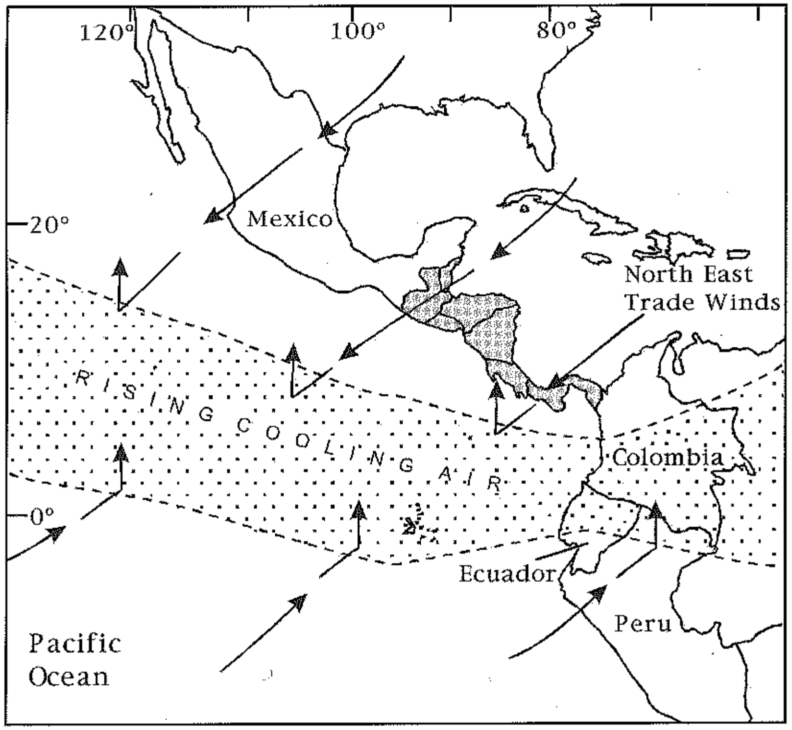
Caribbean coastal waters are warm and salty, with little annual variation in spite of very heavy rainfall most of the year. This constancy is due to the strong, westward flowing Caribbean Current, which bathes the southern Caribbean throughout the year (fig. 2–4). The tidal range is less than 1 meter and generally depends more on local weather than on any regular astronomical cycle. Weak upwelling of nutrient-rich waters



2–2. Meteorological pattern that distinguishes the rainy season in Central America. From about May to December the Intertropical Convergence Zone lies over Central America as shown. In this zone, air from the northeast and southwest trade winds meet and rise. The result is cooling of the air mass, condensation, and widespread rain.

(fig. 2–5) occurs off parts of Venezuela and Colombia, but not along the Caribbean coast of Central America, so levels of nutrients there are very low. Hurricanes occur with increasing frequency, intensity, and devastation northward from Costa Rica to Yucatán. Any particular storm, however, usually affects only a small part of the coast.

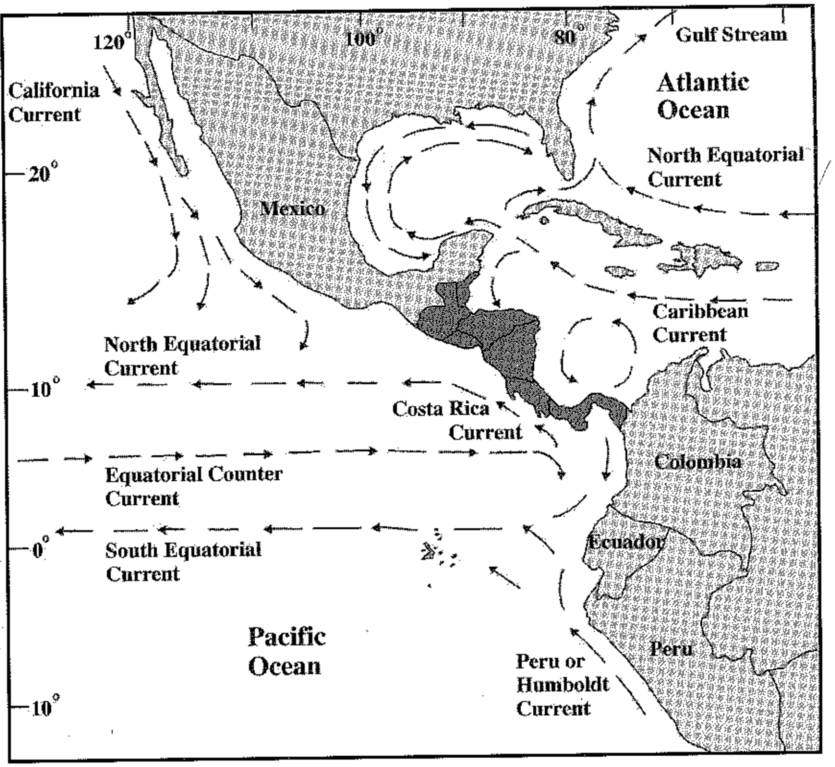
Seasonal climatic and oceanographic fluctuations are much stronger on the Pacific coast than on the Caribbean. This difference is pronounced in areas of wind-induced coastal upwelling adjacent to the Bay of Panama and the Gulfs of Papagayo and Tehuantepec, where the land is low and strong trade winds blowing across these lowland saddles drive the Pacific surface water out to sea (see fig. 2–1). This water is replenished by upwelling of underlying colder, denser water that is very rich in nutrients (see fig. 2–5). Surface seawater temperatures during upwelling may plummet more than 10 degrees in a few days to as low as



2–3. Meteorological pattern that distinguishes the dry season in Central America. From about January to April the Intertropical Convergence Zone migrates to the south, as the earth's axis changes orientation relative to the sun. The northeast trade winds then blow steadily across the Central American isthmus, bringing stable, drier, and less humid conditions.

15 degrees centigrade (pl. 1). Oceanic upwelling also occurs off the Pacific coast of Costa Rica owing to the divergence of the North Equatorial Counter Current. Pacific coastal salinities drop during the rainy season, especially in the Bay of Panama. The daily tidal range is large, reaching 6 meters or more on a regular semidiurnal and lunar schedule.

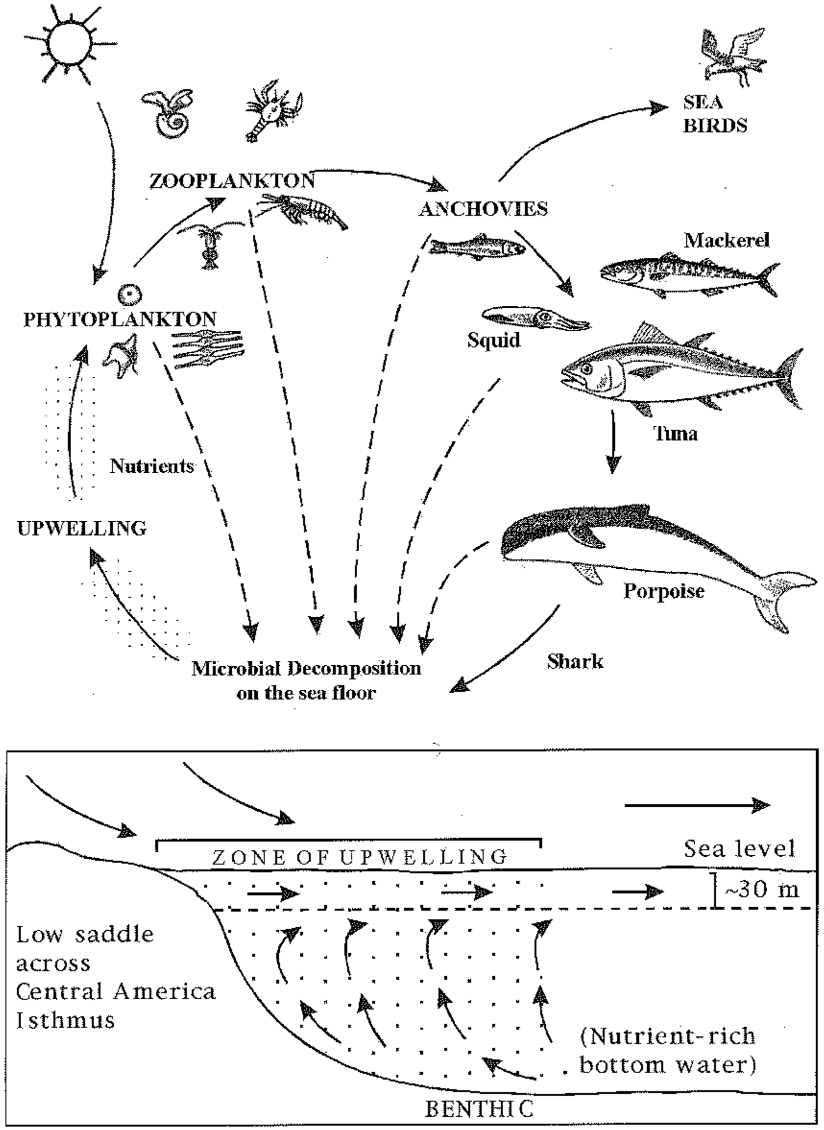
The pattern of ocean currents affecting the Pacific coast is also more variable than that in the Caribbean (see fig. 2–4). The main source of surface water is the Equatorial Counter Current, which flows eastward just north of the equator and then curves back northwestward from Panama as the Costa Rica Current. In addition, the Equatorial Counter Current is bounded by the North and South Equatorial currents flowing to the west, and these are fed by the California and Peru currents, which flow toward the equator along the coasts of North and South America, respectively. The California and Peru currents occasionally impinge on Central America as well.



2–4. Names and flow patterns of the major ocean current systems that impinge on Central America.

This complex system is vulnerable to periodic disturbances in water movement, atmospheric pressure, and sea surface temperatures over the tropical Pacific. The resulting El Niño events occur every three to eight years and vary greatly in intensity. These events involve shifts in the relative position and strength of the various eastern Pacific currents and air masses which cause dramatic changes in rainfall, sea temperatures, upwelling, and biological productivity as well as changes in global climate from the tropics to the temperate zones. In Central America, these effects are greatest along the Pacific coast, where the dry season is extended, sea surface temperatures rise, and coastal upwelling is reduced.

