
Mangrove Swamp Communities: An approach in Belize*

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Abstract

Belize has the longest barrier reef of the northern hemisphere, extending 220 kilometers from 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 the coastline, extend upstream of the countless river mouth and fringe or cover most lagoon cays. Twin Cayss has become our study site and experimental laboratory. The purpose of this chapter is document the biology, geology, ecological balance, economic importance, and aesthetic value of a prominent coastal ecosystem.

The inventory of species has yet to be completed, but the most phyla are represented by species of which 10 to 25 percent, and in some microscopic-sized groups up to 60 percent, are undescribed.

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. The mangrove community itself can be thought of as being composed of three components: the above-water "forest", the intertidal swamp, and the underwater system. The mangrove produce fine sediment and organic detritus and stabilize them by modifying the wave and current regime of the open lagoon. Furthermore, the mangrove swamp is rich in recycled nutrients and high production rates but its occupants are severely stressed by factors such as salinity and temperature fluctuations, desiccation potential, and size grain sediment.

Resumen

Belice posee la barrera arrecifal más grande del hemisferio norte, extendiéndose 220 kilómetros desde el borde Mexicano al norte, hasta el Golfo de Honduras al sur. Detrás de esta barrera se sitúa un enorme sistema lagunar promediando 25 km entre el continente y el mar abierto. Los manglares que bordean la mayor parte de la línea de costa, se extienden río arriba por las innumerables bocas

del río y cubren la mayoría de los cayos lagunares. La localidad de los estudios y laboratorio experimental se encuentra en los Cayos Twin. El propósito de este capítulo es documentar la biología, geología, balance ecológico, importancia económica y valor estético de este notable ecosistema costero.

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El inventario de especies aún **está siendo integrado**, y la **mayor parte de los phyla están representados por especies de las cuales entre el 10 y el 25% no están descritas y algunos son grupos crípticos de tamaños microscópicos. Dentro del ecosistema, el manglar rojo de franja, la vegetación especializada, el ambiente físico y la fauna y flora asociada conforman una comunidad insular compleja y diversa tanto por arriba del agua como por debajo. La comunidad de manglar por sí misma, puede considerarse que está constituida por**

tres componentes: el bosque por debajo del agua, los pantanos de intermarea y el sistema por arriba del agua. Los manglares producen sedimentos finos y detritus orgánico, estabilizándolos por la modificación del oleaje y el régimen de la laguna abierta. Además, el pantano del manglar es rico en nutrientes reciclados y altas **tasas de producción**, pero sus habitantes están severamente estresados por **factores tales como las fluctuaciones de salinidad y temperatura**, la desecación potencial y la granulometría del sedimento.

Introduction

"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 E.F. Ricketts depicted the mangroves in 1941 in the "Sea of Cortez." Many people will agree with them. So why have two dozen scientists from the Smithsonian Institution, primarily 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. 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 the mouth of the Rio de la Plata 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 at least 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 vivipary (producing new plants instead of seeds)**, 4) they are physiologically adapted for salt exclusion or salt excretion, 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, tannins, dyes, and medicines. They resist coastal erosion during storms and have the reputation of promoting land-building processes by trapping sediment and producing peat. The protective subtidal root system of red mangrove is quoted as serving as nursery ground for many commercially valuable species of fishes, shrimps, lobsters, crabs, mussels, and oysters. An attractive 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 water, air, as well as in the 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.

