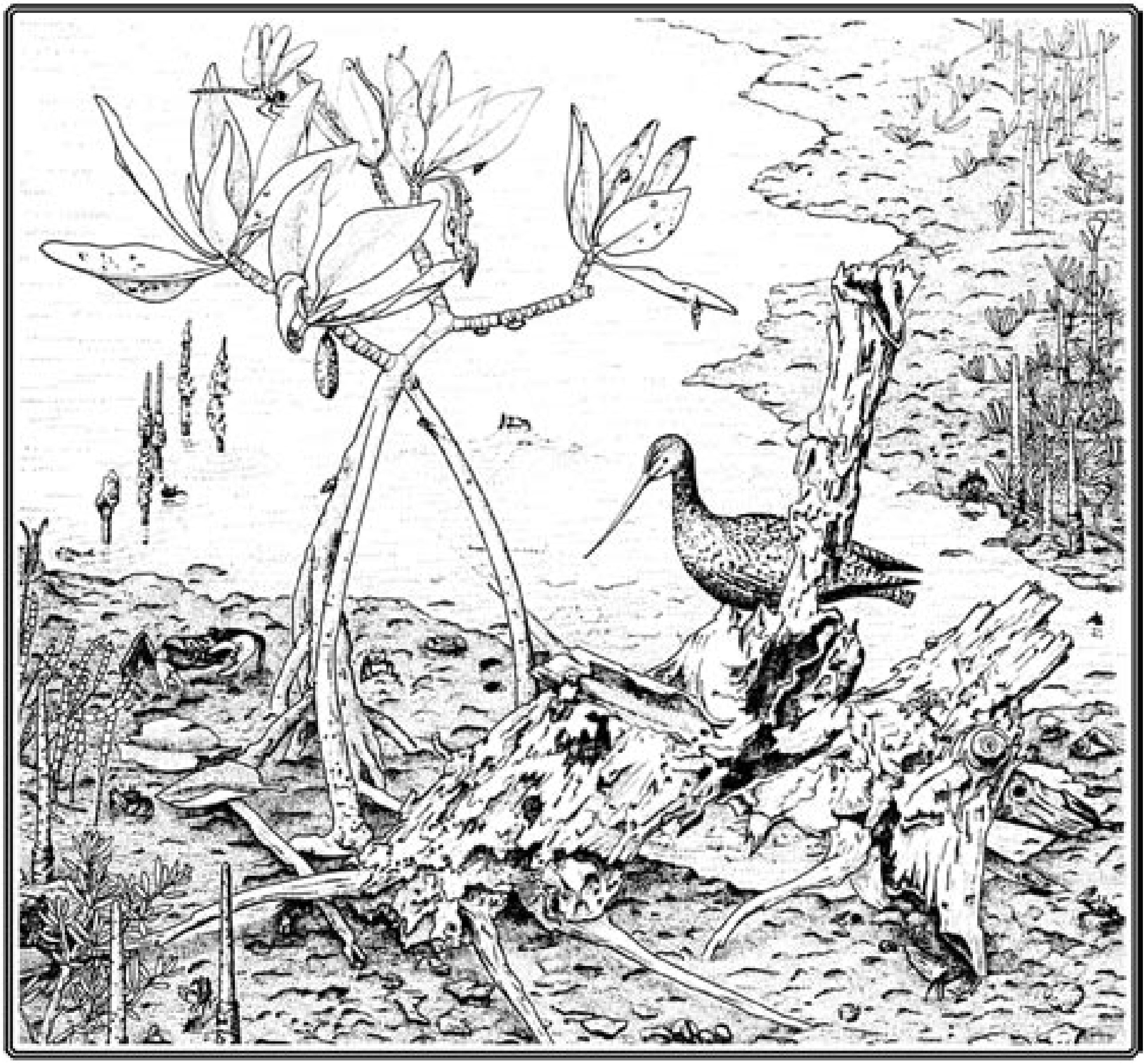

MANGROVE ECOLOGY WORKSHOP MANUAL

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Cover illustration provided by Molly Kelly Ryan, Dept. of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560

MANGROVE ECOLOGY:
A Manual for a Field Course

A Field Manual Focused on the
Biocomplexity on Mangrove Ecosystems

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Editors' preface

Intertidal mangrove swamp communities dominate the world's tropical and subtropical coasts, paralleling the geographical distribution of coral reefs. They survive in substrate salinities ranging from fresh water alongside rivers to hypersaline ponds and mudflats. Mangrove plants are pioneer as well as mature-phase species. They not only help form these environments, they create habitats for a diverse and characteristic community, including numerous mangrove-dependent organisms.

The term "mangrove" refers to an ecological rather than a taxonomic assemblage of plants. Worldwide, 34 species or so in nine genera in five families are considered "true mangroves" and another 80 or so species occur as "minor components" and "mangrove associates." True mangroves are ecologically restricted to tidal swamps and form extensive monospecific stands. They are morphologically adapted with aerial roots and vivipary. As halophytes, they are physiologically adapted for either salt exclusion or excretion. Taxonomically, true mangroves are isolated from their nearest terrestrial relatives, at least at the generic level.

Mangroves are critical, not only for sustaining biodiversity in these intertidal swamps, but also for their direct and indirect benefit to human activities. Energy and nutrients are assimilated and stored in leaves of mangrove trees. As a detritus-based ecosystem, leaf litter from these trees provides the basis for adjacent aquatic and terrestrial food webs. Because most energy and nutrients are biotically stored rather than free in the water or substrate, species diversity of these swamps is directly dependent on primary productivity by mangrove plants. Mangrove swamps function as nurseries for most of the sport and commercial fishes found in deeper waters. Mangrove swamps also provide feeding grounds for large reef fishes. As a result, mangrove-assimilated energy and nutrients are exported to surrounding coral reefs.

Besides supporting and renewing coastal fishing stock, mangrove swamps also benefit human economic development by stabilizing shorelines. This is a critical function in tropical coastal areas that are periodically battered by tropical storms and hurricanes. Bangladesh offers examples of the devastation that can happen when deltaic and island mangrove swamps are deforested. "Land" in mangrove swamps is peat, produced primarily by red-mangrove rootlets. This organic substrate is not soil and cannot sustain human activities such as agriculture, buildings, or dredging. Undisturbed, mangrove swamps can buffer the effects of storms and protect property and human life behind these coastal fringes.

Mangrove forests are generally oligotrophic ecosystems. Human-caused enrichment is one of the major global threats to these and other coastal environments. Our experiments show that nutrients are not uniformly distributed among or even within mangrove forests and that soil fertility can switch from conditions of nitrogen to phosphorus limitation across narrow gradients. Likewise, not all ecological processes respond similarly to the same nutrient. Enrichment affects plant growth, metabolism, and tissue quality, which in turn affect primary consumption. It alters litter quality, thereby linking nutrient enrichment to detritivory, decomposition, and below-ground processes. Interactions and feedback among nutrient availability, microbial communities, nutrient cycling, and higher trophic levels have not been explored in mangrove forests. Enrichment with nitrogen and phosphorus may affect microbial communities and activity, nutrient dynamics, photosynthesis, and ultimately, peat accumulation and habitat stability. Furthermore, hydrology and sediment physico-chemical parameters may also influence these interactions and feedbacks.

Despite their ecological and economic significance, mangrove swamps are an imperiled ecosystem. Throughout the tropics, they are threatened directly and indirectly by commercial development. Tropical and subtropical mangroves support adjacent marine communities and ecosystems, including seagrass beds and coral reefs. However, little is known about the intra-wetland processes that regulate those interactions and how they are affected when the coastal zone is altered by eutrophication.

Increased industrial development as well as destruction of inland tropical forests for agricultural development indirectly impact coastal and island mangrove swamps through water pollution from industrial effluent, oil spills, sewer discharge, and agricultural and sediment runoff. Oils and sediments destroy mangroves by coating their stilt roots and pneumatophores; this blocks air passages that ventilate the submerged root systems and enable aerobic respiration to occur. Sewer discharge and agriculture runoff dump large amounts of nitrogen and phosphorus into coastal waters, drastically changing 'nutrient conditions. Although research is ongoing to determine the effects of nutrient over-enrichment on mangrove plant growth and interactions with other organisms, evidence is accumulating that increased nutrient availability to the primary producers results in increased insect populations and increased damage to mangroves by insect herbivores. This modification at the base of both aquatic and terrestrial food webs may impact the entire mangrove system in ways not yet understood or studied.