These differences in oceanography between the comparatively stable Caribbean and the more variable eastern Pacific underlie equally striking biological variations. But to explain why, we must first consider the pathways of biological production in the sea and how organisms can alter the environments in which they live.



2–5. Upwelling and the pelagic food chain in the tropical eastern Pacific. Upwelling occurs opposite low saddles in the Central American volcanic mountain chain, where wind blows the surface water away from the coast. This water is then replaced by cool bottom water whose rich nutrients allow phytoplankton to multiply in abundance. The pelagic food chain, schematically shown here, is based on the abundant phytoplankton.

Production, Construction, and Environmental Variation

Biological production is the growth and multiplication of life, whereas biological construction is the assembly of biological materials, for example, the conversion of animal skeletons and wood into durable structures such as coral reefs and forests, respectively. Rates of biological production and construction respond to environmental changes in diverse ways.

Biological Production

Primary producers are organisms that do not require organic materials as a source of energy; all other life depends on them. Almost all *primary production* occurs by photosynthesis, whereby plants use chlorophyll and energy from the sun to convert carbon dioxide and water into carbohydrates and oxygen. Photosynthesis occurs only near the sea surface, where penetration of sunlight provides sufficient energy. In clear coastal waters sunlight reaches the sea floor down to 20 or 30 meters depth. In highly turbid waters the limit may drop to only a few meters, whereas in exceptionally clear ocean waters, photosynthesis may occur as deep as 100 meters. Thus, photosynthesis occurs exclusively in the water in the pelagic realm and reaches the sea floor only near land.

Almost all pelagic primary producers are extremely small, unicellular "plants" that drift passively in the current and are referred to collectively as *phytoplankton*. The most important groups are diatoms, dinoflagellates, coccolithophores, blue-green algae, and bacteria; the exception is the abundant, large, floating alga *Sargassum*, which gives the Sargasso Sea in the North Atlantic its name. In contrast, *benthic* primary producers live on the bottom and include typically much larger algae (collectively called seaweeds), sea grasses, and mangroves (an association of shrubs or trees which grow in saline soils in tidal fringes of tropical coasts). The most important exceptions are microscopic single-celled dinoflagellate algae that live symbiotically within the tissues of such plant-shaped animals as reef corals, sea fans, and sea anemones.

The ecology of pelagic and benthic primary producers is dramatically different. Phytoplankton abundance and production depend primarily on currents and upwelling, which supply essential nutrients like nitrogen and phosphorous. Growth and reproduction by simple cell division is rapid, and lifetimes are measured in days or weeks. Populations can therefore double within a day when nutrients increase and may fluctuate wildly in response to changing environmental conditions. Phytoplankton are eaten by *zooplankton*, which also drift with the currents. The most important of these primary consumers are microscopic copepod crustaceans, developing larvae of myriad invertebrates and fishes, and much larger jellyfish and salps (transparent, free-swimming tunicates or sea squirts). Zooplankton are eaten by small predators like anchovies, which in turn are eaten by larger and larger actively swimming predators, including tuna, squid, porpoises, and sharks (see fig. 2–5). Phytoplankton abundance is strongly affected by all of these consumers, but, in general, rates of production probably depend more on changes in nutrients, which means that the system is controlled from the bottom upward.

In contrast, the ecology of benthic primary producers depends more on biological interactions like competition for space, grazing, and disease than on currents and nutrients. Growth and reproduction are slower, and lifetimes are measured in months to centuries. Thus, populations cannot increase as rapidly to take advantage of newly favorable conditions, and numbers fluctuate within much narrower limits except when devastated by rare disasters such as hurricanes or epidemics. Benthic food chains are also more complex than pelagic food chains because there are more ways to feed. For example, such primary consumers as sea urchins, snails, parrot fish, and turtles feed on benthic primary producers like sea grasses and seaweeds, whereas sponges and oysters are suspension feeders that eat microscopic phytoplankton and zooplankton. These primary consumers are in turn eaten by a great variety of invertebrate predators, including worms, snails, and starfish as well as fish, sharks, and stingrays. In addition, a great variety of clams, snails, and worms feed on the detrital remains of dead organisms that accumulate on the bottom. In spite of this diversity, however, the outbreak or disappearance of a single top predator can totally alter the community. Thus, benthic communities appear to be controlled from the top downward except perhaps in strongly upwelling regions.

Biological Construction

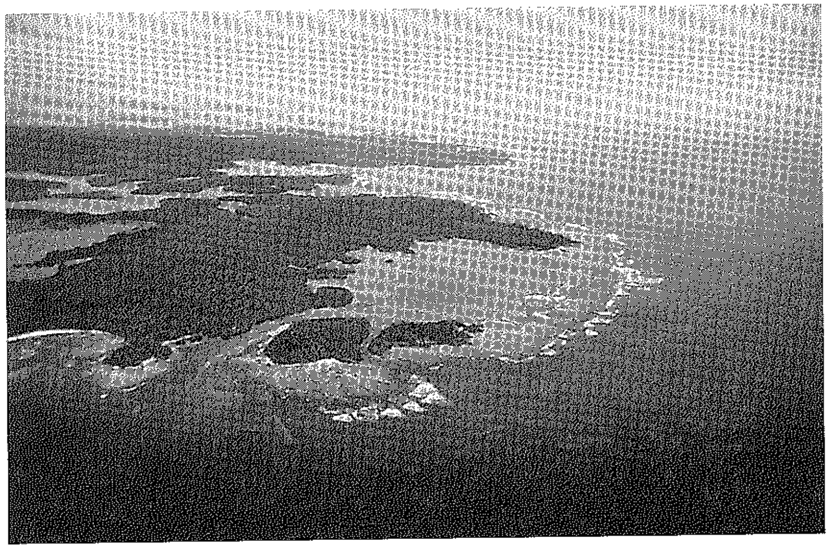
Some phytoplankton and zooplankton produce minute skeletons of silica and calcium carbonate that accumulate as fine-grained sediments on the deep sea floor but are obscured in coastal environments by runoff of vastly greater amounts of sediment from the land. In contrast, many benthic plants and animals produce massive structures of wood, rhizomes (underground stems that anchor sea grasses), and limestone skeletons, which are the building blocks of the enormous biological constructions called mangrove forests, sea grass beds, and coral reefs.

Even sandy beaches and lagoonal sediments can be composed almost entirely of the fragmented calcareous skeletons of benthic animals and plants.

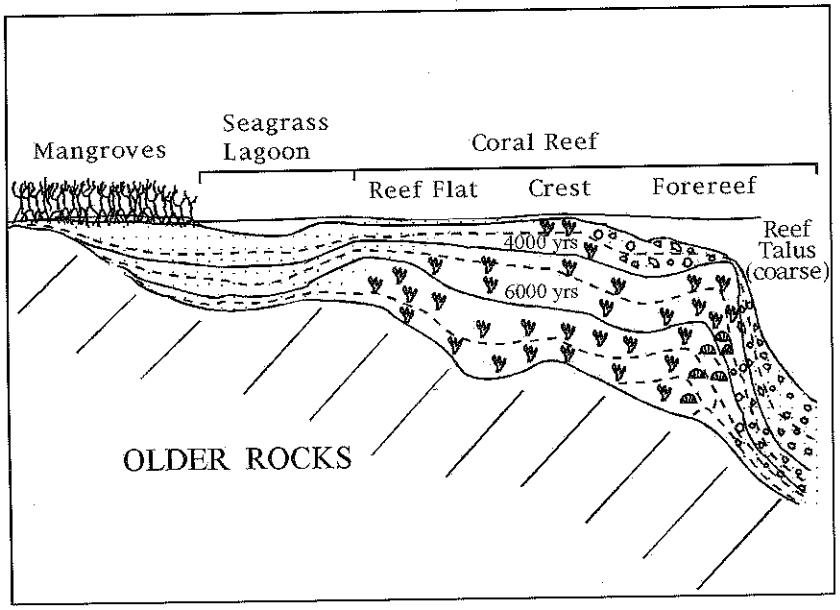
Coral reefs, sea grass beds, and mangroves occur together throughout most of the Caribbean (fig. 2–6), just as they do in the Indian and West Pacific oceans. In contrast, in the eastern Pacific, coral reefs and mangroves are effectively separated ecosystems and sea grasses are absent. In the absence of reefs, however, mangroves and sea grasses are restricted to bays and estuaries, where they are protected from the full force of the sea. When reefs are present, mangroves and sea grasses may occur behind them anywhere along the coast. The dense root systems and rhizome mats of mangroves and sea grasses reduce water circulation, increase sedimentation, and stabilize the bottom. In this way they act as sediment traps that protect coral reefs on wet coasts like Central America, where extensive runoff from the land might otherwise suffocate coral reefs in mud. Where they occur together, then, coral reefs, sea grasses, and mangroves are strongly interdependent: if one is disturbed, the effects are felt throughout the coastal ecosystem.

Where conditions are favorable, coral reefs, sea grasses, and mangroves dramatically change the physical structure and appearance of the coast (figs. 2–6, 2–7). The scale of their biological construction is enormous. Coral reefs are the largest and most durable construction projects on earth. The Panama Canal is still the largest human construction project, but it is paltry in comparison with the size and extent of coral reefs along the Caribbean coast of Panama, and these in turn are tiny compared to the Belize Barrier Reef, the largest reef tract in the Caribbean. Moreover, living reefs, including the Great Barrier Reef in Australia, have grown to their vast size in less than 7000 years, about the same time that humans have been building pyramids and cities. Investigators know this because sea level rose 85 meters between 12,500 and 7000 years ago, after the last glacial advance, including two 1000-year pulses during which it rose faster than 2 meters per century or 20 meters per thousand years! This is faster than coral reefs can grow, so that almost all reefs were drowned, and new reefs started to develop only when the rise in sea level slowed down.

