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Mangrove Swamp Communities

by Klaus Rützler, and Candy Feller

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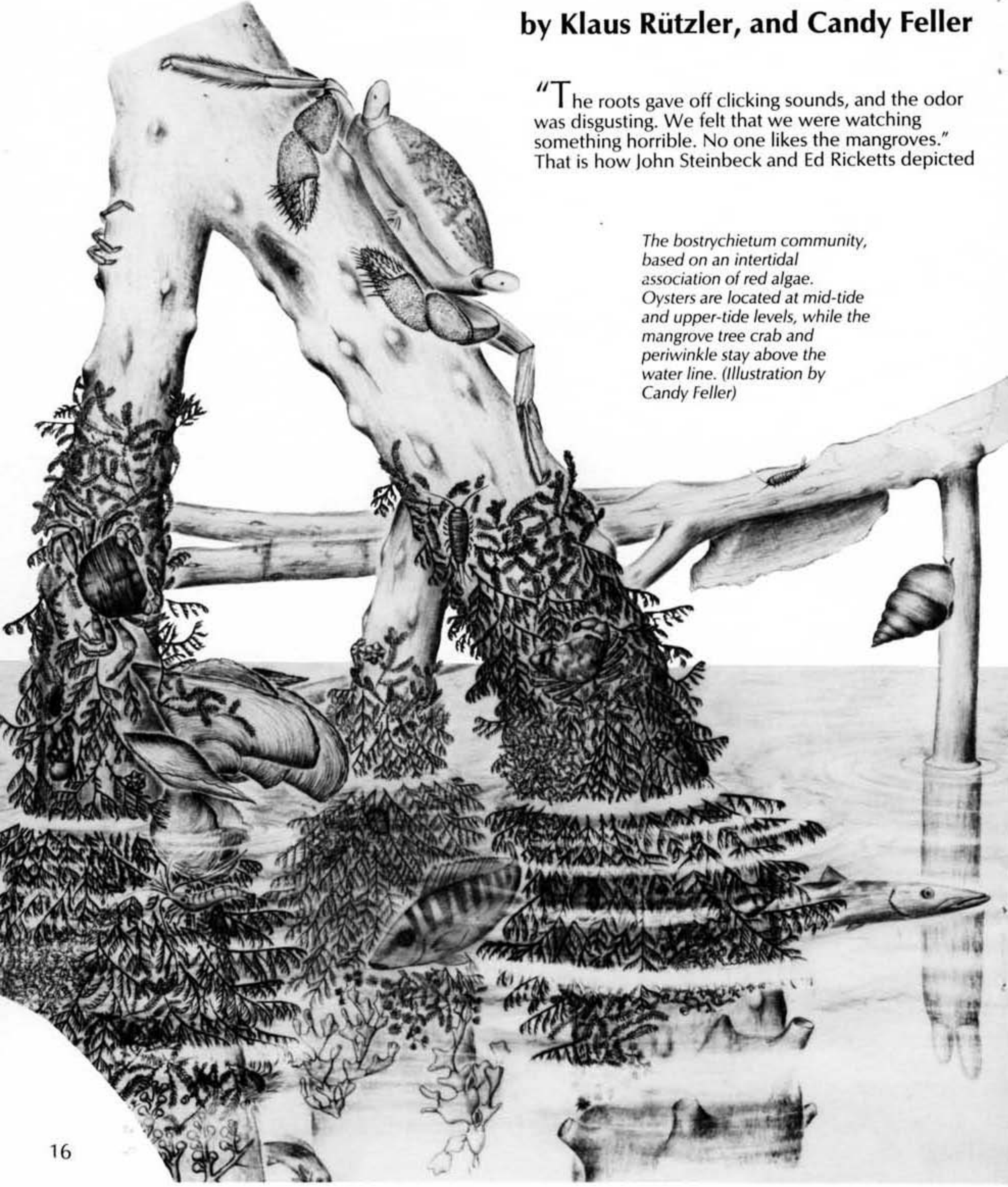
"The roots gave off clicking sounds, and the odor was disgusting. We felt that we were watching something horrible. No one likes the mangroves." That is how John Steinbeck and Ed Ricketts depicted



The bostrychietum community, based on an intertidal association of red algae. Oysters are located at mid-tide and upper-tide levels, while the mangrove tree crab and periwinkle stay above the water line. (Illustration by Candy Feller)

Communities

the mangroves in 1941 in the *Sea of Cortez*. Many people agree with them. So why have two dozen scientists from the Smithsonian Institution, primarily from the National Museum of Natural History, and twice as many colleagues from American and European universities and museums devoted a decade of exploration to one square kilometer of "black mud, . . . flies and insects in great numbers . . ., impenetrable . . . mangrove roots . . .," and ". . . stalking, quiet murder"?