The objectives of this manual are:

1. Introduce students to the biological complexity of mangrove ecosystems;
2. Provide students with training and experience in field ecology;
3. Offer opportunities for students to formulate and test hypotheses in a field setting, to conduct research in a field setting, and to summarize and present results based on data collected in the field;
4. Encourage and foster self education and discovery;
5. Initiate and stimulate cultural interactions and scientific collaborations among students of different backgrounds;
6. Increase the awareness of the ecological roles, economic importance, and cultural significance of mangrove ecosystems

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Marsha Sitnik
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Part I: Lectures

A. Mangrove Ecosystems: Definitions, Distribution, Zonation, Forest Structure, Trophic Structure, and Ecological Significance

By Karen L. McKee

Major Points of Chapter

1. Mangroves are a taxonomically diverse group of tropical trees and shrubs, yet are all adapted to growth in the intertidal zone.
2. The major controls on mangrove distribution are climate, salinity, tidal fluctuation, sedimentation, and wave energy.
3. Mangrove species distributions across the intertidal zone often lead to distinct zonation patterns, which vary depending on floristic composition, geomorphology, and local factors.
4. Mangrove forests also vary in structural attributes such as species richness, canopy height, basal area, tree density, and understory development.
5. Although mangrove ecosystems are typically characterized as based on a detrital food web, a grazing food web also exists.
6. Although once thought of as unproductive, transitional systems, mangrove swamps are now viewed as highly productive, ecologically important ecosystems.

Definitions

The term "mangrove" refers to an assemblage of tropical trees and shrubs that grows in the intertidal zone. Mangroves include approximately 16 families and 40 to 50 species (depending on classification). According to Tomlinson (1986), the following criteria are required for a species to be designated a "true or strict mangrove":

1. Complete fidelity to the mangrove environment.
2. Plays a major role in the structure of the community and has the ability to form pure stands.
3. Morphological specialization for adaptation to the habitat.
4. Physiological specialization for adaptation to their habitat.
5. Taxonomic isolation from terrestrial relatives.

Thus, mangrove is a non-taxonomic term used to describe a diverse group of plants that are all adapted to a wet, saline habitat. Mangrove may typically refer to an individual species. Terms such as mangrove community, mangrove ecosystem, mangrove forest, mangrove swamp, and mangal are used interchangeably to describe the entire mangrove community.

Distribution

Mangrove distribution is circumglobal with the majority of populations occurring between the latitudes of 30° N and S (Tomlinson 1986). At one time, 75% of the world's tropical coastlines was dominated by mangroves. Unfortunately, mangrove extent has been significantly reduced due to human activities in the coastal zone. There are two centers of mangrove diversity: the Eastern group (Australia, Southeast Asia, India, East Africa, and the Western Pacific) where the total number of species is approximately 40 and the Western group (West Africa, Caribbean, Florida, Atlantic South America, and Pacific North and South America) where the number of species is only 8. Thus, New World forests are relatively depauperate compared to Old World forests.

In Belize, there are three true mangrove species: *Rhizophora mangle* (red), *Avicennia germinans* (black), and *Laguncularia racemosa* (white). A fourth species, *Conocarpus erectus*, is an important mangrove associate in Belize that is transitional between the true mangroves and non-mangrove species. At first glance, these species may appear very similar, but closer inspection reveals differences in morphology, physiology, and reproductive biology. These species can be distinguished using characteristics such as growth form, bark, and structure of leaves, twigs, aerial roots, flowers, and fruits/propagules.

Reproductive Strategies

Mangroves have little capacity for vegetative propagation and are thus dependent on seedlings for forest maintenance and spread (Tomlinson 1986). Although some species (*A. germinans* and *L. racemosa*) can resprout from stumps (coppicing), this process is not equivalent to propagation. Mangroves exhibit two relatively unique reproductive strategies: hydrochory and vivipary (Tomlinson 1986; Rabinowitz 1978). Hydrochory (dispersal by water) is a major means which mangrove spreads seeds, fruit, and/or propagules. Tidal action can carry mangrove diaspores great distances from their point of origin. Vivipary refers to the condition in which the mangrove embryo germinates while still attached to the parent tree. A number of mangrove species, including *R. mangle*, for example, may remain attached to the parent tree for 4 to 6 months and attain lengths of 25 to 35 cm at "maturity," they fall to the ground or into the water where they are dispersed by the tides. The embryo of *A. germinans* breaks through the seed coat but remains enclosed in the fruit wall until detachment. Upon falling into the water, the thin pericarp is quickly shed, leaving the seedling, which is composed of two folded cotyledons. *Laguncularia racemosa* is not considered to be viviparous, but germination often occurs during dispersal. Vivipary increases the chances of successful establishment in an unpredictable environment where germination of seeds would typically be inhibited.

Limits on Mangrove Distribution

Extensive development of mangroves has occurred in the estuaries of large rivers flowing over shallow continental shelves, such as the Ganges in Bangladesh, Fly River in Papua New Guinea, and the Mekong Delta in Vietnam. The Amazon and Congo, the two largest rivers in the world, do not have extensive stands of mangroves primarily because of the huge outflow of freshwater. The following factors are considered to be the major determinants of mangrove distribution:

1. Climate. Mangroves are tropical species and are not tolerant of freezing temperatures. Their latitudinal limits worldwide vary depending on air and water temperatures (Tomlinson 1986; Waisel 1972; Sherrod *et al*. 1986; Sherrod & McMillan 1985). The abundance of mangroves is also affected by aridity, and development is much greater along coasts that have high inputs of rainfall (Macnae 1968; Golley *et al.* 1975).
2. Salinity. Salt is generally not a requirement for growth, since most mangroves can grow in freshwater (Tomlinson 1986; Ball 1988). However, they do not develop in strictly freshwater habitats because of competition from freshwater species. Salinity is thus important in eliminating other vascular plant species that are not adapted for growth in a saline habitat.
3. Tidal fluctuation. Tidal influence is also not a requirement, but plays an important indirect role:

a. Inundation with saltwater helps exclude most other vascular plants and reduces competition.
   b. Tides bring saltwater up estuaries against the outflow of freshwater and extend mangrove development inland.
   c. Tides transport sediment, nutrients, and clean water into the mangrove environment and

export organic carbon and reduced sulfur compounds.

d. Where evaporation is high, tides help flush soils and decrease salinity.

The effect of this "tidal subsidy" can be seen on two landscape scales:

1) A regional or geographic scale—mangroves reach their greatest development around the world in low-lying regions with large tidal ranges (Tomlinson 1986; Macnae 1968; Golley *et al.* 1975).
2) A local scale—trees closest to the edges of land masses, which are subject to the largest fluctuations of the tide, are obviously larger and more productive than trees in the interior (Mendelssohn & McKee 2000).

4. Sediment and wave energy. Mangroves grow best in a depositional environment with low wave energy according to Tomlinson (1986). High waves prevent propagule establishment, expose the shallow root systems, and prevent accumulation of fine sediments.

Zonation

Spatial variation in species occurrence and abundance is frequently observed across environmental gradients in many types of ecosystems (Davis 1940; Smith 1992; Mendelssohn & McKee 2000). Zonation of plant communities in intertidal habitats is particularly striking and often results in monospecific bands of vegetation occurring parallel to the shoreline. Although zonation patterns are usually depicted in a manner that suggests a rigid sequence proceeding from the shoreline to upland regions, many patterns resemble a mosaic with vegetational patterns occurring repeatedly where the land mass is interrupted by watercourses or other variations in topography.