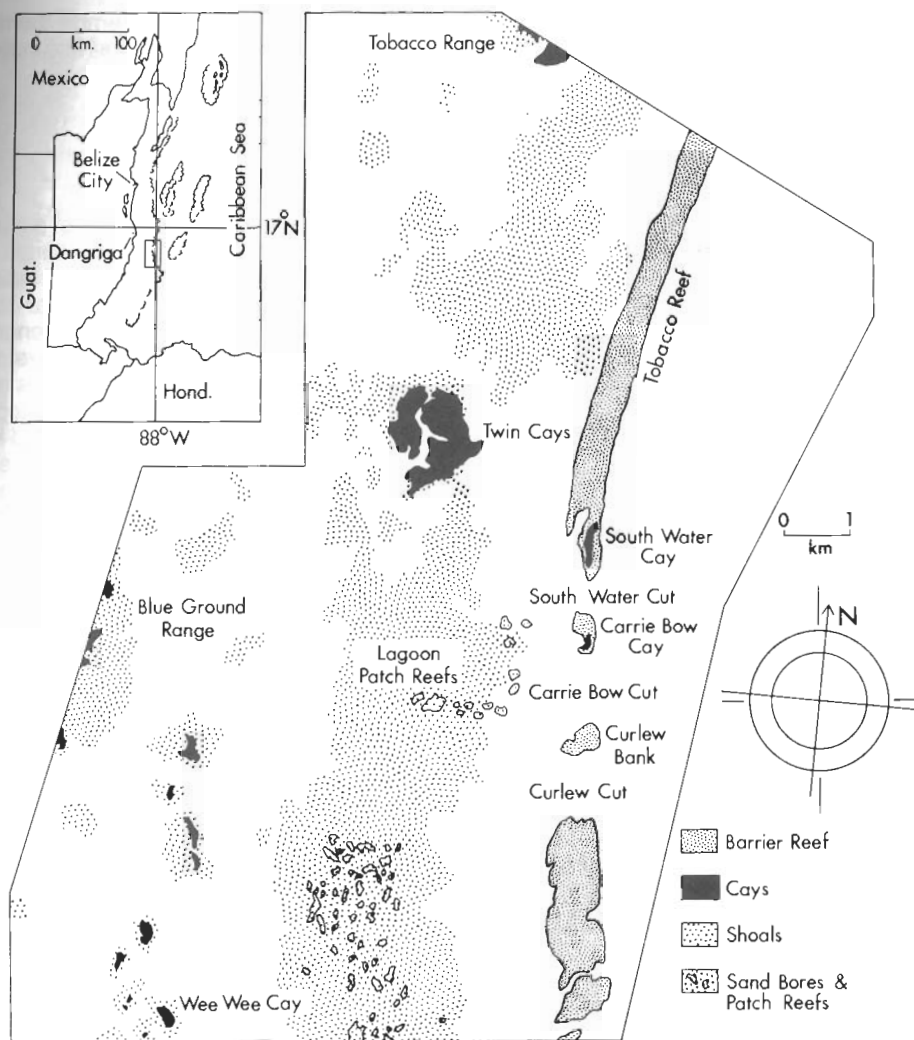


Figure 1. Map of study area, Twin Cays, Belize. The National Museum of Natural History's coral reef field station is located on Carrie Cay, about four kilometers southeast. (from Rützler and Macintyre, 1982, *Smithsonian Contributions to the Marine Sciences* 12)

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 of the countless river mouths, and fringe or cover most lagoon cays.

One of these is Twin Cays (Fig. 1)—an island divided into two by an S-shaped channel. Twin Cays has become our study site and experimen-

tal field laboratory. Although we usually spend the nights and conduct lab bench work on nearby Carrie Bow Cay—site of the National Museum's coral reef field station for 20 years (founded in 1972)—most days and many nights are spent in the mangrove channels, lakes, ponds, mudflats, and even the trees. Many important climatic parameters are monitored by a self-contained weather station on Carrie Bow Cay. Selected oceanographic measurements, such as tides, temperature, turbidity, salinity, are recorded at substations in the swamp. 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