The study started in the early 1980s, and focuses on an intertidal mangrove island known as Twin Cays, just inside the Tobacco Reef section of the barrier reef of Belize, a tiny Central American nation on the Caribbean coast (see article page 76). The principal purpose of this research is to document the biology, geology, ecological balance, economic importance, and aesthetic value of a prominent coastal ecosystem using the example of a diverse and undisturbed swamp community.

Properties of Mangrove Swamps

Mangrove swamp communities dominate the world's tropical and subtropical coasts, paralleling the geographical distribution of coral reefs. Mangroves on the Atlantic side of the American coasts occur between Bermuda and almost to the mouth of the Rio de la Plata (Argentina), and throughout the West Indies. Like reefs, mangrove swamps are environments formed by organisms, but unlike most coral communities, they thrive in the intertidal zone and endure a wide range of salinities.

"Mangrove" refers to an assemblage of plants from five families with common ecological, morphological, and physiological characteristics that allow them to live in tidal swamps. Worldwide, at least 34 species in nine genera are considered to be true mangroves. P. B. Tomlinson's recent book, *Botany of Mangroves*, defines this group of plants by five features: 1) they are ecologically restricted to tidal swamps, 2) the major element of the community frequently forms pure stands, 3) the plants are morphologically adapted with aerial roots and viviparity (producing new plants instead of seeds), 4) they are physiologically adapted for salt exclusion or salt excretion, and 5) they are taxonomically isolated from terrestrial relatives, at least at the generic level. "Mangrove swamp" or "mangal" refers to communities characterized by mangrove plants.

Mangrove trees are used for water-resistant timber, charcoal, dyes, and medicines. They resist coastal erosion during storms and possibly promote land-building processes by trapping sediment and producing peat. The protective subtidal root system of the red mangrove serves as nursery ground for many commercially valuable species of fishes, shrimps, lobsters, crabs, mussels, and oysters. An assorted fauna of birds, reptiles, and mammals is also at home in the mangrove thickets and tidal channels.

Human disturbances have made a heavy impact on many mangroves near populated areas as a result of dredging and filling, overcutting, insect control, and garbage and sewage dumping. The intertidal environment of mangroves is endangered by pollutants in the water, air, and soil. Accidental oil spills appear to be particularly damaging. Oil and tars not only smother algae and invertebrates, but also disrupt the oxygen supply to the root system of the mangrove trees by coating the respiratory pores of the intertidal prop and air roots.

A Mangrove Laboratory in Belize

Belize (formerly British Honduras), boasts the longest barrier reef of the Northern Hemisphere, extending 220 kilometers from the Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and open ocean. Mangroves border most of the coastline, extend upstream from countless river mouths, and fringe or cover most lagoon cays.

One of these is Twin Cays (Figure 1)—an island divided into two by an S-shaped channel. Twin Cays has become our study site and experimental field laboratory. Although we usually spend the nights and conduct laboratory bench work on nearby Carrie Bow Cay—site of the National Museum's coral reef field station for the last 15 years—most days and many nights are spent in the mangrove channels, lakes, ponds, mud flats, and even the trees. A self-contained weather station established on one of the mud flats transmits data on wind, sun, rain, temperatures, and tides to a portable computer on Carrie Bow Cay.