Mangroves exhibit zonation patterns in a number of different geographic regions (Davis 1940; Smith 1992; Mendelssohn & McKee 2000). The large variation in floristic composition of mangrove communities means that patterns of species distribution across the intertidal zone will vary substantially among geographic regions. For example, patterns for Florida and the Caribbean often show *R. mangle* (red mangrove) occupying the seaward zone, followed by *A. germinans* (black mangrove), and *L. racemosa* (white mangrove) in the most landward position. That pattern may be contrasted with a profile for northeastern Australia (Queensland), which is not only more complex due to a higher number of species, but the relative position of congeneric species is reversed from that in Florida (*e.g.*, *Avicennia* spp. in the seaward position and *Rhizophora* spp. in the landward position).

Zonation patterns in mangrove forests may also vary on a local scale. Occurrence of species may differ across an estuary, apparently in response to differences in freshwater input. For example, species found at the seaward end of the estuary may be absent from the headwaters. Although zonation typically refers to patterns created by segregation of different species, differences in stature and productivity of plants across environmental gradients may also result in readily discernible patterns. Zones may be comprised of different architectural forms that represent variations in height and vigor.

Several hypotheses have been proposed to explain species zonation patterns in mangroves: 1) zonation reflects land building and plant succession (Davis 1940); 2) geomorphological processes cause vegetation zonation (Thom 1967); 3) differential dispersal of propagules across a gradient results from a physical "sorting out" of species by tidal action (Rabinowitz 1978); 4) differential predation of propagules across the intertidal zone eliminates some species from certain zones (Smith 1987; *Smith et al.*1989, but see McKee 1995); 5) physiological specialization limits distribution of species to certain portions of the gradient where physicochemical conditions differ (Ball 1988; McKee 1993, 1995); and

6) interspecific competition (Ball 1980).

Succession due to land building is not considered to be a viable explanation for zonation by many mangrove ecologists, since evidence shows that mangroves respond to, rather than cause, coastal propagation (Thom 1967). However, it's clear that some mangrove systems in sediment-poor environments have built vertically through deposition of organic matter (mangrove peat) (Woodroffe 1983; McKee & Faulkner 2000). Mangroves are probably best viewed as steady-state cyclical systems migrating toward or away from the sea depending on sea-level rise or fall, sedimentation rates, topography and tidal energy (Lugo 1980). Coastal geomorphology is important in determining physical and chemical conditions for mangrove development and may explain regional differences in zonation patterns. Geomorphology as an explanation of intertidal zonation patterns is unsatisfactory, however, because it provides no insight as to how the interaction of geomorphological processes with vegetation causes a segregation of species. The remaining four hypotheses—dispersal dynamics, seed predation, physiological tolerance, and interspecific competition—offer clear explanations for mangrove zonation. The relative importance of these processes is currently uncertain, but probably varies among geographic regions.

In addition to horizontal spatial patterns, mangroves exhibit vertical stratification. There are three major strata that are readily observed along tidal creeks: supratidal, intertidal, and subtidal. A unique assemblage of organisms associated with the mangrove vegetative structures characterizes each of these strata. The supratidal stratum includes the arboreal portions of the forest and is occupied by birds, reptiles, crabs, snails, insects, and spiders. The intertidal stratum extends from the high to low water tidal heights and encompasses the aerial root systems of the mangroves and peat banks. The organisms inhabiting this zone (*e.g.*, barnacles, isopods, crabs, oysters, amphipods, snails, and algae) experience periodic submergence by the tides. The subtidal stratum occurs below the low water mark where the mangrove roots and peat banks provide substrate for organisms adapted to constant submergence (*e.g.*, algae, sponges, tunicates, anemones, octocorals, shrimp, polychaetes, brittlestars, nudibranchs, jellyfish, and seagrasses).

Forest Structure

In addition to zonation, mangrove forests are also characterized by attributes such as species richness, canopy height, basal area, tree density, age/size class distribution, and understory development. Lugo & Snedaker (1974) described six mangrove forest types based on size, productivity, and composition in Florida: riverine, overwash, fringe, basin, scrub, and hammock. These forest types reflect differences in geomorphology and hydrology and are generally applicable to forests in the Caribbean Region. Species richness appears to be influenced by temperature, tidal amplitude, rainfall, catchment area, freshwater seepage, and frequency of cyclones (Tomlinson 1986; Lugo & Snedaker 1974).

Another structural characteristic of mangrove forests is the frequent absence of understory species, which are usually found in other forest systems (Janzen 1985). Shrubs, grasses, lianas, and other herbaceous plant species do not usually occur under the closed canopy in the mangrove forests. The lack of understory is probably related to the combination of salinity and flooding stresses and low light levels, which exceeds the tolerance limits of plants (Lugo 1986). An understory may develop, for example, where the canopy is open (allowing light penetration to the forest floor) or where rainfall or freshwater runoff lowers salinity levels. There may also be a second layer composed of mangrove seedlings and juveniles, but densities are greatest in light gaps.

Although mangrove forests are usually described as having an even-aged size class structure, the data supporting this viewpoint are not extensive. It is thought that large-scale disturbances such as hurricanes kill large areas of forest, which then regenerate at about the same time from seedlings or previously established juveniles. This view of even-aged structure in mangrove forests does not agree with what is known about the dynamic processes in other forest ecosystems. Forest systems are now viewed as mosaics of patches that vary in size and contain individuals of different ages or stages of development. These patches have resulted from natural disturbance events that create openings or gaps in the forest. Preliminary work indicates that gap dynamics may be an important process structuring mangrove forests. Natural disturbances such as lightening strikes, wind damage, and frost are often associated with the development of patches or gaps in mangrove forests. Recent work in Belize, however, demonstrates that wood-boring insects are primarily responsible for the creation of gaps in red-mangrove forests (Feller & McKee 2001).

Forest structural characteristics such as canopy height, tree density, and biomass accumulation may be influenced primarily by climatic factors such as rainfall and by nutrient input (Golley *et al*. 1975; Smith 1992). Areas characterized by high rainfall typically have tall canopies, high basal areas, and low tree densities. Similarly, larger, more productive trees typify mangrove forests receiving high inputs of nutrients—for example, those areas used as bird rookeries.

Trophic Structure

Trophic structure refers to the complex interrelationships among the various organisms in an ecosystem through the transfer of food energy from one trophic level to another. The first trophic level (the producer level) is comprised of green plants; the second trophic level (primary consumer level) is comprised of herbivores (plant-eaters); the third trophic level (secondary consumer level) is comprised of carnivores, etc. These trophic levels are linked through food chains; food chains form interlocking patterns called food webs. There are two basic types of food chains: the grazing food chain (green plants to grazing herbivores to carnivores) and the detrital food chain (dead organic matter to detritus-feeding organisms to predators of detritivores).

The traditional view is that mangrove ecosystems are based on the detrital type of food web (Odum & McIvor 1990). Work by Heald (1969) and Middleton & McKee (2001) demonstrated that the leaves of the mangroves fall into the water where they are then consumed by various detritivores, which are in turn eaten by fish and other organisms that feed on the detritus consumers. The grazing pathway is considered to be unimportant in mangroves, since it has been estimated that only 5% of the leaf material is removed by grazing insects before leaf abscission. This value may be an underestimate, however, since work by Onuf *et al.* (1977) shows substantial variation in leaf herbivory among mangrove species and locations. In addition, the contribution of wood-feeding insects to the grazing pathway has not been quantified. Wood-boring beetles may consume living wood and in the process kill branches or whole trees (Feller & McKee 1999; Feller 2002). These activities produce standing dead wood that is then utilized by secondary wood feeders such as termites, which in turn support secondary consumers such as arthropods, lizards, snakes, and birds (Feller & Mathis 1997).

Ecological Significance

Although early workers regarded mangrove forests as unimportant, transitional communities with a low productivity, most ecologists today view them as highly productive, ecologically important systems. Four major roles of mangrove swamps are recognized:

1. Mangroves contribute to soil formation and help stabilize coastlines.

2. Mangroves act as filters for upland runoff.
3. Mangrove systems serve as habitat for many marine organisms such as fish, crabs, oysters, and other invertebrates and wildlife such as birds and reptiles.
4. Mangroves produce large amounts of detritus that may contribute to productivity in offshore waters.