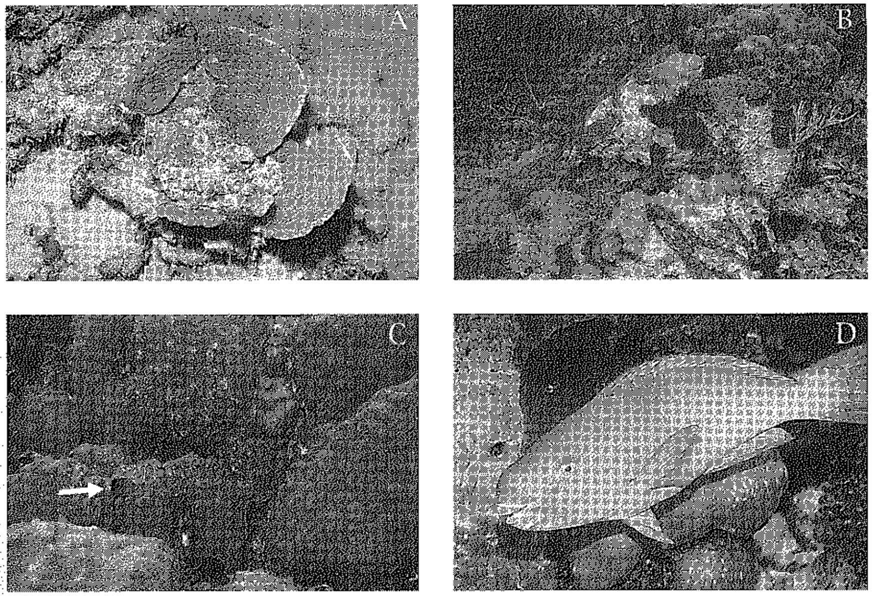
The impressive size of coral reefs, sea grass beds, and mangroves gives a false impression of stability that belies an underlying turmoil of growth, death, and destruction of the organisms that construct these communities. For example, reef growth is determined by how much production, accumulation, and cementation of skeletons, especially of corals and coralline algae (a very important group that make skeletons



2–6. Caribbean coastal ecosystem along the north coast of Panama. Extensive fringing coral reefs are marked by the line of breaking waves to the right. Behind the reefs is a broad lagoon floored by turtle grass, inland of which is a broad zone of mangroves. Photograph by Carl Hansen.



2–7. Idealized cross section of the internal structure of a Caribbean mangrove / sea grass / reef coastal ecosystem. Dashed lines show the profile of the reef at various stages in its history; the profiles for 4000 and 6000 years ago are picked out in solid black lines.



2–8. Processes of reef destruction: (A) accumulation of sediments killed the central portion of this lettuce coral (*Agaricia sp.*); (B) the black-spined sea urchin *Diadema antillarum* has scraped away most of the large brain coral at the center; (C) the tiny (5-centimeter-long) three-spot damselfish *Stegaster planifrons* (arrow) is killing the coral in the background by biting away tissue to expose the skeleton beneath (white spots). This allows algae to grow on the skeleton. These algal gardens provide food for the fish, who vigorously protects them from intruders; (D) the large midnight parrotfish *Scarus rubrovidaceus* bites away large pieces of coral with its strong beak (white spots on the coral below). Photographs by Carl Hansen.

in the manner of corals), exceed destruction due to storms (pl. 2D), grazing, and excavation by animals and plants (*bioerosion*) that can penetrate the reef limestone chemically or physically (fig. 2–8). Similarly, expansion of mangrove forests and sea grass beds depends on the ability of these plants to trap, stabilize, and accumulate sediment to grow on. The crucial point is that the distribution and extent of these communities are sensitive to even small changes in rates of construction or destruction. For example, most eastern Pacific coral reefs virtually disappeared within a decade after the strong El Niño of 1983 because of coral death and intense bioerosion. There is evidence now of recovery in many areas.

Most of the primary production of sea grass beds and mangroves is due to photosynthesis by the bioconstructing organisms themselves or, in the case of corals, by their symbionts, rather than by pelagic phytoplankton. Much of this production is directly invested in the physical structure of the habitat in the form of wood, rhizomes, or limestone skeletons that tend to be recycled within the coastal ecosystem rather than exported to other environments. Net productivity and biomass are greatest for mangroves and least for coral reefs. Productivity of phytoplankton is variable in mangroves but low over sea grass beds and coral reefs, except in cases of overenrichment by man. Low nutrient content appears to be critical for extensive reef growth, and this sensitivity to nutrients is a major determinant of the differences in ecological communities on the opposite coasts of Central America.

Production and Construction in the Two Oceans

How, then, do all of these differences in biological production and construction relate to the physical oceanographic variations between the two coasts of Central America? The two critical factors are the amount of nutrients available and the physical stability of the environment. In general, high pelagic nutrient concentrations result in dense populations of rapidly multiplying phytoplankton that decrease light penetration and rob nutrients from slower-growing benthic primary producers. Similarly, high nutrients near the bottom greatly favor seaweeds and animals without massive skeletons over corals, sea grasses, and mangroves because they grow much faster than the latter. Rapidly fluctuating environments also tend to tip the balance in the same direction as high nutrients.

Pelagic Systems

Pelagic primary production during seasonal upwelling in the Bay of Panama and the Gulfs of Papagayo and Tehuantepec is the highest in Central America and supports extremely rich pelagic fisheries that may produce half a million metric tons per year. Anchovies account for most of this biomass (pl. 3A, B). These small fish feed directly on the plankton. Their abundance varies from as little as a few thousand tons annually when El Niño events suppress upwelling to as much as 200,000 tons when upwelling is very strong. Anchovies and other small fish in turn feed abundant tuna, dolphins, and seabirds like brown pelicans and boobies (see fig. 2–5, pl. 3A) that nest by the millions in the Bay of Panama during upwelling. When upwelling failed during the extreme El Niño of 1983, every baby pelican died. Comparatively little is known about pelagic fisheries along the Caribbean coast of Central America, largely because low nutrients and lack of upwelling result in such low abundance of pelagic fish that no one has bothered to study them in detail. Caribbean seabirds are also rare.

Benthic Systems

The sandy, muddy bottoms of estuaries, bays, and the continental shelves are inhabited by diverse populations of worms, clams, snails, shrimps, crabs, lobsters, sea urchins, starfish, and flatfish like flounders. These broad sediment plains are physically unstable and extensively burrowed by animals, so that bioconstruction is inhibited. The composition of these benthic communities is strongly influenced by levels of production in the waters above. In the eastern Pacific, abundance and spawning of scallops and other fast-growing shellfish that feed directly on plankton and detritus increase dramatically during most strong upwelling years. Mollusks in general are extremely abundant, and dredge hauls in the eastern Pacific are almost always full of shells, which is rarely the case in the Caribbean.

The extent of the two Central American coasts dominated by corals, sea grasses, and mangroves is exactly the opposite of that of productive pelagic and benthic fisheries. Large coral reef tracts, sea grass meadows, and mangrove forests border about half of the Caribbean coast (see fig. 2–1). The chief exceptions are the Mosquito Gulf in Panama, most of Costa Rica, and the Mosquitia of Honduras and Nicaragua, where sediment discharge from large rivers inhibits near-shore development of reefs. In contrast, eastern Pacific reefs are small and widely scattered, sea grasses are absent, and mangroves occupy less than one-third of the area they cover in the Caribbean.

Wood and tough skeletons provide structural support and protection against most predators and grazers. For example, only animals like parrot fishes and sea urchins that are armed with strong beaks can scrape through the skeleton of corals and other stony species to graze on the soft tissues below (see fig. 2–8B–D), when other more palatable foods are not available. On the other hand, making a skeleton takes time and costs energy, so corals grow slower and reproduce less than most seaweeds or sponges, which do not invest so heavily in skeletons. Moreover, skeletons are not the only form of protection against predators. Many seaweeds, sponges, and other attached (*sessile*) animals produce toxins that make them unpalatable or poisonous.

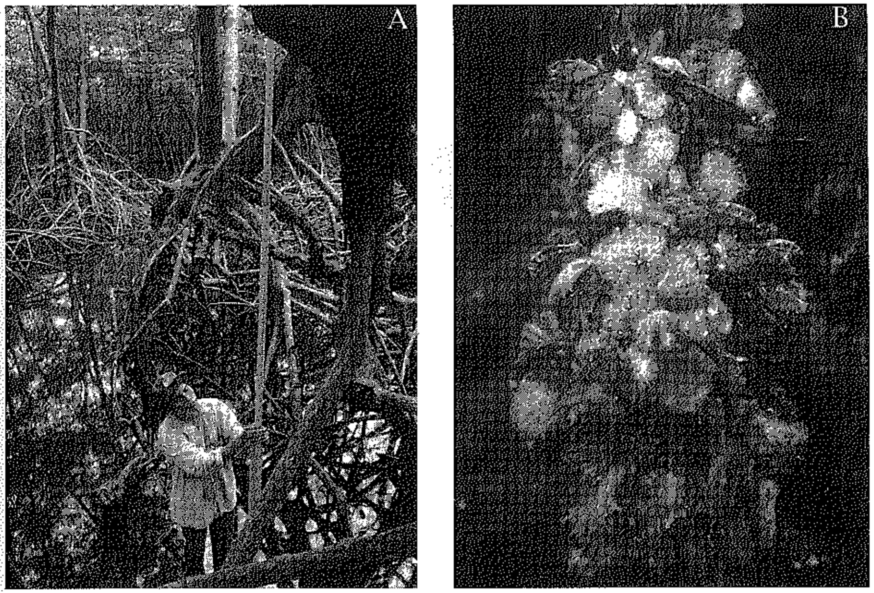
These trade-offs among skeletal support, protection, and growth rate, along with the differential effects of nutrients on phytoplankton and corals, help to explain why coral reefs are extensive on the Caribbean coast of Central America but not the eastern Pacific. Sessile animals that feed on phytoplankton in the water—for example, sponges, bryozoans (small, colonial, mostly calcified marine animals), and oysters—grow and reproduce extremely rapidly on the Pacific coast, especially in zones of upwelling. Moreover, because abundant nutrients favor seaweeds as well as phytoplankton, both seaweeds and plankton-feeding animals tend to rapidly colonize and overgrow substrata suitable for corals, and reefs are small and ephemeral. Similar arguments may apply to sea grasses, which are absent from the tropical eastern Pacific.