The bibliographies on mangroves show that during the last 200 years more than 6,000 papers have been published describing biological and geological details from almost as many different swamps over the world. Our ongoing study aims to

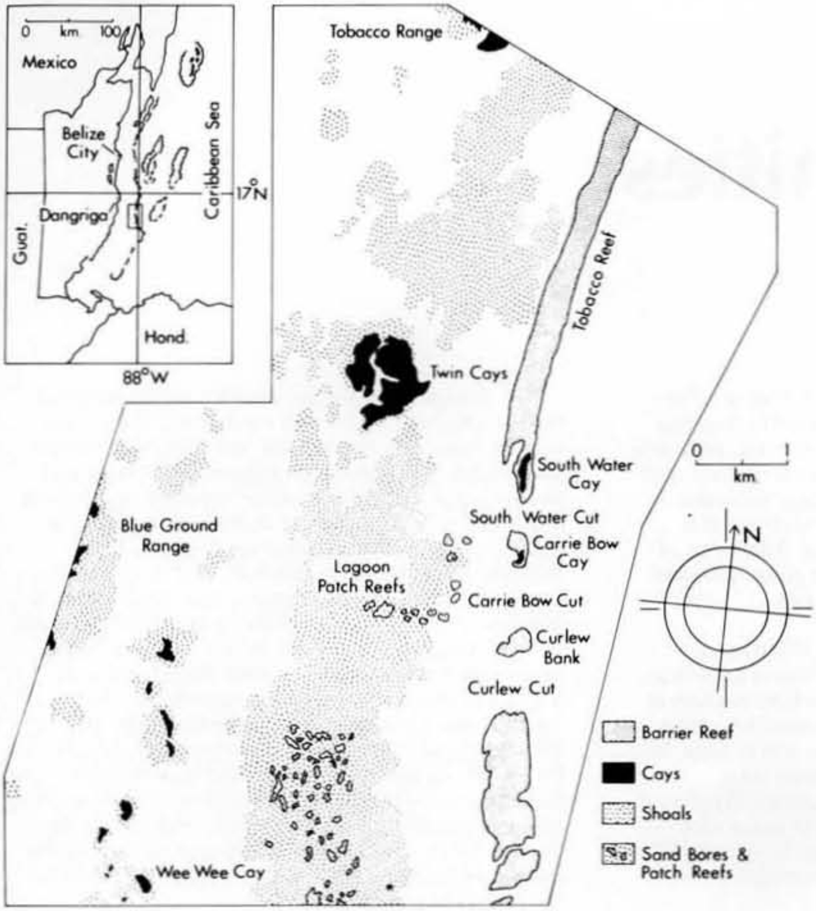


Figure 1. Mangrove ecosystem study area, Twin Cays, Belize. The National Museum of Natural History's coral reef field station is located on Carrie Bow Cay, about 4 kilometers southeast. (From Rützler and Macintyre, 1982, Smithsonian Contributions to the Marine Sciences 12*)*

analyze as many components as possible of a single mangrove swamp and, ultimately, assemble them to a mosaic reflecting structure as well as function of this unique ecosystem.

Geological History of Twin Cays

A popular theory holds that mangroves are builders of land because they trap and hold fine sediments. Early on in our study we discovered that this is not necessarily true. We tried to reclaim nearby Curlew Cay, which had been lost to a hurricane (it is now known as Curlew Bank), by planting an assortment of young red mangroves, but were unsuccessful. So the question arose, if islands are not built by mangroves, how do they get started?

To learn more about the Holocene (recent time—back to 18,000 years before present) stratigraphy under the present island, Ian G. Macintyre of the Smithsonian Department of Paleobiology, along with Robin G. Lighty and Anne Raymond of Texas A&M University, drove pipes 8 meters into the sediment, down to the Pleistocene level (marks the beginning of the Holocene), and retrieved sediment cores that date back 7,000 years.* They also collected rock cores below this level.

What they found below the mangroves was a carbonate substrate consisting of a dense limestone formed mostly by finger corals (*Porites*) with abundant mollusk fragments, indicating an environment of deposition similar to today's calm-water patch reefs. The sequence of peat, algal-produced sand, and mangrove oysters in the sediment cores indicates that this mangrove was apparently established on a topographic high formed by a fossil patch reef, and kept pace with the rising sea level. However, there is also evidence that the island repeatedly changed its size and shifted position, generally building with lagoon sediments on the windward coasts, while eroding at the leeward edge, which is characterized by shallow-water bottoms formed by stranded peat deposits.

The mangrove community itself can be thought of as being composed of three components: the above-water "forest," the intertidal swamp, and

* Although the Holocene can date back as much as 18,000 years, there are only 7,000 years of sediment accumulation in this particular area, as sea level did not flood the Belize lagoon until the upper Holocene.