In addition to these ecologically important roles, mangrove forests possess attributes that are specifically important to humans:

1. Mangrove forests serve as protection for coastal communities against storms such as hurricanes. It has been suggested that the large loss of life (300,000 to 500,000 lives) in Bangladesh during the 1970 typhoon was partly due to the fact that many of the mangrove swamps protecting those populated coastal regions had been removed and replaced by rice paddies.
2. Mangrove forests serve as nurseries and refuge for many marine organisms that are of commercial or sport value. Areas where widespread destruction of mangrove has occurred usually experience a decline in fisheries.
3. Many threatened or endangered species reside in mangrove forests.
4. Mangrove forests are also important in terms of aesthetics and tourism. Many people visit these areas for sports fishing, boating, bird watching, snorkeling, and other recreational pursuits.

B. Mangrove Forest Structure

By Thomas J. Smith III

Major Points of Chapter

1. A noted feature of mangrove forest structure is the zonation of tree species into monospecific bands parallel to the shoreline.
2. Several hypotheses have been put forth to explain zonation, including a) plant succession due to land building b) geomorphological factors, c) physiological adaptation to gradients, d) differential dispersal of propagules, e) differential predation on propagules, and f) interspecific competition.
3. The structure of mangrove stands is relatively simple, consisting of only the main canopy and, in some forests, a layer of seedlings beneath it. Understories usually only develop in areas with abundant year-round rainfall and freshwater runoff.
4. In Florida, agents of local natural disturbance in mangrove forests include wind storms, lightning strikes, and frost damage. Hurricanes are sources of large-scale disturbance.
5. Conditions in light gaps differ from those under the canopy in both physical parameters (*e.g.,* temperature and salinity) and biotic characteristics (*e.g.,* crab fauna and frequency of propagule predation). Seedling survival and growth has been demonstrated to be greater in gaps.

Description of a forest's structure may include measures of species composition, diversity, stem height, stem diameter, basal area, tree density, and the age-class distributions and spatial distribution patterns of the component species in the forest. A noted feature of mangrove forest structure is the often-conspicuous zonation of tree species into monospecific bands parallel to the shoreline. Zonation has been a dominant theme in the voluminous literature on mangroves as well as in that on other vegetation types. Zonation, however, is not the only manifestation of structure in mangroves. Lugo & Snedaker (1974) described six types of mangrove forests in Florida, a region with only three mangrove species. Their classification of forests into riverine, overwash, fringe, basin, scrub, and hammock was based on differences in size, productivity, and composition of Florida mangroves, which were caused by differing geomorphic and hydrologic factors.

Mangrove Zonation Patterns

Zonation patterns have been described for Malaysia, East Africa, Australia, Papua New Guinea, Indonesia, India, Burma, Florida, West Africa, and Panama to name but a few. In Belize, the red mangrove *(Rhizophora mangle)* often grows in the low intertidal, while the white *(Laguncularia racemosa)* and black *(Avicennia germinans)* mangroves are more common in the high intertidal zones. Sometimes a species may have a "double distribution." This is a situation in which a species may be abundant in two different zones of the forest.

For example, in the Indo-Pacific region, *Avicennia marina* is often the dominant species in both the lowest and highest intertidal zones and is rare or absent in the middle intertidal. Observations such as this make interpreting zonation patterns difficult.

Several hypotheses have been advanced to explain zonation, including the following:

1) plant succession due to land building
2) response to geomorphological factors
3) physiological adaptation to gradients across the intertidal zone

4) differential dispersal of propagules
5) differential predation on propagules across the intertidal
6) interspecific competition.

At the present time, there is a lively debate among scientists as to just what factor or factors cause zonation in mangrove forests.

1. **Land building and plant succession**. The view that zonation in mangroves represents a successional sequence from pioneer colonizers to mature climax forest is by far the most popular and most often cited mechanism. The idea is that species that grow in the lowest intertidal zone successfully trap sediments. Over time, the sediment builds up and new mangroves are able to invade and outcompete the colonizers. The process continues until the land is no longer intertidal. The key to this explanation is the ability of the colonizer to trap and hold sediment and thus build land.

   Criticism of the “zonation represents succession” hypothesis appeared early in the literature. Watson (1928) claimed that mangroves responded to depositional processes rather than causing them. In Watson’s view, frequency of tidal inundation, salinity, and soil type were the important determinants of mangrove zonation. Egler (1950) presented evidence that each mangrove zone behaved differently in terms of its development and control. He emphasized the roles of disturbance from fire and hurricanes as factors influencing the distribution of *R. mangle, L. racemosa,* and *A. germinans* in Florida.

   The idea of succession in mangroves still appears in the literature. Putz and Chan (1986) analyzed over 60 years of forest composition and growth data from permanent plots in the Matang mangroves of Malaysia. They reported increased species diversity of the forest over time, as shade-tolerant species invaded the understory. *Bruguiera gymnorrhiza*, one of the most shade-tolerant mangrove species, increased most in abundance. It is obvious that within a mangrove forest classical ecological succession can and does occur, as it does in every other of the world’s forest types. This succession, however, is not the result of mangroves building land.
2. **Geomorphological influences**. It is now widely recognized that mangroves respond to geomorphological changes rather than cause the changes themselves. Detailed studies by Thom, Woodroffe, and coworkers have established that mangrove vegetation is directly dependent on the dynamics of sediment topography. Mangroves do not override abiotic land-building processes. Detailed analyses of long-term stratigraphic records from peat deposits also show the dependence of mangrove forest development on geomorphic factors, in particular on relatively stable sea level. During periods of rapid sea-level rise, the size and extent of mangrove forests decrease. Results of these studies, however, leave unanswered questions regarding explanations of zonation based in terms of different biological adaptations of individual species to contrasting physiographic factors within the intertidal environment.
3. **Physio-chemical gradients and zonation**. A dominant theme in vegetation ecology is the idea that a species adapts physiologically to physico-chemical gradients in the environment. Two forms of the “gradient” hypothesis exist: the distinct-preference hypothesis and the same-preference hypothesis. The distinct-preference hypothesis states that each species has its optimum along the gradient which controls where that species occurs. Because different species have different optima, zonation results. An alternate view is that all species share

the same optimum and that other factors (*e.g.,* competition, seed dispersal, predation) cause zonation. The idea of physiological adaptation has been used to explain the zonation patterns observed in a variety of plant communities, including mangroves.

Many environmental parameters vary across the intertidal zone. The most obvious of these, and most often cited, is the frequency of tidal inundation. Low intertidal areas are inundated much more frequently than high intertidal regions. Tidal action introduces two other gradients: soil pore-water salinity and soil waterlogging. These two gradients may not vary in the same way as frequency of inundation. The pattern of soil pore-water salinity across the intertidal is influenced by the salinity of the flooding tidal water, rainfall, and freshwater runoff and seepage. Porewater salinity in the lowest intertidal area tends to approximate the salinity of the flooding water: 35‰ near the ocean and <1‰ at the up stream end of riverine mangrove systems. The pattern of salinity variation in the high intertidal zone is complex. In arid regions, pore- and surface-water salinities in the high intertidal may exceed 90‰. In regions with abundant rainfall and freshwater runoff and seepage, high intertidal salinities are often lower than that of the flooding water. Other factors that vary across the intertidal zone include nutrients such as nitrogen and phosphorus, oxidation-reduction potential, and soil texture. These gradients are often correlated. For example, fine-grained, clay sediments are usually the most highly reduced, whereas coarser sands are more oxidized.

Salinity is one of the most investigated gradients in mangrove distribution ecology. Mangroves, however, are not obligate halophytes. They are fully capable of growing in freshwater. Propagules are capable of survival, but with less than optimal growth, over a broad salinity range (0-100‰ depending on species). Maximum seedling growth for a variety of species occurs between 8-15‰ based on laboratory culture studies.

Seedling establishment by *A. germinans* in Texas was not related to salinity. Survival of experimental seedlings was 100% for salinities 0-57‰, 80% at 65 ‰ and 10% at 75‰. Detailed comparisons between the observed seedling distributions of *Ceriops tagal* and *C. australis* (two Australian mangroves) in the field and their survival and growth performance along a laboratory salinity gradient have been made. The salinity at which seedlings of both species reached their maximum abundance in the field did not correspond to the laboratory salinity at which maximal growth or survival was measured. Both species grew best at l5‰ in the laboratory. In the field, seedlings of *C. tagal* were most abundant between 20-35‰, whereas *C. australis* reached greatest abundance between 50-60‰. Together, these studies indicate that although many mangrove species probably share an optimal salinity range for growth (10-20‰), they are physiologically capable of tolerating an extreme range of soil salinity.