In contrast, low nutrients on the Caribbean coast favor the coral-algal symbiosis because the symbiosis recycles scarce nutrients much more effectively than seaweeds or phytoplankton, and corals are also better protected against grazing parrot fish and sea urchins by their stony skeletons. The greater environmental stability of the Caribbean also favors longer-lived corals over shorter-lived seaweeds and animals. Nonupwelling regions of the Pacific coast like the Gulf of Chiriquí present an intermediate situation. Here, productivity and environmental fluctuations are less common than in upwelling regions but greater than in the Caribbean and, as might be expected from the above arguments, can support only reefs of intermediate development.

The Community Ecology of Coral Reefs, Sea Grasses, and Mangroves

Coral reef, sea grass meadows, and mangrove forests are built by relatively few species. In Central America, there are fewer than 100 species of corals, a dozen species of mangroves, and half a dozen sea grasses; even the Great Barrier Reef has only about 600 species of corals. Thus, the very existence of these habitats depends on the well-being of relatively few species. Moreover, Central American reefs, sea grass beds, and mangroves provide habitat and shelter for thousands of species of fishes, shrimps and other crustaceans, starfish, sea urchins, snails, clams, oysters, worms, bryozoans, sponges, algae, and myriad other groups (fig. 2–9B); just as canopy-forming trees provide habitat for the spectacular array of birds, insects, mosses, and herbs of a tropical forest.

Most of these associated species exhibit preferences for specific reef, sea grass bed, or mangrove habitats, where they may spend their entire lives. Others begin life in one habitat and migrate elsewhere when they are big enough to escape from predators and defend themselves or are better equipped to eat different foods. The migrators include commercially important shrimps and fishes like snappers, which explains why mangroves are so vital as nurseries to fisheries in other habitats, such as those along the Pacific coast, where sea grasses are absent and reefs few and small. Very few species except the larger vertebrates range freely among habitats throughout their lives.

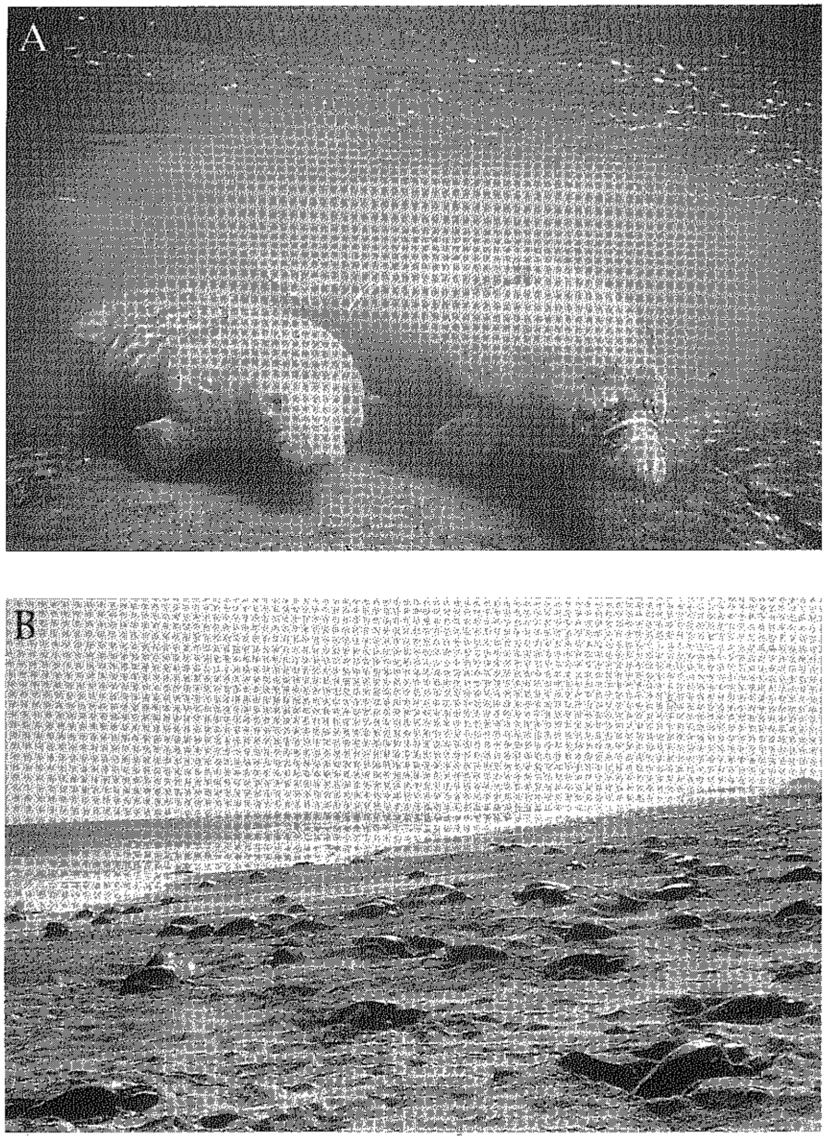


2–9. Mangrove root systems: (A) large red mangrove roots (*Rhizophora mangle*) on the Caribbean coast of Panama tower above the scientist below. The maze of roots protects the coast from waves and traps sediment running off from the land; (B) abundant edible oysters growing underwater on a red mangrove root in the Chiriquí Lagoon, Bocas del Toro, on the western north coast of Panama. Photographs by Marcos Guerra.

Many species that live among corals, sea grasses, and mangroves have little positive or negative effect on their habitat. But others eat, clean, and protect the corals, sea grasses, or mangroves on which they depend and can therefore greatly affect the distribution and abundance of their hosts. The best studied examples of these *keystone species* are crabs that feed on mangrove seedlings (pl. 4C), turtles, manatees, and sea urchins that feed on sea grasses (fig. 2–10), and starfishes, snails, and fishes that feed on corals and algae (see fig. 2–8B–D).

Coral Reefs

Reef corals are cylindrical polyps similar to sea anemones that secrete a hard, calcareous skeleton at their base (pl. 5A). Most corals grow by repeated budding of polyps, which remain attached to form a colony (pl. 5B–D). Corals are animals, but all reef-forming species contain extremely abundant symbiotic algae within their tissues, and the same is



2–10. Historically abundant, large Caribbean grazing vertebrates: (A) the manatee *(Trichechus manatus)* in Nicaragua, a species approaching extinction in many locations. Photograph by Jim Reid, U.S. Department of the Interior, Sirenia project; (B) green turtles *(Chelonia mydas)* nesting at Tortuguero on the northeast coast of Costa Rica. Photograph by U.S. Department of the Interior. Turtle populations are now vastly reduced throughout the coastal waters of Central America.

true of sea fans and most of the other relatives of corals that inhabit reefs. Photosynthesis by the symbiotic algae during daylight supplies most of the energy for coral growth. Even under normal conditions, however, the polyps also feed as animals, using their tentacles to catch zooplankton, because the food that the algae provide is "junk food," insufficient in protein to meet all of the coral's needs.

The symbiosis between corals and their algae is extremely complex but is normally stable over a wide range of environmental conditions. Reef corals placed in the dark stop growing, release their algae, and eventually die. Similar "coral bleaching" occurs in natural reef populations when the coral expels its algae (or perhaps the algae abandon ship) when the water is too hot or too fresh, among other factors (pl. 6). At present, there is great controversy about whether the frequency of coral bleaching is increasing and is therefore a harbinger of global warming. Whatever its cause, however, bleaching is definitely a sign of stress. High concentrations of nutrients in the water are also unfavorable for corals because they disrupt the regulatory balance between the algae and their coral hosts and increase photosynthesis by phytoplankton.

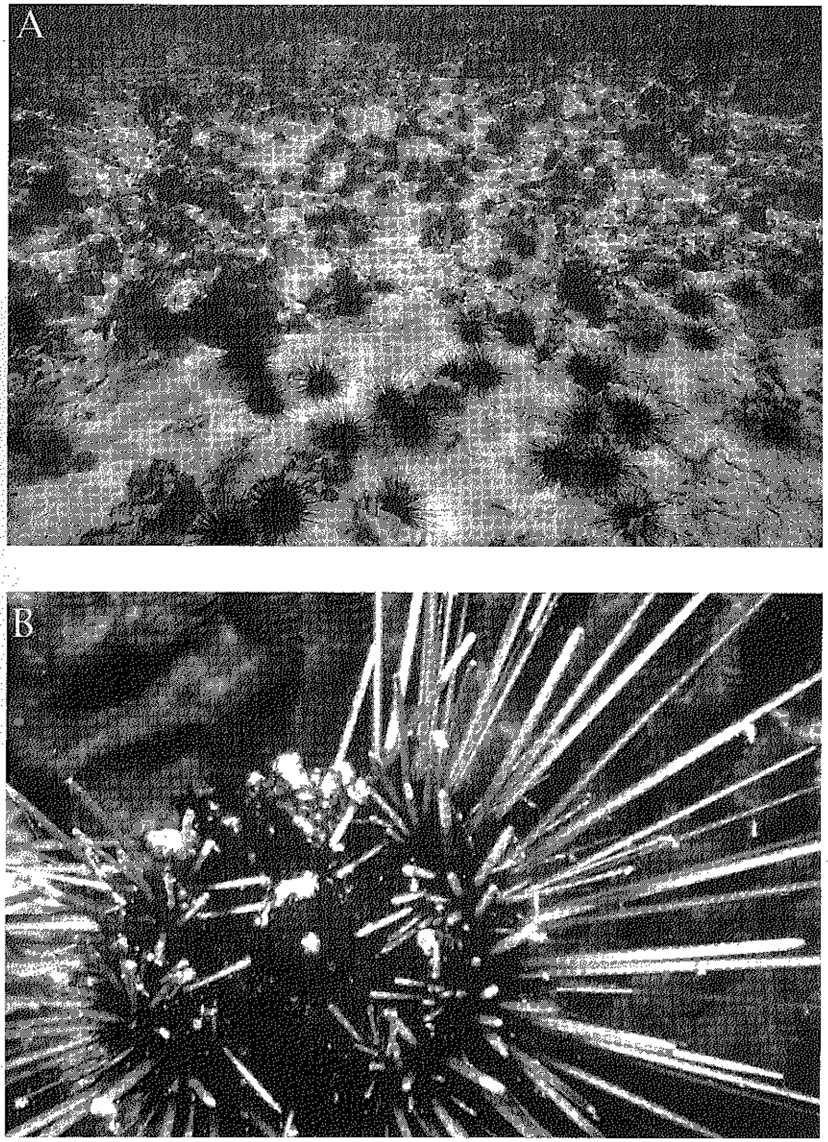
The plantlike shape of corals is determined by patterns of budding of the polyps (see pl. 5B–D), which vary among species and, to a lesser extent, in response to changes in light and water movements. The most common forms are branching, massive, and foliaceous. In the Caribbean, branching corals typically dominate from the reef crest down to 5 or 10 meters (see pl. 2A,B), at which point they are replaced by mostly massive, dome-shaped species that in turn give way to flat, platelike forms that extend downward to 50 meters or more. Zonation is similar in the eastern Pacific but diversity within any zone is typically much less. Branching corals grow up to ten times faster than brain corals and other skeletally massive forms, but there is also great variation among branching species. The champions are the staghorn and elkhorn corals in the genus *Acropora*, which grow from 10 to nearly 30 centimeters per year. These are the competitively dominant species on wave-swept Caribbean shores (see pl. 2A, B) but are absent from the eastern Pacific. In contrast, smaller branching finger corals like *Pocillopora* and *Porites* grow only 2 to 3 centimeters per year. Nevertheless, *Pocillopora* is extremely abundant on eastern Pacific reefs, where it commonly forms dense, single-species stands in shallow water (see pl. 2C); branching *Porites* commonly do the same on more sheltered Caribbean reefs.