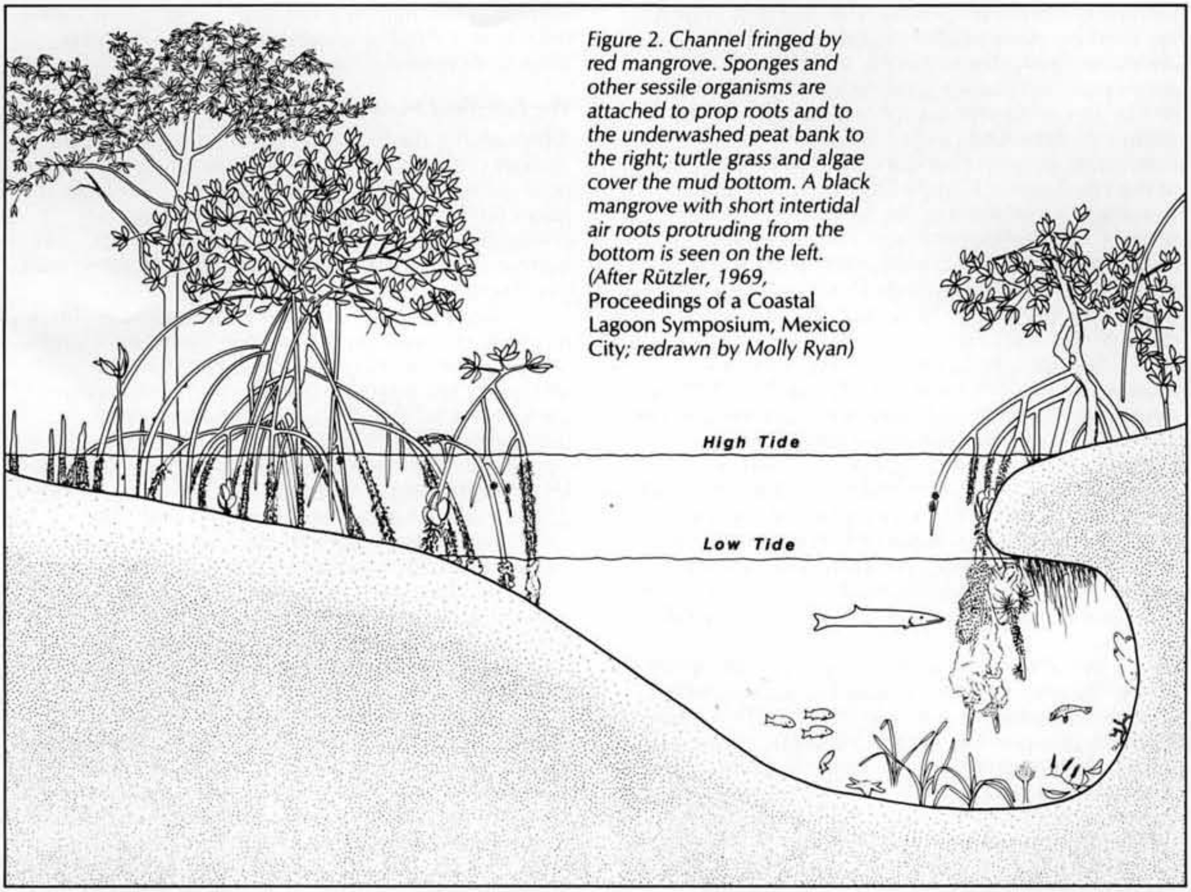


Figure 2. Channel fringed by red mangrove. Sponges and other sessile organisms are attached to prop roots and to the underwashed peat bank to the right; turtle grass and algae cover the mud bottom. A black mangrove with short intertidal air roots protruding from the bottom is seen on the left. (After Rützler, 1969, Proceedings of a Coastal Lagoon Symposium, Mexico City; *redrawn by Molly Ryan)*

the underwater system (Figure 2). In our descriptions, we will start from the bottom and work up.