The studies conducted to date clearly demonstrate that many mangroves can grow over the broad range of conditions found across the intertidal zone. Data relating species distributions to soil salinities suggest that two groups of mangroves exist. The first has very broad tolerances and can grow and survive in salinities two to three times that of seawater. The second group appears to be restricted to salinities less than 40‰. This latter group is composed of species that have predominantly upstream distributions in river-dominated estuaries (*e.g.*, *R. mucronata)* or those restricted to geographic areas of abundant rainfall (*e.g.*, *Pelliciera rhizophoreae*). In this regard, it seems that some adaptation to salinity gradients may have occurred which influences distributions within and between estuaries. Not enough data for other physical gradients (*e.g*., soils, nutrients, redox potential) have been collected to examine adequately the physiological adaptation hypothesis.

4. **Propagule dispersal and zonation**. It was hypothesized that zonation in Panamanian mangrove forests was controlled by the influence of tidal action on mangrove propagules. (Because most mangroves are viviparous the unit of dispersal is a propagule, not a true seed.) The mangroves were distributed from low to high intertidal in a manner inversely related to the size of their propagules. *Avicennia germinans* and *L. racemosa* were restricted to high intertidal zones because they had small propagules that high tides would carry the farthest inland. Large propagules, such as those of *R. mangle* and *P. rhizophorae,* would become snagged and not get carried into higher intertidal areas. Thus, tidal action "sorted" the propagules across the intertidal inversely according to their size, which resulted in species zonation.

   Observations of species distributions in Australia and elsewhere, however, indicate that tidal sorting was not a mechanism that influences mangrove zonation patterns. *Sonneratia* spp. routinely colonizes the lowest intertidal zone. The seeds of *Sonneratia* spp. are only some 10-15 mm in length, which is small in comparison to most other mangroves. *Aegiceras* spp. and *Avicennia* spp. also have small propagules and are typically abundant in low intertidal areas. They are also common in the highest intertidal areas. It is obvious that tidal action delivers propagules of all species to all portions of the intertidal zone. The question is not so much whether or not dispersal takes place, as much as it is what factors regulate post-dispersal establishment, survival, and growth.

5. **Propagule predation and forest structure**. Predation on seeds has been recognized as an important process in a variety of ecosystems. Watson (1928) commented on the role of crabs as consumers of mangrove propagules, particularly in the managed forests of west Malaysia. He stated, "The most serious enemies to mangroves are crabs." The crabs to which he referred belong to the family Grapsidae. This group is a ubiquitous feature of mangrove forests, especially in the Indo-Pacific region. Crabs are the dominant macrofauna of mangrove forest soils in terms of both numbers and biomass.

   Consumption of mangrove propagules by grapsid crabs greatly affects natural regeneration and influences the distribution of certain species across the intertidal zone. A series of experiments were performed in which mangrove propagules were tethered in the forest and then the amount of consumption was determined over time (Smith & Duke 1987; Smith 1987a, 1987b). The initial experiments were conducted in northeastern Queensland, Australia. For *A. marina, R. stylosa, B. gymnorrhiza,* and *B. exaristata* there appeared to be an inverse relationship between the dominance of the species in the canopy and the amount of predation on its propagules. This relationship was not found for *C. australis,* however. Caging experiments were used to study the establishment and growth of *A. marina* in middle intertidal forests. *Avicennia marina* is usually absent from this region of the intertidal zone. The results indicated that when protected from crabs, *A. marina* propagules survived and grew. The conclusion was that virtually crabs consumed 100% of the A. marina propagules that were dispersed into middle intertidal forests; hence, propagule predation was an important determinant of the forest's species composition and structure (Smith 1992).

   Subsequent studies indicated that propagule predation was important over a much larger geographic region than northeast Queensland (Smith *et al*. 1989). Data from Malaysia and Florida revealed high levels of predation on the propagules of A. *officinalis* and *A. alba* in Malaysia and on *A. germinans* in Florida. For all three species, predation was higher where the species was absent from the canopy, and it was lower in forests where conspecific adults were present. For *Rhizophora* spp. and *Bruguiera* spp., however, equivocal results were obtained. In Malaysia, results for *B. cylindrica* supported the predation hypothesis, whereas results from *B. gymnorrhiza* did not. No predation on *R. mangle* in Florida was observed, but in Panama more *R. mangle* propagules were consumed in a forest where the species was present in the canopy than were consumed in a forest where it was absent. Studies at Twin Cays in Belize have shown that both *R. mangle* and *A. germinans* propagules are consumed but not in the manner predicted (McKee 1995). The predation hypothesis thus explains only a portion of the observed patterns of mangrove forest zonation.

6. **Competition and forest structure**. Competition has been studied in a variety of wetland plant communities, but few studies have examined the role of competitive interactions in mangrove forests. Competitive interactions between *C. tagal* and *C. australis* have been studied over a salinity gradient in the laboratory. Seedlings were grown in mono- and polycultures at salinities from 0-60‰. *Ceriops tagal* grew better than *C. australis* did at lower salinities, whereas the reverse was true at higher salinities. Competition was gauged by comparing the reduction in growth of each species in the presence of the other to the growth of that species alone. Growth of *C. tagal* was reduced less at salinities from 0 and 15‰ than was *C. australis* at all densities. The effect of *C. tagal* on *C. australis* was some two to four times greater than *C. australis* effect on *C. tagal.* For salinities >45‰, however, this result was strongly reversed, suggesting that *C. australis* was the superior competitor at higher salinities. In the field, however, it was observed that both species were shifted to salinities higher than their growth optima salinities in the laboratory. Additional experimental analyses and long-term studies of permanent forest plots would be very helpful at unraveling the role of competition in mangrove forests.

Stand Structure in Mangroves

Stand structure in mangrove forests is relatively simple when compared to that of other forest types, such as tropical rainforests. The number of strata is often reduced to one: the main canopy. In some forests, a carpet of seedlings may form a second layer, but the abundant lianas and subcanopy trees and shrubs common to most tropical forests are largely absent in mangrove forests. Several hypotheses have suggested that the combination of salinity stress and the need for light are enough to prohibit the development of understory vegetation and, therefore, pose an evolutionary hurdle that has not been crossed. There are mangrove forests with understories, however. These tend to be in areas with abundant year-round rainfall and freshwater runoff. In this situation, a number of smaller tree and shrub species can be found in the forest as mangrove associates, but these species are much more common in freshwater swamp or rainforest environments.

The age- (or size-) class structure of mangrove forests is also characteristic of pioneer, or early successional, formations. Many mangrove forests have an even-aged size-class structure. The question of how this arises in mangroves has not been studied. The possibility exists that a large-scale disturbance will destroy large tracts of forest, which then regenerate at approximately the same time. It has been hypothesized that mangroves in Florida have adapted to a 25-year disturbance cycle, the approximate return time for major hurricanes.

Stand height, density, and biomass accumulation appear to be related to climatic factors, particularly rainfall. A "complexity index," which combines measures of species richness, stem density, canopy height, and basal area, has been used to make geographic scale comparisons across the Caribbean region. The least complex stands were in arid regions. High stem density, but low species richness, height, and basal areas marked these stands. Complex stands, characterized by tall canopies, high basal areas, and lower stem densities, were common in wet, high rainfall areas. Complementary results that are based on different methods are available from the Indo-Pacific region. Rainfall and freshwater runoff appear to be major determinants of stand structure.

Natural Disturbance in Mangroves

A variety of natural disturbance regimes affect mangrove forests. These may be relatively local-scale events such as breakage of branches during windstorms, lightning strikes, frost damage (in more northern areas), and whole-scale destruction of the forest by hurricanes. Gradients in the types and frequency of disturbance are also present across the geographic range of mangrove forests. For example, the mangroves of Panama are not subjected to frost or hurricanes, but are vulnerable to lightning strikes. In south Florida, disturbances from frost, hurricanes, and lightning are common (Odum *et al.* 1982). The influence of disturbance on the structure and function of mangrove forests is poorly investigated and most reports are anecdotal.