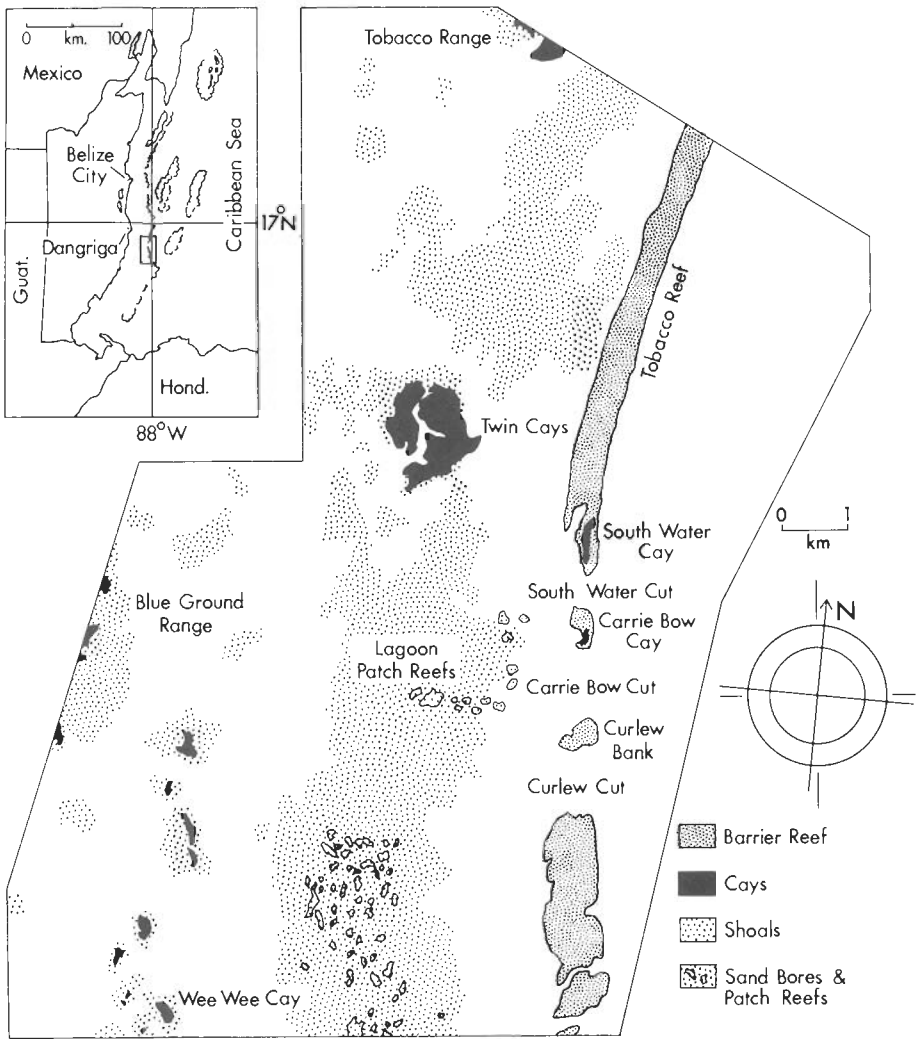


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almost as many different swamps over the world. Our ongoing study aims to analyze as many components as possible of a single mangrove

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 Ann 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 which date back seven thousand years, the maximum sediment accumulation in this particular area. 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 indicate 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 transgressing 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 the underwater system. In our descriptions, we will start from the bottom and work up.

Environments Below the Tides

The bottom of the mangrove (Fig. 2), from the intertidal to three 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 siliceous 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 three 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 coworkers 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 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