Environments Below the Tides

The bottom of the mangrove from the intertidal to 3 meters, the greatest depth of the main channel, is composed of what most people would call muck. To us, it displays many varieties, such as carbonate silt, mud, and sand with varying amounts of mucus, organic detritus (products of plant and animal decay), peat, and silicious skeletons derived from diatom algae and sponges. Many fine-grained limestone sediments are produced by physical and biological erosion on the nearby reef and carried into the mangrove by water currents. Sands, on the other hand, are primarily produced within the community by digestion or decay of calcareous green algae (*Halimeda*).

The most abundant and ecologically important plant on the submerged mangrove bottoms is the turtle grass (*Thalassia*). It stabilizes the muddy bottom, offers substrate for egg cases and many small sessile organisms, and provides food and shelter to animal groups ranging from microbes to 2-meter manatees. Jörg A. Ott, a seagrass ecologist from the University of Vienna, determined that turtle grass in the Twin Cay mangrove is more dense, and grows 3 times faster than *Thalassia* in the nearby open lagoon, resulting in an almost 10-fold net leaf production.

Red mangrove stilt roots line all channels, creeks, and ponds and, below tide level, support spectacularly colored clusters of algae, sponges, tunicates (sea squirts), anemones, and many associates. They also provide hiding places for many mobile animals, such as crabs, lobsters, sea urchins, and fishes.

Algae without the ability to root in mud bottoms abound on the stilt roots. Mark Littler, from the Smithsonian Department of Botany, and co-workers Diane Littler and Philipp Taylor found that, curiously, fleshy algae seem to prefer roots that had penetrated the water surface, but had not yet reached the bottom of the channel or lake. Calcifying algae (such as the sand-producing *Halimeda*), on the other hand, are common on the submerged parts of anchored roots and along the channel banks. Experiments demonstrated that the hanging roots offer palatable plants protection from benthic (bottom-living) herbivores such as sea urchins and many fishes, whereas *Halimeda* has its own skeletal protection.

Certain algae and many sessile invertebrates on the subtidal mangrove roots are protected from predators by toxic substances stored in their tissues and produced by their own metabolism. Sponges are particularly well-known for their antibiotic and feeding-deterrent properties. The sponges, in turn, are used by many smaller organisms, such as anemones, polychaete worms, shrimps, crabs, amphipod crustaceans, gastropod mollusks, and brittle stars as an effective physical and chemical shelter. Collaborating with our Smithsonian colleagues, Kristian Fauchald, Gordon Hendler (now at the Los Angeles County Museum), and Brian Kensley, we extracted up to 40 species and 400 specimens of endozoans (species living within another) larger than 2.5 millimeters from, as an example, a 1-liter fire sponge (*Tedania*), a species that causes burning, itching, and even severe dermatitis in humans.

Sponges are among the most common, massive, and colorful invertebrates in the submerged mangrove. To settle and metamorphose, their larvae need solid substrate with low exposure to sedimentation, although we observed grown specimens surviving for months buried in light mud after they had fallen from their place of original attachment. Only two kinds of firm substrate are available to such settlers, red mangrove stilt roots, and vertical or overhanging banks composed of a felt of peat and mangrove rootlets and flushed by tidal currents.

In both locations, the competition for space is fierce, not only among sponges, but also between sponges and other sessile organisms, such as algae, hydroids (the polyp-generation of many medusae), corals, anemones, bryozoans (moss animals), and tunicates (sea squirts). With our colleagues Dale Calder, Royal Ontario Museum, Ivan Goodbody, University of the West Indies, and Jan Kohlmeyer, University of North Carolina, we are analyzing the sequence of settlement of species at different seasons, following their growth and methods and hierarchies of competition.

We have found that within days new substrates (wood, plastics) are colonized by ubiquitous bacteria, fungi, and lower algae. Next to arrive are coralline algal crusts, sponges, hydroids, scyphozoan polyps (the polyp stage of the upside-down jellyfish *Cassiopea*), anemones, serpulid and sabellid worms, bryozoans, and ascidians (the latter two are colonial, encrusting organisms). After 3 to 6 months, substrates are fully covered by a spectrum of organisms. This spectrum varies greatly, and depends on the season in which the experiment was started, the habitat position of the substrate, and the environmental endurance of the settlers.