A positive relationship between large-scale disturbance (cyclones) and species richness in the mangrove forests of northeastern Queensland, Australia, has been reported. Forests that were impacted, on average, by one cyclone every *5* years had more species than forests affected by fewer storms. Species in the Rhizophoraceae often dominate these forests. In the Sunderbans mangroves of Bangladesh, the Rhizophoraceae is a minor component of the forest community. The Sunderbans are struck by to 40 cyclones a year. The Rhizophoraceae's inability to coppice, in comparison to other groups may account for their vulnerability to cyclones.

Gap Dynamics in Mangroves

Canopy gaps are common in mangrove forests. In addition to what most forest ecologists would recognize as a canopy gap, the low intertidal, accreting mudbanks also act as "light gaps." Individuals in these areas are exposed to more light than are individuals under the nearby canopy. In south Florida, many gaps are created by lightning strikes. Lightning strikes create relatively circular patches in the forest from the top of the canopy to the forest floor. An interesting aspect of lightning strikes is that a number of trees are usually killed rather than a single individual, and those dead trees often remain standing for several years. Seedlings that are present under the canopy are often killed as well. Gaps ranged in size from <10 m^2 to >500 m^2 with the modal size 40-60 m^2. Gaps were evenly distributed across the forest from low to high intertidal zones and from upstream to downstream along the length of the estuaries. Saplings of several species, including *A. marina, B. parviflora, B. exaristata,* and *R. apiculata,* were found to be significantly more abundant in these gaps than under the surrounding canopy.

The physical environment in light gaps is substantially different from that under the surrounding canopy. Measurements made in light gaps in high and low intertidal areas in Australia indicated differences in photosynthetically active radiation (PAR), porewater salinity, and soil temperature. The canopy was so dense that it dampened the annual cycle in PAR, which was pronounced in nearby gaps. There were consistent differences in soil temperature. Sediments in gaps were 3-5°C warmer than were soils under the canopy. Pore-water salinity was also lower in gaps, by 1-2‰ than under nearby canopies.

Seedling survival and growth for several mangrove species have been examined in gap and understory habitats in both high and low intertidal zones. In Australia, survival of A. *marina, R. stylosa, B. gymnorrhiza* and *C. australis* was higher in gaps than under the canopy and greater in high intertidal gaps than in low intertidal gaps. Relative growth rates for all species except *B. gymnorrhiza* were also greater in light gaps.

In Australia, canopy gaps may provide some mangroves with a refuge from seed predators. Predation on propagules of *A. marina* was higher in small gaps and decreased with increasing gap size. Fiddler crabs (primarily *Uca* spp.) dominated the crab fauna in gaps, whereas grapsids dominated under the canopy. Fiddler crabs are not known to consume mangrove propagules, but grapsids do. The increase in soil temperatures that accompanies gap formation may underlie this shift in the crab fauna, as *Uca* spp. appear to prefer warmer sediments.

Conclusion

Despite several thousand publications concerning mangrove forests, a clear understanding of the dynamics in mangrove ecosystems is just beginning to emerge. Of the several hypotheses advanced to account for species zonation, several warrant further attention, but others should be laid to rest. In particular, hypotheses concerning zonation as plant succession and the tidal sorting of propagules clearly are not supported by the available data. Geomorphological factors establish much, but not all, of the framework within which mangrove forests develop. Climatic factors, particularly rainfall, are important determinants of species richness, stand structure, and growth dynamics in mangrove forests. Two groups of mangroves can be identified based on salinity tolerance data, one has a very broad range (0-80‰) and the other has a narrower range (<40‰) of tolerance. Physiological responses to other environmental gradients in the intertidal zone (*e.g.*, soil texture, redox potential, nutrients) do not appear to be sufficient to influence observed zonation patterns. However, more data are needed to address this question adequately. Biotic factors such as predation on propagules are important influences on the distributional patterns of some groups of mangroves and in certain geographic regions. Competitive interactions may be important in determining some aspects of forest structure, but much more experimental and long-term observational work is needed.

A more important consideration is that the dynamics of mangrove forest systems fit within current theories and paradigms developed for other vegetation systems. Ideas of gap-phase dynamics, natural disturbance, and forest mosaics are applicable to mangrove ecosystems and will provide a fruitful avenue for further research.

C. Biodiversity in the Mangrove Supratidal Zone

By Ilka C. Feller

Major Points of Chapter

1. The mangrove supratidal zone consists mainly of arboreal communities.
2. Although the mangrove canopy shows little or no vertical stratification in structure or floristics, the fauna associated with the canopy is distinctly stratified.
3. Several land birds, wading birds, and aquatic birds are permanent residents of mangrove forests.
4. Mangrove forests in the Caribbean are important stopover sites for neartic and neotropical migrant birds.
5. In addition to birds, the mangrove canopy supports many other species including snakes, lizards, crabs, snails, and insects.
6. Insects are the most abundant and species-rich group in mangrove forests above the tide.
7. Insect herbivores play major roles in mangrove ecosystems, affecting plant fitness, nutrient cycling forest structure, and community development.

Because the land that supports mangrove forests is in the intertidal, the principal supratidal habitats available to terrestrial fauna are arboreal. When viewed from a distance, the monotonous canopy dominated just a few tree species gives the impression that the mangrove forest has little habitat diversity and would support few species. Contrary to these first impressions, the above-water portions of mangrove trees support a diverse fauna that includes birds, lizards, snakes, snails, crabs, spiders, and insects. On offshore islands in Belize, biogeographic studies of bird, reptile, insect, and fish populations indicate that these animals are a subset of the mainland fauna, and that they probably reached the islands via swimming flying or rafting on (or inside) pieces of wood and other floating debris (Rützler & Feller 1996).

Vertebrates

The diversity of vertebrates associated with mangrove islands in Caribbean is low, and there are no endemic species. Most vertebrates found on offshore islands and cays occur in greater numbers on adjacent mainland mangrove forests. This situation is strikingly different from Australian mangrove communities, where there are many endemic species, especially birds.

Birds: In Belize, the most common land birds residing on offshore mangrove cays are the Mangrove Warbler and the Yucatan Vireo. They can be found on all but the smallest cays. Both species are insectivorous. The Mangrove Warbler typically feeds by gleaning insects from leaves in the outer canopy, and the Yucatan Vireo feeds in the mid-canopy. The Mangrove Cuckoo, Great-tailed Grackle, Osprey, White-crowned Pigeon, Yucatan Woodpecker, and Green-breasted Mango also reside in these swamps. At Turneffe Islands, the White-crowned pigeon and Great-tailed Grackle use some of the small cays along the eastern side of the atoll for their rookeries.

Belize's mangrove forests also provide nesting sites for several species of resident aquatic birds, including the Clapper Rail, Magnificent Frigatebird, Brown Booby, Great Blue Heron, Green-backed Heron, Yellow-crowned Night Heron, Tricolored Heron, Little Blue Heron, and Brown Pelican. Although the Clapper Rail is more often heard than seen, one can occasionally catch a glimpse of it walking in the intertidal region under red mangrove prop roots and feeding on crabs. Frigatebirds, boobies, and pelicans typically nest in large colonies in the mangrove canopy, but feed offshore. Great Blue Herons and other wading birds can be found nesting in the canopies of large black mangrove trees and feeding in adjacent shallow ponds and dwarf red mangrove stands. Green-backed Herons frequently build their nests low in the branches of red mangrove fringe along protected channels. Besides supporting these resident species, Belize's mangrove forests on the cays and along the coast also provide important stopovers for neotropical and nearctic migratory land and wading birds, such as the Northern Water Thrush, American Red Start; Ruddy Turnstone, Whimbrel, Black-bellied Plover, Sanderling, Least Sandpiper, and Spotted Sandpiper. The aquatic species spend their summers in North America and overwinter in the South American tropics. Small groups of Ruddy Turnstones, mainly first-year birds, linger in the Belize cays for the entire summer.