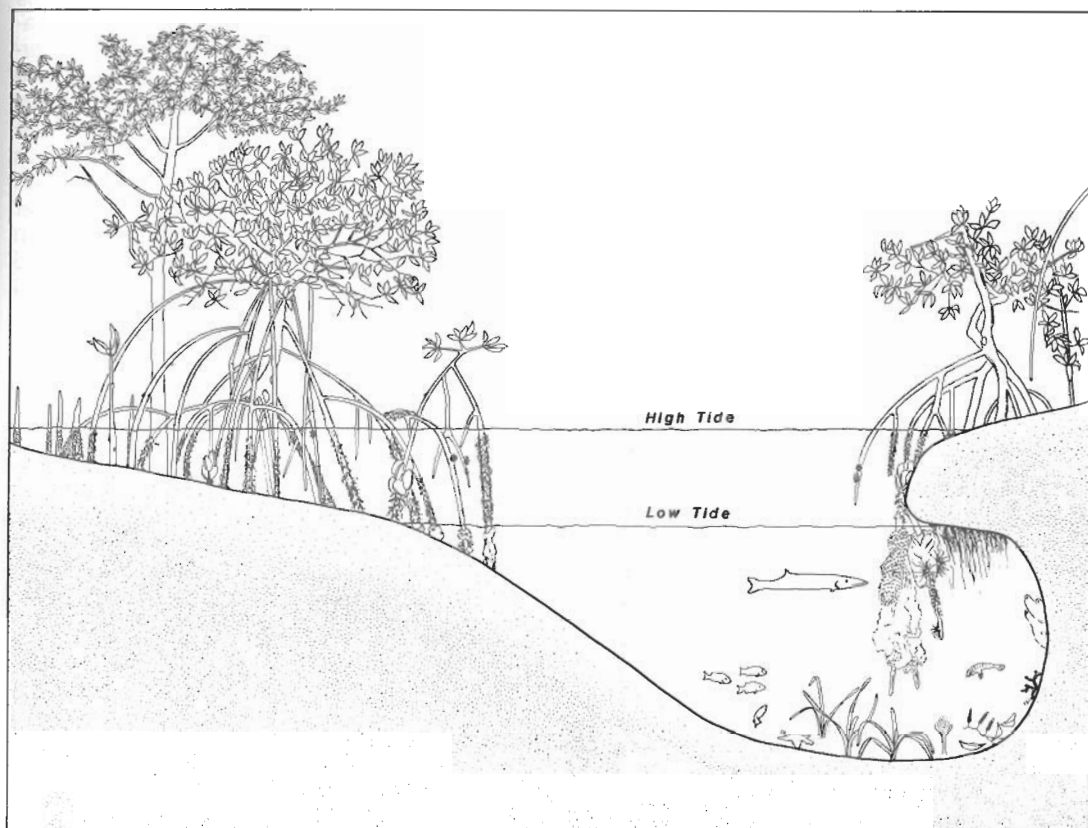


Figure 2. Channel fringed by red mangrove. Sponges and other sessile organisms are attached to prop roots and to the underwashed peat bank to the right; turtle grass and algae cover the mud bottom. A black mangrove with short intertidal air roots protruding from the bottom is seen on the left. (After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

their antibiotic and feeding-deterrent properties and 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 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 sub-

strate are available to such settlers, red mangrove stilt roots, and vertical or overhanging banks composed of a peat and live 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 subsequently the methods and hierarchies of competition.

We have found that within days new substrates (wood, plastics) are colonized by ubiquitous bacteria, fungi, and lower algae. The 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. After 3 to 6 months, substrates are fully covered by a spectrum of organisms. The 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 copepod and mysid crustaceans, for food. Mem-

bers 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 two thousand 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 1000-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 astro-nomic, geomorphologic, and meteorologic factors can cause a range of more than a half meter.

Red mangrove (*Rhizophora*) prop roots, black mangrove (*Avicennia*) pneumatophores (aerial roots), peat banks, and mudflats 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 *Catenella* and *Caloglossa*).

The bostrychietum (Fig. 3) 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 Marine Laboratory, 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 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, 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, National Institutes of Health, is experimentally 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.



Figure 3. The bostrychiatum 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: Candy Feller)

Mangrove Forest Above the Tide

Unlike the adjacent marine systems, the supratidal 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 mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). On cays with slightly higher ground, additional woody and herbaceous halo-

phytes 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 mudflats and shallow ponds. Numerous stumps throughout the mudflats 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 mudflats 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 over 1.5 meters tall. A. Lugo and S. Snedaker, in their 1974 review of mangrove ecology, estimated the age of comparable dwarf trees in south Florida and the Florida Keys to be 40 years old. Our collaborators Irving A. Mendelssohn, Karen McKee, and Colin D. Woodroffe (Wetland Biogeochemistry Institute, Louisiana State University) suggest that abiotic factors, such as high sulfide levels in the soils, may be responsible for the die-back and reduced tree vigor.

The supratidal 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 birds species have established permanent breeding populations on the mangrove islands. James F. Lynch (Smithsonian Environmental Research Center) reports that the mangrove yellow warbler is the most characteristic land bird throughout the cays, but the Yucatan vireo is also a well-established resident on most of the cays. Both of these species are insectivorous. The hummingbird, *Anthracoceros*, has been observed nesting in red mangrove on Twin Cays but not on smaller islands. Mangrove cuckoos, grackles, and white-crowned pigeons, common on the large mangrove islands, are also thought to be 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 clapper rail with its loud, rather sudden clattering is more often heard than seen, although occasionally one can catch a glimpse of it walking under the prop roots of red mangrove where it feeds on crabs. The green-back heron is the most commonly observed wading bird at Twin Cays. 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 frigate bird, which can always be seen flying overhead or perched in mangrove trees.

Only four or five reptile species are known from the Belizean mangrove cays. James F. Lynch has found one species of lizard (*Anolis sagrei*) to be ubiquitous on the islands. It is commonly seen in red mangrove trees, feeding on ants, termites, and other insects. Less common is the boa constrictor (*Boa*) which populates most of the larger islands. The ground iguana (*Ctenosaura*) and a couple of gecko species are present only on a few of the islands.