Not all subtidal mangrove life is restricted to the bottoms and roots. Fishes of all size and age classes hide or feed in the water column around the red mangrove roots and along the banks. Many of these depend on plankton, such as copepods and other small crustaceans (shrimp-like animals), for food. Members of both groups form characteristic swarms during the day. Smithsonian's Frank Ferrari teamed up with Julie Ambler, Texas A&M University, Ann Bucklin, University of Delaware, and Richard Modlin, University of Alabama, to study the systematics, ecology, and genetics of the swarms and found population densities much greater than expected. They counted more than 2,000 copepods per cubic meter of water in a small bay at night, and estimated 100 million individuals congregated during the day in a band of swarms along a 1,000-meter stretch of channel bank.

The Intertidal Mangrove Swamp

Although the tidal range in the Caribbean is small, in shallow coastal areas it can strongly influence current flow and distribution of organisms. At Twin Cays, the mean tidal range is only 15 centimeters, yet a combination of astronomical, geomorphologic, and meteorologic factors can cause a range of more than a half meter.

Red mangrove (*Rhizophora*) prop roots, black mangrove (*Avicennia*) pneumatophores,* peat banks, and mud flats are the typical substrates of the intertidal zone supporting distinctive communities. Barnacles (*Chthamalus*), wood boring isopods (*Limnoria*), oysters (*Crassostrea*), and "mangrove oysters" (*Isognomon*, not a true oyster) are the best known indicators of intertidal hard substrates, while fiddler crabs (*Uca*) are typical for the mud flats. Green algal mats (*Caulerpa, Halimeda*) are found exposed on peat-mud banks during low tide. The most abundant and characteristic intertidal mangrove community, however, is called the bostrychietum, named after the principal components of an association of red algae (*Bostrychia*, with *Catanella* and *Caloglossa*).

The bostrychietum (see page 16) has a remarkable water-holding capacity, which allows the plants and their associated animals to survive extended dry periods. We measured water loss rates in two of the substrate species and found evidence of two different methods of water retention. *Bostrychia* is a delicate, tufted plant that holds water primarily interstitially (between the branches). *Catenella* is more fleshy and less elaborately branched, and holds water intracellularly (within the cells), in its tissues.

Loren Coen, Dauphin Island Sea Lab, examined the animal associates of the bostrychietum, particularly in respect to grazing. He found that amphipods (*Parhyale*) become concentrated in the algal mats in high numbers during receding tides, and that their grazing on *Bostrychia* can match or exceed the algal growth. The mangrove tree crab, *Aratus*, and other crabs from the low-tide level were also found with large quantities of *Bostrychia* in their guts.

Desiccation and related problems of increased temperature and salinity in organisms subjected to exposure at low tide became particularly apparent during an extreme low tide in June 1983. A 20-centimeter zone below mean low-tide level became exposed during noon hours under a clear sky.

Large communities of low intertidal (rarely exposed) and subtidal (never exposed) organisms,

* A feature of many mangroves is that some part of the root system is exposed to the atmosphere. In an oxygen-poor substrate, oxygen is absorbed directly from the atmosphere. In the black mangrove, these aerial roots, termed pneumatophores, occur as direct upward extensions of the subterranean root system.

such as occupants of seagrass meadows (including the turtle grass itself), and mangrove mud banks and stilt roots, were killed during the long exposure to desiccation. Estimates indicate that more species of algae and invertebrates, and much more living matter (biomass), were destroyed during those days of June than during two hurricanes combined (Fifi, 1974; Greta, 1978).

Collaborating eco-physiologist Joan Ferraris, Mt. Desert Island Biological Laboratory, is examining a number of organisms (sponges, sipunculan worms, shrimps, crabs) that are exposed to strong salinity-temperature stress in their natural environment. Results so far show a fine correlation between experimental tolerances in the animals and range of variability of stress factors in their natural habitat. In the case of sponges, regulatory mechanisms controlling water-ion balances are still unknown, but in the absence of organs, they must take place inside individual cells.

Unfortunately, the intertidal swamp is not only an exciting biological study zone, but also a gallery of pollutants. Even in this remote location every imaginable piece of floating debris discarded by man can be found, washed in by currents among the mangrove roots and deposited by the receding tides.

Mangrove Forest Above the Tide

Unlike the adjacent marine systems, the above-water flora and fauna of the mangrove-covered islands appear less complex and diverse. From the water, an unbroken, monotonous barrier of red mangrove trees confronts, and frequently intimidates, the casual explorer.