Rookeries in mangrove forests can affect both biotic and abiotic components of this ecosystem. At the Frigatebird and Brown Boobie rookery on Man-of-War Cay in Belize's Stann Creek District, increased availability of nutrients from the bird guano results in higher mangrove productivity and growth rates, in comparison with nearby islands that are not rookeries. Unlike the tangled maze of stems and roots that typify the low-stature fringe forests of most of the nearby cays, the mangrove trees on Man-of-War Cay are tall (10-15 m) and straight trunked, with few buttressing prop roots. Under the canopy, this forest is relatively open. Although Man-of-War is a very small cay, the insect fauna associated with these tall trees is more species-rich than on much larger, nearby islands (Feller & Mathis 1997). In addition, insect herbivory of mangrove leaves, stems, and roots on the tall trees at this rookery is greater than is suffered by mangroves on these other islands (Feller & Mathis 1997). The input of nutrients from the guano also leads to increased decomposition rates in the substrate and affects nutrient-cycling processes. Adjacent marine communities also respond to this naturally occurring nutrient enrichment. Some marine fungi and algae grow densely in the waters around Man-of-War Cay (Kohlmeyer & Kohhneyer 1987). Some of these species of algae, such as *Ulva* sp. and *Enteromorpha* sp., are typically associated with marine environments that are more eutrophic than the oligotrophic waters typical of Belize's coastal zone.

Reptiles: Only a few reptile species are known from Belize's mangrove cays (Campbell 1998; Platt *et al.* 1999). One small lizard, *Anolis sagrei,* is virtually ubiquitous in these mangrove swamps. It is commonly seen on tree trunks and limbs, where it feeds on ants, termites, and other insects. This species lays its eggs in tree holes. Although more cryptic in their behavior, the boa constrictor *(Constrictor constrictor),* ground iguana or "Wish Willie" *(Ctenosaura similis),* and two gecko species *(Thecadactylus rapicauda* and *Aristelliger georeensis)* are also commonly encountered on the cays. The coastal scrub adjacent to the mangrove community at Turneffe provides habitat for the furrowed wood turtle (*Rhinoclemmys areolata*) and a green tree snake. The islands at Turneffe, particularly in the northern cays, are also home to a large population of the American crocodile (*Crocodylus acutus*) (Platt *et al.* 1999). Although crocodiles are extremely shy and difficult to observe, their trails or "slides" are commonly seen among the mangrove roots along narrow creeks.

Invertebrates

Snails: A species of periwinkle *(Littoraria angulifera*) is common in Belize mangrove forests. It migrates between mean high water level and the tops of red-mangrove trees. It feeds on fungi found in a very narrow zone just above the mean high water level (Kohlmeyer & Kohlmeyer 1987). Brown, semicircular scars on leaf surfaces are evidence of the damage caused by these snails.

Crabs: The mangrove tree crab (*Aratus pisonii*) is found throughout the neotropics. It moves up and down the bole and aerial roots of red mangrove. This omnivorous crab feeds on red mangrove leaves and propagules in the canopy, on algae and detritus in the intertidal zone, and on insect larvae. Its feeding damage in the canopy is recognized by the presence of distinctive, rough-edged cuts and scrapings on the upper surface of leaves. The red-clawed mangrove tree crab *(Goniopsis cruentata*) also climbs trees and moves about under the prop roots. It has been observed feeding on mangrove propagules, leaf litter, insects, and organic material it drags from the water. The hairy land crab *(Ucides cordatus)* is the largest land crab on Belize's mangrove islands. This species frequently occurs in large colonies under dense mangrove cover, builds extensive burrows near the upper limits of the high tide, and scavenges mangrove leaf litter. In areas where these crabs are abundant, they clean the forest floor of leaf litter and propagules. Their flooded burrows are havens for the mangrove rivulus, *Rivulus marmoratus,* a tiny hermaphroditic fish (Davis & Taylor 1987). The Soldier Crab *(Coenobita clypeatus),* a terrestrial hermit crab, is frequently found in mangrove areas with slightly higher tidal elevation, as well as on sand cays and in the coastal scrub adjacent to the mangrove community. The mangrove forest floor and open mud flats also teem with several species of fiddler crabs (*Uca* spp.), which build burrows in the peat. The male of each of these species has a distinctive enlarged fiddler claw.

Insects: Insects are, by far, the most abundant and species-rich group of animals in the mangrove habitat. Because of the difficulty of conducting research in these swamps, few attempts have previously been made to characterize the insect fauna associated with mangroves. Based on relatively few scattered records in scientific literature, most workers have concluded that the mangrove-associated insect fauna, like the flora, is depauperate and unspecialized and plays a minor role in these ecosystems. However, recent studies in Belize's mangrove swamps have revealed quite a different picture (Chemsak & Feller 1988; Mathis 1989, 1990, 1991, 1992, 1993; Spangler 1990; Feller 1995, 2002; Rützler & Feller 1996, 1999). The tropical sun and lack of freshwater in the mangrove create harsh environments for insects, and only a few species are active during the day. Nocturnal and endophytic feeding are common features among many of the mangrove-associated insect species. Because of these cryptic behaviors and the difficult environment for collecting, the complexity of the insect fauna associated with mangroves frequently has been underestimated.

The huge nests (termitaria) and extensive covered walkways, made of chewed wood, of the termite *Nasutitermes* sp. are the most conspicuous signs of insect activity on many of the islands in Belize's coastal zone. However, ants (Formicidae) are ubiquitous and are clearly the most abundant terrestrial animals on these mangrove and coral cays. At least 20 of the 34 species known from the Belizean cays live in direct association with the mangroves, utilizing hollow twigs and branches as nest sites (Feller 2002).

The saltwater surface and mudflats on mangrove islands provide habitats for aquatic and semiaquatic insects, including species representing several families of Diptera, Hemiptera, Odonata, and Coleoptera. Comparable habitats in the mainland mangrove support much greater diversity than the cays in this part of the insect fauna.

The shore-fly family Ephydridae is particularly species-rich in mangrove habitats in Belize. So far, 55 species in this family have been collected along the margins of mangrove islands in the Stann Creek District and Turneffe Atoll (Mathis 1989, 1990, 1991, 1992, 1993). Most species in this family are detritivores. They live on decaying vegetation along the shore. Like other taxa, shore-fly species occupying the cays is a subset of Belize's mainland fauna.

Mangrove vegetation provides numerous supratidal habitats for herbivorous (*i.e.,* plant-eating) insects, along with their parasites and predators. The foliage of each species of mangrove supports a distinctive suite of leaf-feeding herbivores (Feller 1995). However, the damage to leaves is more apparent than are the insects themselves. In Belize, the leaf-feeding guild of insects associated with red mangrove is composed primarily of a mangrove puss moth *(Megalopyge dyeri),* a microlepidopteran leaf miner *(Marmara* sp. nov.), an io moth *(Automeris* sp.), a bagworm *(Oiketicus kirbii),* a bud moth *(Ecdytolopha* sp.), the mangrove tree crab *(A. pisonii),* and several species of crickets (Orthoptera). Each of these species has a distinctive feeding pattern. Except for the leaf miner, which feeds only on red-mangrove leaves, these herbivores are generalists (*i.e.,* they feed on leaves of several plant families).

In addition to the animals that feed directly on leaves, each mangrove species supports a set of arthropods, including insects and their kin, which feed internally within the wood. More than 35 species of wood-feeding insects have been collected from mangrove trees on the cays and mainland in Stann Creek District (Feller 1995, Rützler & Feller 1999). Although some of these woodborers feed on any available dead wood, several species specialize on living trees of a single species of mangrove. For example, live twigs on red mangrove host a feeding guild composed of seven species of specialized wood-boring beetles and moths (Feller & Mathis 1997). Larval stages of these insects feed internally on these twigs, killing them in the process, and creating hollow cylinders of dead wood. Another group of woodborers feed opportunistically on these dead twigs. These wood-boring insects modify trees by constructing galleries and pupal chambers in living and dead woody tissue. These spaces provide critical habitats for ants and numerous other arthropods in the canopy that use them for food, nest sites, prey sites, and diurnal refuge. The animals that use these spaces include ants, spiders, isopods, myriapods, pseudoscorpions, scorpions, crickets, scales, psocopterans, mites, moths, roaches, thrips, buprestids, tenebrionids, anobiids, termites, and cerambycids. More than 70 species of arthropods associated in some way with twigs in the red mangrove canopy.