Two common land crab species occur on the islands. The mangrove tree crab (*Aratus pisonii*, currently under study by Kim Wilson, Central Connecticut State University) moves up and down the bole and aerial roots of red mangrove. *Ucides*, the largest land crab on the islands, lives on the ground under the dense mangrove canopy where it builds large, extensive burrows near the upper limits of the high tide. Belizean fishermen consider the burrows of *Ucides* to be the primary breeding sites for sandflies and mosquitoes. William P. Davis (Environmental Protection Agency, Gulfbreeze, Florida) and D. Scott Taylor (Vero Beach, Florida) have found *Ucides* burrows to be havens for the mangrove *Rivulus*, a hermaphroditic fish.

The periwinkle (*Littoraria angulifera*) is widespread on all the mangrove islands. These arboreal snails migrate slowly between the mean high water level and the tops of red mangrove trees; they are the subject of thesis research conducted by Laurie Sullivan, University of Alabama. Brad Bebout and Jan Kohlmeyer, University of North Carolina determined that these snails feed on a fungus that is restricted to a very narrow zone on the prop roots, just above the mean high-water level.

Insects are, by far, the most Species-rich and abundant group of supratidal 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 the mangrove fauna. As in other tropical ecosystems, a large percentage of the insect species that we have found associated with mangroves is undescribed.

The surface of the salt water, the interior ponds, and the mudflats provide habitats for aquatic and semiaquatic insects, including members of five families of true bugs (Hemiptera) and three families of beetles (Coleoptera). Paul J. Spangler and Robin Faitoute (Department of Entomology, Smithsonian Institution) studied this group alongside similar fauna