The species composition of the above-water plant community around Twin Cays is relatively simple. Three halophytic* tree species, known collectively as mangroves, dominate the natural vegetation on most of the islands: Red mangrove (*Rhizophora*), black mangrove (*Avicennia*), and white mangrove (*Laguncularia*). On cays with slightly higher ground, additional woody and herbaceous (soft-stemmed) halophytes are associated with the mangrove, such as buttonwood (*Conocarpus*), saltwort (*Batis*), and sea purslane (*Sesuvium*).

In general, mangrove forests have well-defined horizontal zonation. On these mangrove islands, the seaward and channel margins typically are fringed by dense, 4- to 10-meter-tall stands of red mangrove. Behind this fringe, the red mangrove is usually more open and shorter, with black and white mangroves intermixed. The zonation is easily recognized: dull gray-green spires of black mangrove, and flattened, yellow-green crowns of white mangrove stand slightly above and behind the dark green dome of the fringing red mangrove.

The interiors of some of the larger islands off Belize, like Twin Cays, have several extensive, unvegetated mud flats and shallow ponds. Numerous stumps throughout the mud flats are evidence that the trees that once grew there fell victim to some environmental stress. The red mangrove trees growing around the margins of the mud flats and in the ponds are severely stunted and widely spaced. Over the years, these natural bonsai have been distorted and pruned by their environment into fantastic forms, seldom more than 1.5 meters tall.

The above-water fauna on the cays is considered by most investigators to be introduced from the Belizean mainland. Even on the largest mangrove islands, most of the "land" is intertidal; therefore, the only environments available to terrestrial animals are arboreal. The fauna is limited to birds, lizards, snakes, snails, and arthropods, such as land crabs, spiders, and insects. These animals probably reached the cays from the mainland by flying, or rafting on or in pieces of wood and other floating debris.

A few land bird species have established permanent breeding populations on the mangrove islands. Warblers, vireos, hummingbirds, cuckoos, grackles, and white-crowned pigeons are among the permanent residents. Several of the islands also provide nesting sites for ospreys. These birds frequently build their nests atop tall snags of black mangrove.

At Twin Cays, the green-back heron is the most commonly observed wading bird. It breeds on the island, and builds its twig nest in the red mangrove fringe along the channels. It is frequently seen diving for small fish in the shallow, interior ponds. The most conspicuous birds of the area are the brown pelican and frigatebird, which fly overhead or perch in mangrove trees.

Insects are, by far, the most diverse and abundant group of above-water animals inhabiting the Belizean mangrove cays. Ants, in 28 or so species, are clearly the most abundant. Termites, because of their huge nests and extensive covered walkways, are the most conspicuous. Some major groups of insects, such as bees, are poorly represented in mangrove fauna. As is other tropical ecosystems, a large percentage of the insect species that we have found associated with mangroves are undescribed.

Conclusions

The red mangrove fringe, the specialized vegetation, the physical environment, and the associated fauna and flora form a complex and diverse island community above water as well as below. We have learned that mangroves produce fine sediments and organic detritus, and stabilize them by modifying the wave and current regime of the open lagoon. The inventory of species has yet to be completed, but already we have shown that most phyla are represented by species of which 10 to 25 percent, and in some cryptic (having a hidden or concealed lifestyle) microscopic-sized groups, up to 60 percent, are undescribed. The mangrove swamp is rich in recycled nutrients and high in production rates, but its occupants are severely stressed by factors such as

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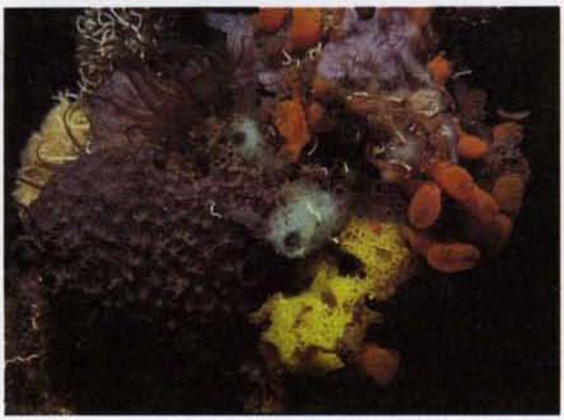
* A plant growing in salty soil or salt water, termed a halophyte, has unique physiological characteristics that enable it to obtain fresh water, excrete salt, and reduce fresh water loss.