Catastrophic declines of reef corals have occurred around Jamaica and at many other sites throughout the Caribbean during the past ten to twenty years. Extreme overfishing in Jamaica had long ago resulted in a severe decrease in parrot fishes and other grazing fishes that consume seaweeds. These fish were replaced ecologically, however, by extremely abundant, long-spined sea urchins and other small invertebrate grazers that kept the seaweeds down (fig. 2–11A). Then in 1983 an unidentified plague swept through the Caribbean, killing more than 95 percent of the long-spined sea urchins (fig. 2–11B). This left seaweeds free to overgrow the corals. During the following decade, the coverage of live corals on Jamaican reefs plummeted to only a few percent of that before the plague. Now the same thing is slowly happening all along the Caribbean coast of Central America wherever the deadly combination of overfishing, increased nutrients due to deforestation and fertilizers, and sea urchin death is tipping the balance of power to seaweeds over corals. These effects of overfishing and sea urchin mortality are dramatic examples of the importance of keystone species on coral reefs.

Sea Grass Beds

Caribbean sea grasses are most abundant from the intertidal zone down to about 10 meters (see pl. 4A, D), although they may reach 30 meters in areas of exceptionally clear waters; different species are abundant at different depths. The most common species are the broad-leaved turtle grass and slender-leaved manatee grass, common names that evoke the abundance of animals that have practically disappeared from these ecosystems. Sea grasses form extensive carpets of green leaves that grow upward from the sediment and become more ragged and encrusted toward their tips. Turtle grass leaves may grow more than half a meter long before they break off, but more commonly they are cropped down by grazers to less than half that length. Leaf growth may be as fast as 1 centimeter per day, and gross primary production rivals that of a field of corn. Beneath the surface, turtlegrass builds an extraordinarily dense, nearly impenetrable mat of roots, stems, and rhizomes that stabilizes the bottom and helps to protect burrowing animals from being excavated by stingrays and other benthic predators.

Numerous animals feed directly on sea grass leaves and considerably more feed on sea grass detritus. The most important leaf eaters today are sea urchins, which can destroy entire sea grass beds, and small herbivorous fishes. Only a century ago, however, the most important grazers on sea grasses were green turtles, manatees (see fig. 2–10), and much larger fishes. Columbus and other early voyagers were amazed by the abundance of turtles that littered the vast turtle grass beds of the Mosquitia Bank and elsewhere like so many millions of stones. In ad-



2–11. Black-spined Caribbean sea urchin *Diadema antillarum* : (A) grazing horde on a reef pavement before the massive die-off in 1983; (B) a specimen dying from the unknown pathogen that killed more than 90 percent of the species throughout the entire Caribbean. The urchin's spines on top have fallen off, exposing bare flesh beneath. Photographs by Haris Lessios.

dition, the giant queen conch processes large amounts of turtle grass and its detritus in order to feed upon the associated microorganisms on the blades. Early descriptions of conchs are not so dramatic as those of turtles, but their shell middens (piles of shells from which the meat has been extracted) are so enormous that they tower above the surrounding landscape at some once-rich conch fishing grounds.

Conchs are rare now because of overfishing, but when placed in dense experimental populations they damage or destroy the turtle grass while trying to feed; and the abundance of conchs in ancient middens suggests that they may have had a similar natural effect before overfishing. Feeding by green turtles is potentially even more destructive, although by processing vast amounts of sea grass leaves through their guts turtles must have greatly increased the rate at which sea grass entered the detrital food chain. Indeed, the extensive migrations of green turtles probably evolved because dense local populations of turtles were unsustainable, just as wildebeest must migrate on the East African grass plains. Only 150 years ago, a large part of the productivity of sea grasses was harvested as turtle, manatee, fish, and conch meat by people; but today, that productivity has been lost to small, mostly unpalatable invertebrates. This is another example of the importance of keystone species in communities dominated by bioconstructional species.

Mangroves

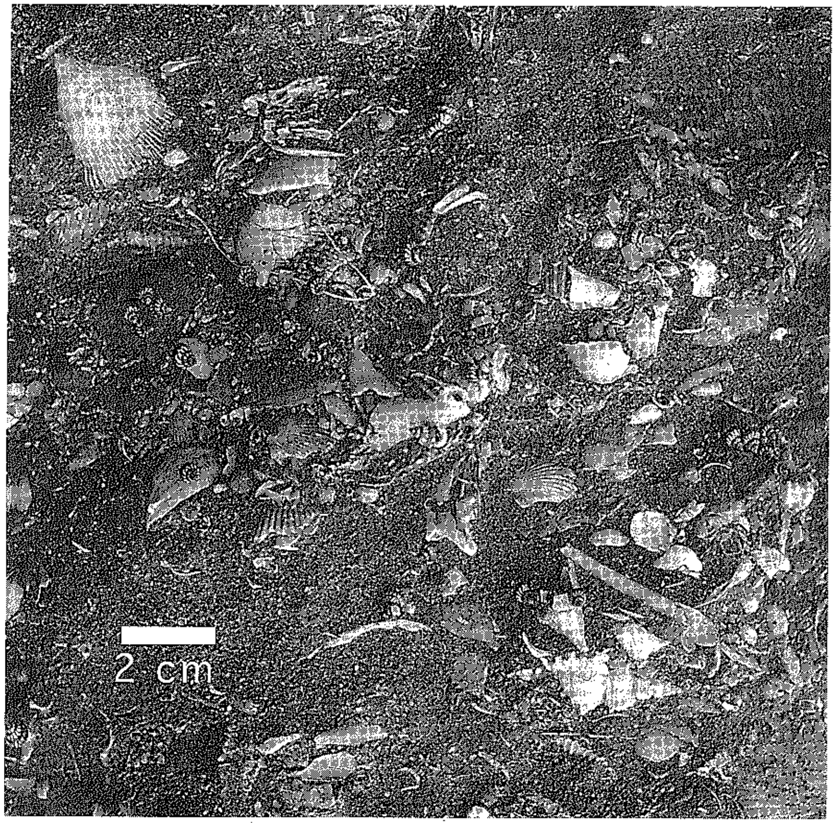
Mangrove forests mark the boundary between marine and terrestrial environments in tropical zones in the same way that salt marshes do in the temperate zone (see fig. 2–9A; pl. 4A, B). The most important factors for mangrove development and productivity are low wave energy, protected shorelines, abundant freshwater and nutrients, mixed salinities, and the deposition and accumulation of fine organic mud. All of these conditions occur along both coasts of Central America, although the absence of large reef tracts in the eastern Pacific restricts mangrove development to bays and estuaries, where they are protected from the open sea. In contrast, the much larger tidal amplitude on the Pacific coast allows mangroves to extend farther inland than in the Caribbean.

Zonation of different mangrove species is due to the interaction of all these environmental factors as well as to grazing on mangrove seedlings and catastrophic storms. Consumption of seedlings is almost entirely by crabs (see pl. 4C) and snails, although large vertebrates may also have been important previously. Rates of grazing vary greatly among different mangrove habitats, forests, and regions. For example, in a recent study, crabs in Panama and snails in Florida consumed about 10 percent of experimentally tethered seedlings every four days. In contrast, consumption rates in Malaysia and Australia were 25 percent over a four-day period, making it quite remarkable that any seedlings ever survive! Consumption rates may also be high on the Pacific coast of Central America, where similar crabs and snails are commonly more abundant than in the Caribbean. Other experiments in Australia have also shown that mangrove species can colonize areas in which they are normally absent when herbivores are excluded by cages. Thus, the zonation of mangroves is controlled more by these small animals than by the direct effects of the physical environment, which is yet another example of the importance of keystone species.

Export of the biological production of mangroves from the forests toward the coast occurs mostly as detritus derived from mangrove leaves, and secondarily as the bodies of abundant fishes and shrimp that live as juveniles in the mangroves before migrating elsewhere. Leaf production may be as high as 10 to 15 metric tons per hectare per year but is not immediately available as food for animals until the leaves are converted into detritus. This conversion involves the leaching of lignin and tannic acids, biological transformation through the metabolism of bacteria and fungi, and physical manipulation of the leaf fragments by myriad worms and small crustaceans. After several weeks only a small fraction of the original leaf remains, but the concentration of nutritious compounds is increased more than tenfold. Mangrove leaf detritus is the most important food for many coastal species, which is why the volume of fisheries in a region increases with the amount of mangroves present.