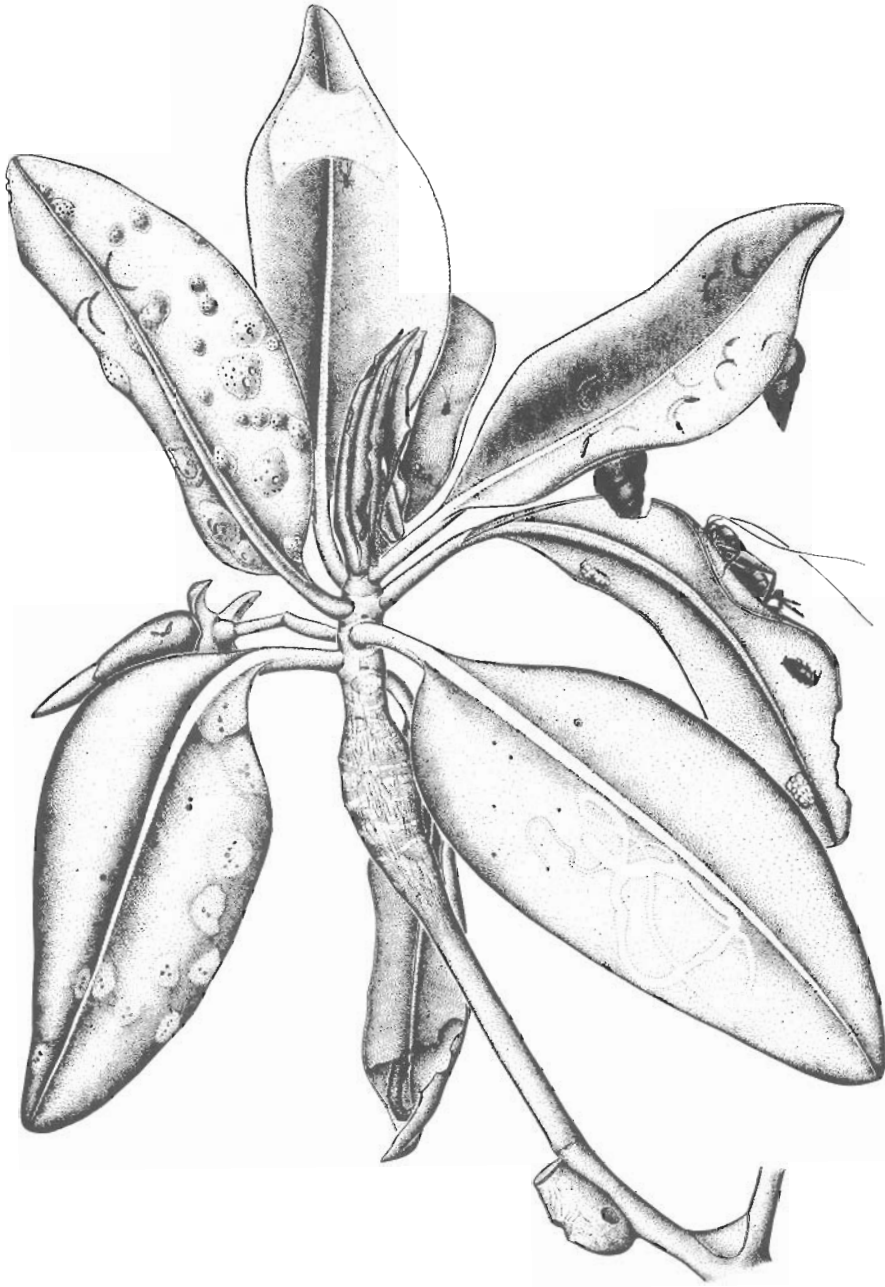


Figure 4. Red mangrove twig terminal with associated organisms. (Illustration: Candy Feller)

on the mainland. The cays have fewer kinds of aquatic habitats, and a corresponding lower species diversity in this part of the insect fauna.

Wayne N. Mathis (Department of Entomology, Smithsonian Institution) found an astounding 51 species of shore flies (Ephydriidae) along the margins of these mangrove islands although none of these species is endemic. Most of these

species are detritivores, living on the peat-based muck or in decaying seagrass and algae that wash ashore.

The mangrove trees and mangrove associates provide numerous supratidal habitats for primary and secondary phytophagous insects as well as their parasites and predators. Because most of these species have cryptic behavior, the diversi-

ty of insects in mangroves can easily be underestimated. The foliage of each species of mangrove supports a unique suite of leaf-eating insects, although the damage to the leaves is much more apparent than the insects themselves.

Leaves and twig terminals of red mangrove, in particular, serve as an important habitat for a diverse assemblage of insects (Fig. 4). Because vegetative growth in the canopy is derived almost exclusively from apical buds in twig terminals, herbivore damage here is particularly important to the tree. The apical bud is commonly attacked by a moth larva (*Ecdytolopha* sp) that causes the enveloping stipules to turn black. A larva usually eats only a portion of the young, folded leaves in a bud, leaving the meristematic tissue intact. However, sometimes the entire apical bud is destroyed as a result of this form of herbivory and any potential for further growth by the damaged twig is lost. A number of other moth larvae feed on red mangrove leaves, but because insect taxonomy is based primarily on adult specimens, identifications of these larvae are almost impossible without rearing them. Moth larvae that feed on leaf surfaces encase themselves in a variety of protective coverings, such as frass tubes or portable cases built of mangrove twigs and bark. Serpentine galleries of a leaf, twig, and propagule mining moth larvae (Microlepidoptera, Gracillariidae) are also common on red mangrove, although both larval and adult specimens are rare. Adult insects that feed on these leaves are primarily nocturnal. A guild of at least six species of wood-boring insects are primary herbivores on the twigs of red mangrove. Ordinarily, each twig hosts only one

individual. As it feeds, the larva hollows the twig. When the adult wood-borer emerges via an exit hole, access is provided to the hollow twig. These spaces are critical to many small arthropods, including ants, other insects, and spiders, that are not wood-eating and are dependent on finding suitable spaces in which to build nests or to take refuge. So far, we have found more than 70 species associated with hollow red mangrove twigs.

At least 35 species of xylophagus (wood eating) beetles and moths have been extracted from the three mangrove species. More than half of these are wood-borers in the Long-Horned Beetle family (Cerambycidae). Although some of the species are generalists, feeding on any available dead wood, a few specialist species appear adapted to a single mangrove species. Our research indicates that these arboreal wood-borers play significant roles in the mangrove ecosystem. The larval stages of these insects are the primary herbivores. They modify the trees by constructing galleries and pupal chambers in the living and dead woody tissue. These spaces are used as habitats by numerous invading arthropods, such as ants, termites, other beetles, spiders, isopods, scorpions, pseudoscorpions, scale insects, centipedes, crickets, katydids, and roaches. The infestation by wood-borers is extensive on the islands; all species of mangroves and almost every tree sampled have hosted at least one and usually several species. Wood-borers girdle, as well as hollow, mangrove stems and boles. In red mangrove, these activities frequently result in death, weakening, and subsequent pruning of all branches beyond the point of attack.

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 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 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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