A Gallery

"Boston Bay," Twin Cays. In the foreground are prop roots of red mangroves (Rhizophora). (Photo by K. Rützler)

Stinging sea anemone (Bunodeopsis) on turtle grass. (Photo by G. Miller)

Black mangrove (Avicennia) pneumatophores. (Photo by M. Parrish)



Sponges, ascidians, and anemone on a submerged root. (Photo by K. Rützler)

Clapper rail. (Photo by S. Canupp)

# of Mangrove Life

Seahorse (Hippocampus). (Photo by G. Miller)

Young upside-down jellyfish (Cassiopea) on mud bottom. (Photo by K. Rützler)

Mangrove oysters (Isognomon). (Photo by K. Rützler)

Starfish (Oreaster). (Photo by K. Rützler)

Drift goods deposited by the tides under black mangroves. (Photo by M. Parrish)

Carrie Bow Cay Field Station

A small field station located just behind the barrier reef in Belize has served as a base for research by the Smithsonian Institution and other scientists since 1972. The facility has been made possible largely through the generosity of the Bowman family, whose members have lived in the Stann Creek District of Belize for several generations. Being naturalists in their own right, the Bowmans were easily convinced to dedicate part of the island to research on the biology and geology of Belize's barrier reef.

Since its founding in 1972, the National Museum of Natural History's coral reef field station has undergone continuous improvements. Some changes were necessitated by research requirements, others by the devastating effects of hurricanes Fifi (1974) and Greta (1978). The original buildings on the small island of Carrie Bow (at present, about 0.4 hectares, or 1 acre), consist of an old plantation house, carried disassembled across from the mainland, and two smaller cottages. During most of the 1970s, the small cottages and parts of the big house provided sleeping space for only six persons, and necessitated combining the laboratory and workshop into a single room. A small kitchen provided cooking space. Electricity supplied by a small portable generator was limited to short periods during the day and evening.

After damage from hurricane Greta in 1978, the laboratory cottage had to be rebuilt. It was enlarged by adding a second story, thus providing additional sleeping space and allowing the research laboratory and workshop areas to be separated. The old outdoor aquarium system with low-volume seawater flow was improved by increasing capacity and enclosing the area with wood siding and windows to protect it from the weather.

In 1985, a new agreement with the Bowman family allowed expansion of living and laboratory space to the upper level of the big house. The resulting renovations added badly needed dry space for instruments, library, and computer. At the same time, the smallest cottage was replaced by a better designed, larger building serving as a dormitory, and a new, separate, and sound-isolated compressor and generator house was built. Other renovations include boat moorings, water tanks and showers, kitchen, and replacement of all electric wiring and fixtures. Some new equipment was added, such as a 4-kilowatt diesel generator, two new 5-meter dive boats, two microscopes, a centrifuge, an electronic balance, air and water filtration systems, and two propane-gas refrigerators. To improve safety, the boats were provided with radiophones compatible with the station's main radio, and a radio-telephone line was established to the Royal Air Force Helicopter Detachment in Belize City, who helped develop logistics for emergency evacuation in case of a diving accident. Plans for 1988 call for an increased seawater capacity with larger pumps, a solar power system, and a 6,000-liter storage tank, and for improved water quality by extending the water intake pipe to the fore reef.

Finally, in step with the upscaled mangrove study, we established a self-contained weather station in Twin Cays, 4 kilometers to the northwest. Meteorological and oceanographic sensors are automatically scanned every half hour, and data sent via radio to a portable computer on Carrie Bow Cay. By mid-1988, transmitted data will also be received at the International Airport, Belize, for evaluation and use by the Meteorological Office.

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salinity and temperature fluctuations, desiccation potential, abundance of fine sediments, and shortage of firm substrates. Space, from the sea bottom to the tree tops, is distinctly partitioned by the animals that exploit this specialized plant community. These intertidal islands, because of their isolation from the Belizean mainland, provide us with ideal locations to study pure mangrove communities in the Caribbean.

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