The Fossil Record of the Oceans

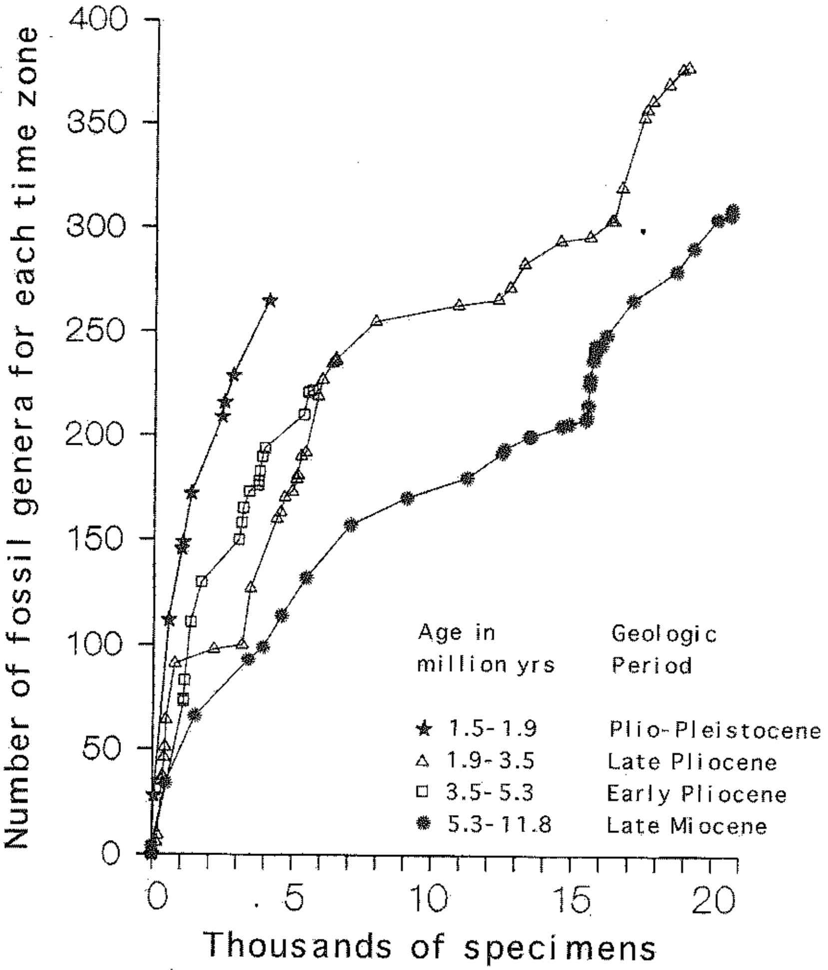
The marine fossil record of Central America is extremely rich but is more complete for the Caribbean coast than for the Pacific (fig. 2–12). Most of the Pacific record has been subducted beneath the tectonically active Pacific margin. Structural deformation of marine sediments is also greater on the Pacific side, with the result that preservation and stratigraphic ordering of Caribbean fossils are generally much better than those of the Pacific. For these reasons we will be largely discussing events on the Caribbean side of Central America.



2–12. Abundant fossil snails, clams, tooth shells, and corals (*upper left*) on the shore of Cayo Agua, Chiriquí Lagoon, Panama. The fossils are from the Pliocene epoch and are about 3.5 million years old. The small black-and-white snails are living periwinkles. Photograph by Marcos Guerra.

Changes in Diversity through Time

The diversity of Caribbean fossils is extremely high, as shown for mollusks from Costa Rica and western Panama (fig. 2–13). The curves are for hundreds of collections of fossils sorted into four time periods over the past 12 million years. Each curve plots the cumulative numbers of different genera against the numbers of specimens collected. These are the largest such collections ever made from Central America, but even 75,000 specimens are not enough to ensure that the full complement of common mollusks have been identified. Paleontologists know this because additional samples continue to unearth new kinds of mollusks for each time period. Only when new collections do not significantly add new genera and the slope of the curves levels off will the true diversity be known. The oldest fauna is apparently the least diverse because the rate of increase is much less, whereas diversity for the three younger faunas appears roughly similar.

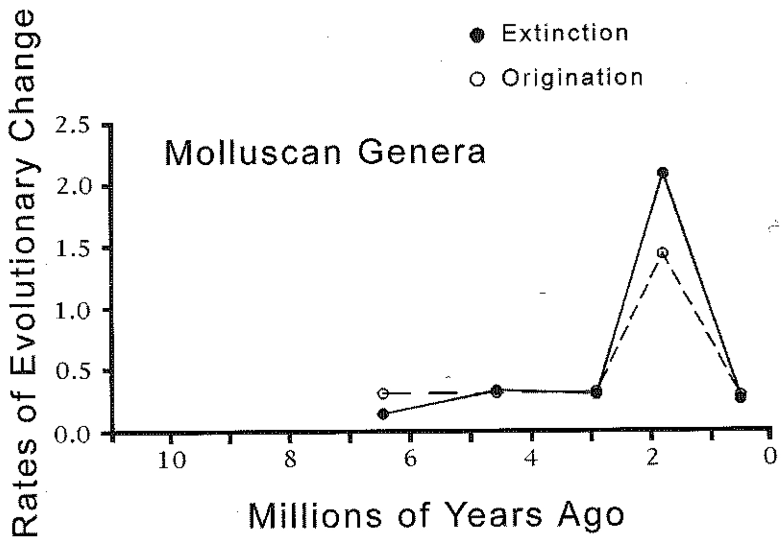


2–13. Diversity of fossil mollusks from four different ages that were collected along the Caribbean coast of Costa Rica and Panama. The numbers of different kinds of mollusks from each age are still increasing sharply as new specimens are obtained.

The first and last stratigraphic occurrences were determined for 1237 genera of mollusks identified as living during the past 12 million years. The purpose was to calculate rates of origination and extinction of molluscan genera through time and to determine whether these were constant processes or whether some times witnessed especially high rates of change. There was a striking pulse of origination and extinction about 2 million years ago, when nearly half of the earlier forms became extinct but were replaced by new ones within a few hundred thousand years (fig. 2–14). Before and after the turnover, however, rates of evolution were much less. Rapid turnover of mollusks also occurred at about the same time in Florida, where it was accompanied by a dramatic turnover of seabirds and marine mammals.

Species of Caribbean reef-building corals also experienced a strong evolutionary pulse about 2 to 3 million years ago, when rates of extinction increased more than tenfold. Turnover of corals, however, began earlier and was slower than for the mollusks. Only one-third of more than 100 coral species alive before the turnover survived, and extinction and speciation dropped sharply afterward so that the modern Caribbean coral reef fauna is about 2 million years old. The period of coral turnover also saw the explosive increase in abundance of branching corals in the genus *Acropora,* which grows more than twice as fast as any other corals and now dominates most living shallow water reefs around the world (see pl. 2A, B), except in the eastern Pacific.

Similarly comprehensive data for mollusks and reef corals are unavailable from the Pacific coast, so it is not possible to compare events on the two sides of Central America. There are, however, excellent collections from both coasts of a highly diverse and well-studied family of snails called strombinids. These are mostly small, live on sand or mud, and have an exceptionally rich fossil record of more than 100 tropical American species. Strong turnover of strombinid species occurred on both coasts but in different ways. Initially there were many more species in the Caribbean than in the eastern Pacific, but the pattern was reversed about 2 million years ago owing to a pulse of extinction in the Caribbean and one of origination in the Pacific. The history of reef corals was also very different in the two oceans. Large *Acropora* replaced small *Pocillopora* finger corals as the dominant branching species in the Caribbean but never became established in the eastern Pacific, where *Pocillopora* dominates all other species (pl. 2C).

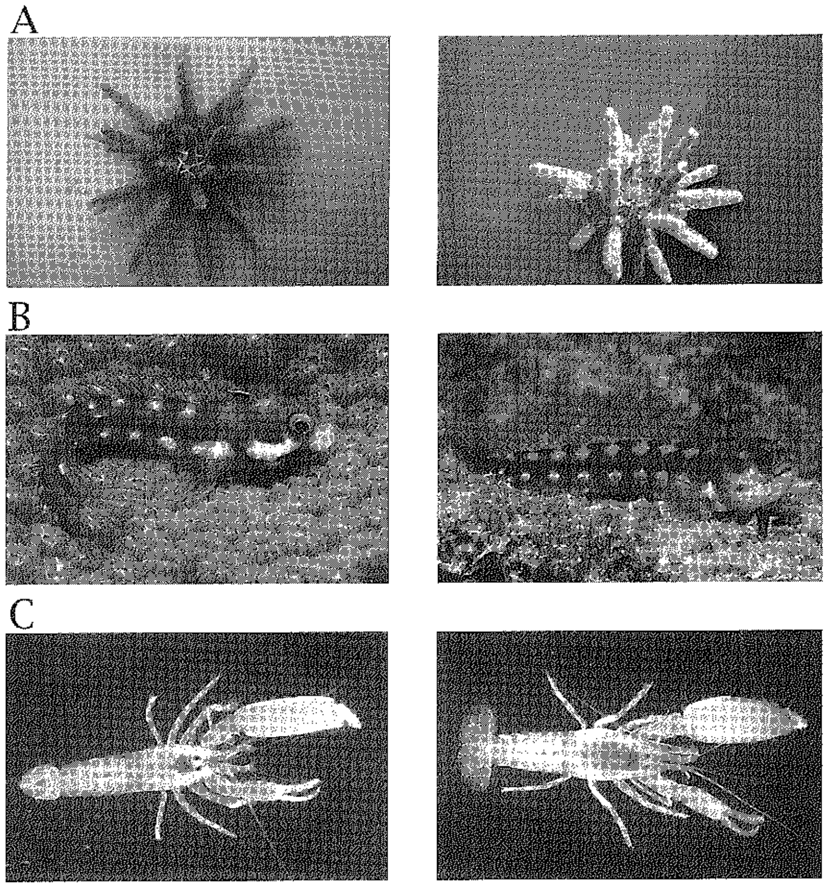


2-14. Curves showing the rate at which genera of mollusks have appeared and gone extinct during the past 10 million years. A sharp pulse of extinction coincides with a peak of origination two million years ago. A similar curve for coral species shows a peak of origination spread over 1 to 2 million years.

The very different histories of reef corals and strombinids on opposite sides of Central America may not be typical. Most transisthmian pairs of closely related sea urchins, shrimps, snails, and fishes are so similar morphologically that only taxonomists can tell them apart (fig. 2–15). Greater resolution is possible by fingerprinting the DNA of sister species on opposite sides of the isthmus, but even these molecular differences are relatively small. Thus, it appears that evolution due to geographic isolation alone is rather slow, especially compared to the pulse of origination and extinction affecting corals and mollusks 2 to 3 million years ago.

The most complete biological data for how the rising isthmus affected the timing of divergence are those for seven pairs of sister species of snapping shrimps, one of each pair living on the Pacific coast and the other on the Caribbean (fig. 2–15C). The extent of divergence of these species was measured by molecular differences in proteins and DNA and by the amount of aggression in experimental combats. Close correspondence of all three parameters in each species pair strongly suggests that they measure time since divergence in a clocklike manner (fig. 2–16).

Isolation of pairs of snapping shrimps did not occur at the same time. The four most similar pairs probably separated 3 million years ago, when the last marine connections were severed. If one assumes constant rates of divergence, then the most dissimilar pairs must have started to diverge more than 7 million years ago, when the oceans were still connected by shallow seaways. These results coincide closely with the ecology of the shrimps. The four most similar pairs occur in the midintertidal zone along the mainland, presumably one of the last habitats to be isolated by the isthmus. In contrast, the most divergent

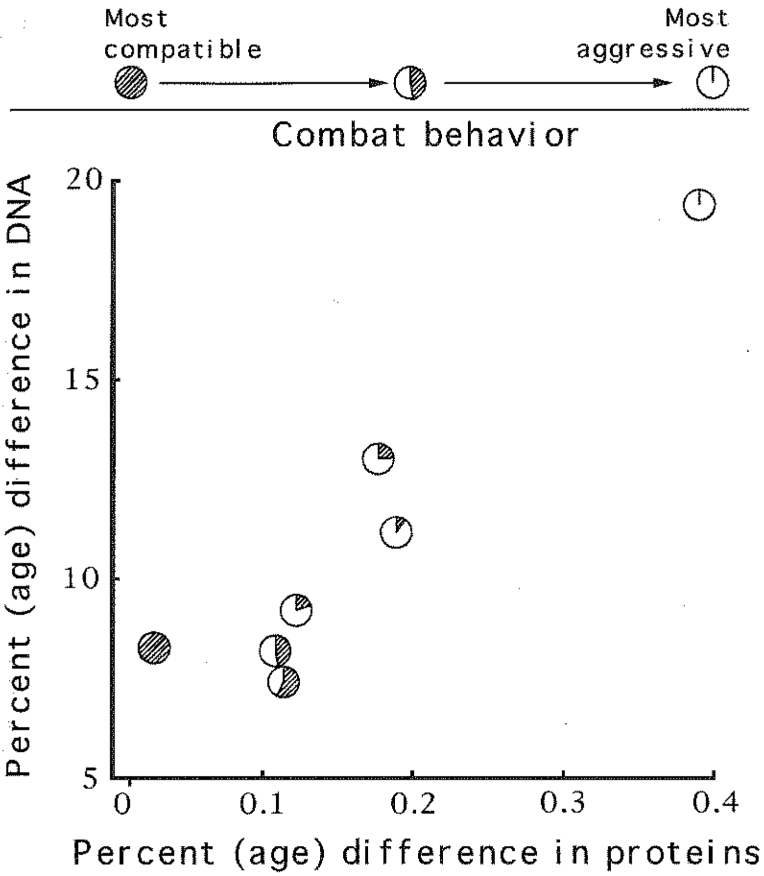


2–15. Pairs of sister species from the eastern Pacific (*left*) and Caribbean (*right*) coasts of Panama: (A) pencil sea urchins: (*left*) *Eucidaris thouarsi;* (*right*) *Eucidaris tribuloides* . Photographs by Haris Lessios; (B) tube blennies: (*left*) *Acanthemblemaria castroi;* (*right*) *Acanthemblemaria rivasi*. Photographs by Ross Robertson; (C) snapping shrimps: (*left*) *Alpheus cylindricus* ; (*right*) *Alpheus cylindricus*. Photographs by Carl Hansen.

pairs require deeper water or more offshore habitats, which would have been isolated earlier.

Evolution and Environment

The progressive isolation of the two oceans by the emerging isthmus caused major changes in primary productivity in the two oceans that are correlated with origination and extinction. Three sorts of evidence suggest that primary productivity was high in both oceans until about 3 million years ago, when it increased in the eastern Pacific and declined dramatically in the Caribbean. First, fossil mollusks, seabirds, and marine mammals are exceptionally abundant from Florida to California prior to 3 million years ago and then decline in the Caribbean but not in the Pacific. Second, microfossils and sediments rich in phosphates (deposits that are characteristic of upwelling regions) disappear from the Caribbean at about the same time. Third, fluctuations in oxy-



2–16. Genetic and behavioral divergence between species pairs of snapping shrimp whose ancestors were separated by the formation of the isthmus. The data points form a straight line, showing that sister pairs have the same level of DNA differences as they have protein differences; the pattern of combat behavior also goes from compatible to aggressive as the differences in DNA and protein get larger. The correlation between the three different kinds of measurements suggests that they measure time like a clock; the species pairs with the largest differences have been separated the longest. Modified from N. Knowlton, L. A. Weigt, L. A. Solórzano, D. K. Mills, E. Bermingham, "Divergence in Proteins, Mitochondrial DNA, and Reproductive Compatibility across the Isthmus of Panama," *Science* 260, no. 5114 (June 11, 1993): 1629–32.

gen isotopes from within annual bands in fossil mollusk shells have been used to infer seasonality and productivity (as described in chapter 1). Some of these isotopic data suggest a gradual decline in Caribbean productivity and others a rapid decline, while eastern Pacific productivity increased.

Surface temperatures of both oceans must also have declined by several degrees during the time of faunal turnover because of the intensification of northern hemisphere glaciation. This conjecture is supported by isotopic analyses of the elements strontium and calcium and by the restriction of latitudinal ranges of tropical Atlantic species. Fossil and paleoenvironmental evidence are not yet sufficient to resolve whether changes in temperature or productivity were the chief agents of turnover: probably both were important.

The Effects of Humans

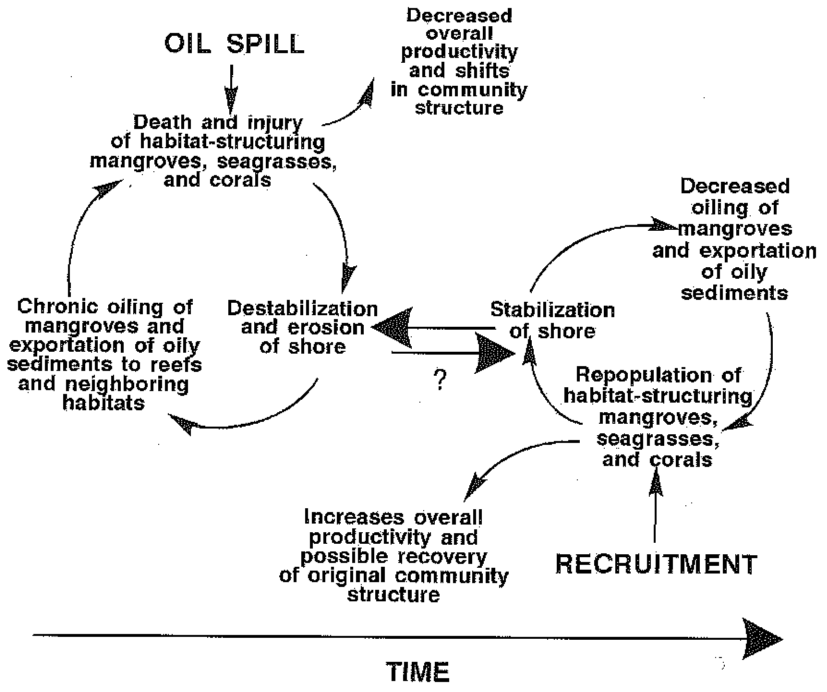
Less than 1000 years ago in western Panama, the Caribbean people living on the shores of the Chiriquí Lagoon derived most of their nutrition from the sea. Their garbage dumps are full of remains of turtles, fish, and shellfish, and remains of terrestrial animals and plant crops are comparatively rare. At about the same time, however, Pacific people living along the Gulf of Chiriquí consumed mostly terrestrial prey and plant crops like maize. These patterns are now completely reversed. Tourists in mainland Caribbean hotels innocently consume great quantities of what they think is fresh corvina, snappers, and groupers, which in reality are trucked over the mountains each day from the Pacific coast because Caribbean snappers and groupers are virtually gone. Scuba divers and snorklers in the same hotels have to be satisfied with beautiful but tiny reef fishes that dart about isolated remnant corals on reefs covered by piles of seaweed that have smothered once luxuriant corals. Offshore, on islands like Roatán, San Andrés, and Providencia, live corals are still abundant, but the fish are mostly gone and destruction is imminent.

The Pacific coastal communities of Central America are naturally more variable than those on the Caribbean, which probably explains why the effects of humans have been so much greater in the Caribbean. This is not to say that the Pacific coast has been unaffected. Much of the Pacific mangroves have been cut down for wood and to make way for human settlement or mariculture. The consequences of these losses are unknown, but it is not unlikely that the increased returns from shrimp farming, for example, are more than offset by decreases in fisheries offshore. It is difficult to understand how such mariculture projects can be implemented without attempting to demonstrate their projected costs and benefits to the economy as a whole.

The damaging effects of trawling are also unstudied in Central America, but extensive research in northern Australia has shown that the habitat structure is destroyed and that production shifts from desirable to undesirable species. Intensive trawling for shrimp has almost certainly transformed bottom communities in places like the Gulf of Nicoya and the Bay of Panama (see pl. 3C, D), where many formerly abundant species are absent or rare. For example, scientists have been unable to collect species of snails that were dredged commonly in the Bay of Panama during the first half of the century. Intensive trawling also occurs all along the Mosquitia Coast, but the effects are unknown.

In general, however, human effects on Caribbean marine communities are obvious and catastrophic. That the loss is so manifest is due to the communities' great bioconstruction, which still dominates Caribbean coastal processes even though it is in serious danger of collapse. Almost everything people do along the Caribbean coast is harmful to this bioconstruction, although adequate planning and management would reduce such damage. Uncontrolled deforestation (see pls. 15, 16) and increased land use for housing and agriculture without soil conservation measures increase sedimentation and nutrients that harm corals, increase bioerosion, and favor seaweeds and phytoplankton. Increased runoff of chemical fertilizers and sewage and overfishing do the same. As the habitat structure is destroyed, surviving fish depart, and the community is taken over by small invertebrates.

Bioconstructional communities are strongly interdependent, so that once destroyed, a great many things must happen for recovery to begin. The intricate nature of such interconnections was demonstrated after a major oil spill dumped nearly one-third as much oil as the Exxon Valdez spill in Alaska into a complex coastal lagoon at Bahía las Minas along the Caribbean coast of Panama (pl. 7). The oil quickly killed a band of mangroves along the shore, several sea grass beds, and most of the living coral on reefs that received heavy oil deposits (pl. 8A, B). But this was not the end of the story. Most of the oil that was not recovered was buried in the mangrove sediments. Erosion of these sediments increased as the dead mangroves and sea grasses rotted away, exposing the oil-soaked shore. Heavy rains at the beginning of each rainy season flushed the newly exposed oil and sediments out into the bay, causing new oil spills, injury, and death (pl. 8C). Sedimentation on reefs in-



2–17. Model of habitat damage and recovery after a major oil spill. Stabilization of the shoreline by mangroves and sea grasses is necessary for corals to become reestablished. Reprinted from B. D. Keller and J. B. C. Jackson, eds., "Long-term assessment of the oil spill at Bahía Las Minas, Panama," synthesis report, volume II: technical report. OCS Study MMS 93–0048. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, La., 1990, 1,017 pp.

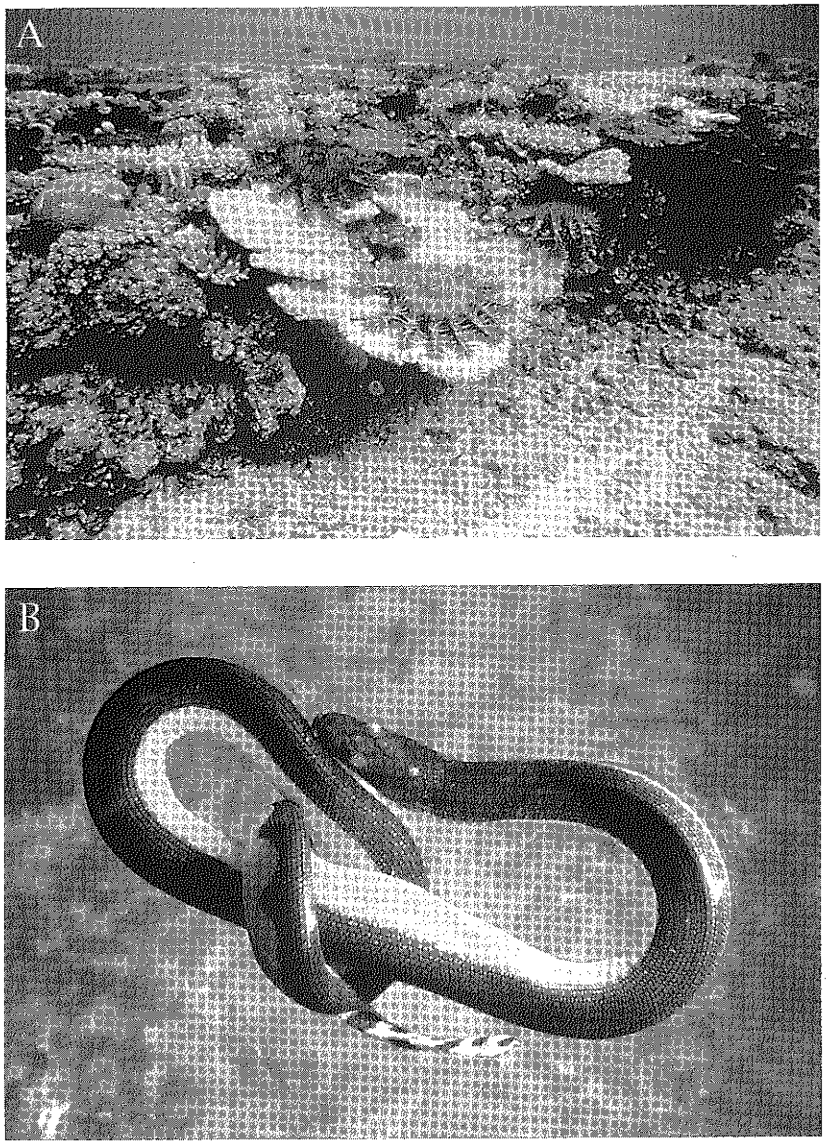
creased fourfold over as many years, and there has been virtually no recovery of corals, sea urchins, or oysters at any of the most affected sites.

Although the causes are different, the consequences of this oil spill serve as a model for thinking about the long-term consequences of other, more pervasive human destruction (fig. 2–17). Bioconstruction depends on the stability of the shore, low levels of nutrients that suppress nonconstructional species like plankton and seaweeds, and abundant predators and grazers that consume potential competitors. Moreover, because adjacent systems interact, serious disturbance to one sets off a chain reaction of events harmful to the rest, so that the entire ecosystem degrades more and more. Even worse, all of the important bioconstructing organisms grow very slowly, as do the turtles, groupers, and sharks that used to dominate the food chain in these communities. Thus, the pace of recovery is extremely slow. Reversal of these events will require not only much more careful national and regional planning, but also the reevaluation of economic, social, and cultural priorities for almost everything people do along the coast! The alternative is the loss of the entire productivity of the Caribbean coast for human consumption and tourism and increasing erosion of the shore.

The one thing that human activity has apparently not yet seriously affected in Central American marine communities is the isolation of Caribbean and Pacific species. The Panama Canal is a freshwater canal, and plans for a sea-level canal have been widely discredited because of their cost and effects on ground water as well as other environmental risks. A far greater threat than a sea-level canal, however, is emerging from the indiscriminant transport of organisms in the seawater and sediments of the enormous ballast tanks of modern ships. Such unwitting importation has already resulted in invasions by exotic species worldwide, especially in estuaries and bays. The consequences can be highly destructive, as in the case of introduced parasites or predators that prey on commercially important shellfish and toxic phytoplankton that cause fish kills and red tides.

Similar introductions of transisthmian species could dramatically alter Central American coastal communities. Several species are of particular interest for their demonstrated ecological importance. Such predators on corals as puffer fishes and snails are larger and more voracious in the eastern Pacific. In addition, the crown-of-thorns starfish *Acanthaster planci* (fig. 2–18A) is absent from the Caribbean, although it readily consumes Caribbean corals when they are offered in experiments. The crown-of-thorns is famous for undergoing population explosions in the Indo-Pacific region, which produce hordes of starfish that consume almost all living corals before dying themselves of starvation. The reason for these starfish eruptions is strongly debated, and tens of millions of dollars have been spent in Australia alone trying to understand what sets them off. The basic question is whether they are natural events or are somehow caused by human activities like fishing, which seems increasingly probable. Crown-of-thorns starfishes do not undergo such population explosions in the eastern Pacific, probably because of the limited development of coral reefs. But a very different scenario is likely if the starfish were introduced into the Caribbean, where the extent of reefs is much greater and overfishing is extreme.

Another species whose introduction would probably cause great ecological change is the unidentified pathogen that caused the epidemic mortality of the long-spined Caribbean sea urchin *Diadema antillarum* (see fig. 2–11). The eastern Pacific *Diadema mexicanum* is ex-



2–18. Pacific species whose introduction could dramatically change conditions in the Caribbean: (A) the crown-of-thorns starfish *Acanthaster planci,* seen here eating a large table *Acropora* on the Great Barrier Reef, is a voracious predator of reef corals throughout the Indo-Pacific. Photograph by John Ogden; (B) the venomous sea snake *Pelamis platurus*. Photograph by Carl Hansen.

tremely similar genetically and dies quickly in experiments when exposed to sick Caribbean relatives. Presumably the introduction of the pathogen to the eastern Pacific would cause similar mass mortality. Finally, introductions may be harmful for many reasons besides their ecological effects. For example, the venomous eastern Pacific sea snake *Pelamis platurus* (fig. 2–18B) causes only rare fatalities to unsuspecting fishermen who catch them accidentally by trawling. *Pelamis*'s danger could be blown out of all proportion, however, if it were accidentally introduced into the Caribbean, with unknown consequences for Caribbean tourism.

There is growing regional concern about the degradation of Caribbean coral reefs, sea grasses, and mangroves, and the economic consequences of such losses for subsistence and tourism. The world's first regional coral reef monitoring program, the Caribbean Cooperative Monitoring Program, was founded to establish baseline information on the status and trends of these communities throughout the Caribbean. Experimental marine reserves are being set up in Belize, Honduras, and Costa Rica to test the effects of stopping fishing on coral reefs and of protecting green turtles on the beaches where they lay their eggs. Preliminary results are encouraging, but there is increasing evidence that coral reefs and related ecosystems are closely linked throughout the region. For example, the floating larvae of corals and fishes are commonly transported hundreds of kilometers from their parents before they settle down, so the recruitment of a particular species in Honduras may depend on its reproduction in Colombia or Panama. Sustainable use will therefore require dramatic action at both local and regional levels.