On the mangrove cays in the coastal zone of southern Belize, woodborers kill branches, which contributes more to the total leaf area lost from the canopy than do all of the leaf-feeding herbivores combined (Feller 2002). In addition to the tiny twig borers, branches of red mangrove host larger woodborers. In particular, the larvae of the beetle *Elaphidion mimeticum* (Cerambycidae) feed on the wood of live red mangrove trees and deeply girdle wood under the bark. This type of herbivory causes death of branches and boles distal to the girdled area. Frequent attacks by this beetle create numerous small gaps in the red-mangrove canopy (Feller & McKee 1999). Thus, insect population dynamics and herbivory have a direct impact on ecosystem-level processes such as forest regeneration, seedling dynamics, nutrient cycling, habitat diversity, and other factors related to light gaps.

Some previous studies have suggested that mangroves do not host a characteristic or specialized fauna (Huffaker *et al.* 1984; Tomlinson 1986). However, surveys of the insects associated with Belizean mangrove islands provide clear evidence to the contrary. For example, a group of tiny moths (microlepidopterans), which are specialized miners of plant tissue of specific species, are particularly diverse in these mangrove communities. In the Caribbean, red mangrove hosts at least four species of miners in the genus *Marmara,* each of which is adapted and restricted to a single type of tissue in this host plant. One *Marmara* species makes winding serpentine mines in leaves. Of the other three, one mines the periderm associated with the distal portion of propagules, another mines the periderm of young stems, and the third mines the periderm of young prop roots.

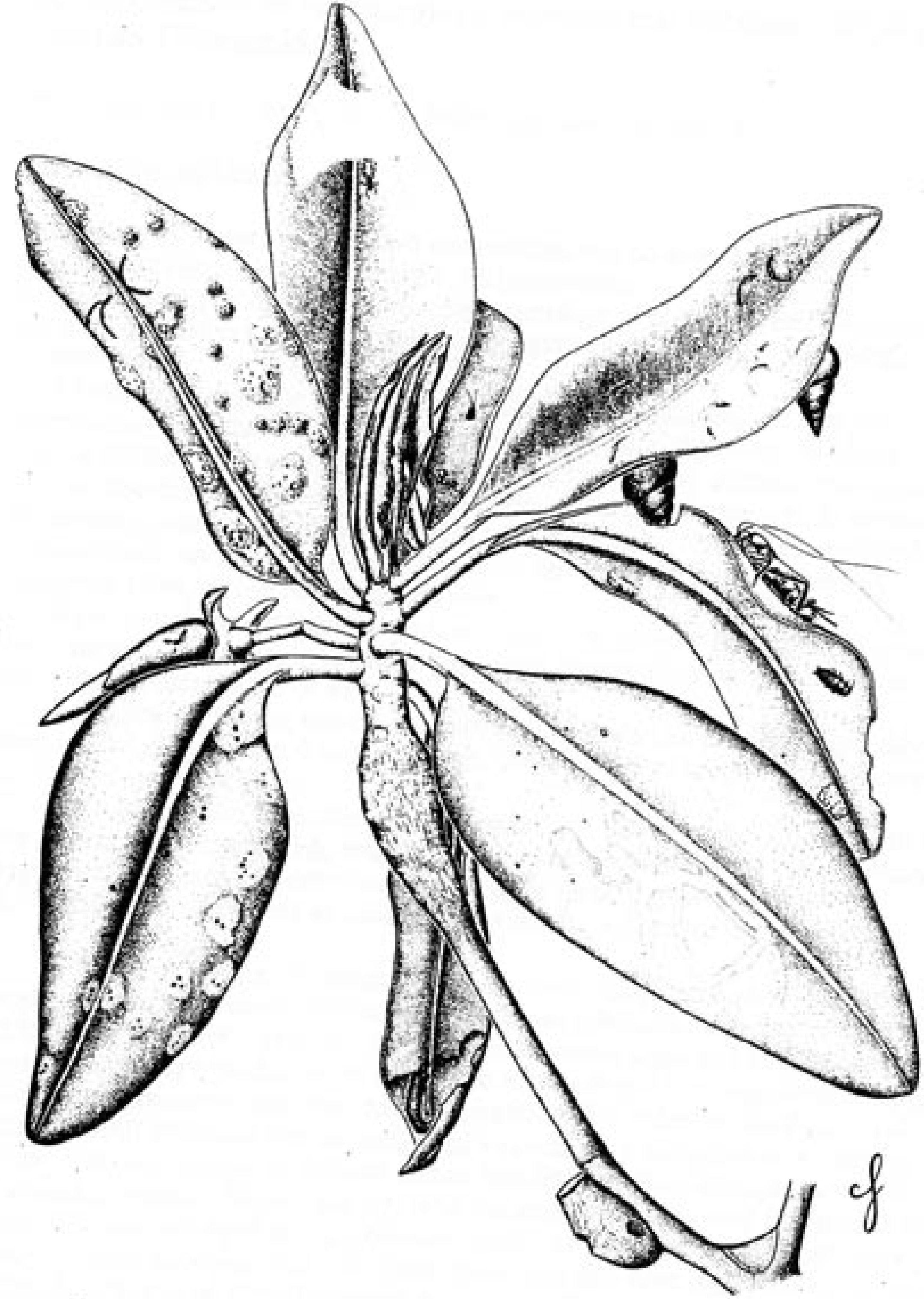


Figure C-1. Leaf-feeding insects on a red-mangrove branch.

Mangrove Fauna and Flora

Argiopes sp., The Mangrove Garden Spider

Cricket

Family Saturniidae, Subfamily Hemileucinae

Stinging Caterpillar, *Acharia horrida* (Limacodidae)

Genus Marmara, undescribed species

Leaf Mines. Marmara

Mangrove Fauna and Flora (*cont.*)

Stinging Caterpillar, The Mangrove Puss Moth, *Megalogyge dyerii* (Megalopygidae)

Mantid On Mangrove

Boaconstrictor, *Constrictor constrictor*

Mangrove Anole, *Anolis sagrei*

Mangrove Tree Crab, *Aratus pisonii*

Uca sp., Fiddlers Fighting

Mangrove Fauna and Flora (*cont.*)

Grackle

Whitecrowned Pigeon

Mangrove Yellow Warbler

Wood Storks

Woodpecker

Epiphytic Mangrove Orchid, *Brasavola nodosa*

D. Biodiversity in the Mangrove Intertidal and Subtidal: Algal and Seagrass Communities

By Christopher E. Tanner, Ilka C. Feller, and Aaron M. Ellison

Major Points of Chapter

1. Primary producers in mangrove communities and adjacent areas include microscopic algae, macroscopic algae, and seagrasses.
2. Algae are a phylogenetically diverse assemblage of photosynthetic organisms that are distinguished primarily by pigmentation and other biochemical and cellular characteristics.
3. Microscopic algae are found in the plankton (phytoplankton), on mangrove roots (periphyton) and other substrates (epibenthic), and within the tissues of corals (zooxanthellae), sea anemones, ascidians, sponges, and other animals (endobionts).
4. The distribution of macroscopic algae, commonly called seaweeds, is determined by substrate availability, light and nutrient levels, salinity, competition, and herbivory. Characteristic assemblages of seaweeds occur on mangrove roots (epiphytes), mangrove peats, and surrounding substrates.
5. Algae contribute a substantial portion of the total primary production of mangrove communities. Also, epiphytic and benthic algal communities provide habitat and food for a diverse assemblage of animals.
6. Seagrasses are marine flowering plants that are grass-like in appearance, although they are not closely related to true grasses. Five species of seagrass are common in the coastal waters of Belize.
7. Turtle grass forms extensive and very productive beds that provide food and shelter for marine invertebrates, fish, and manatees. Many species that are commercially important in Belizean fisheries use these beds as nursery grounds.
8. Turtle grass also serves as substrate for a diverse epibenthic community.

Although species of mangroves are the most conspicuous photosynthetic organisms along the coast of Belize and contribute substantial amounts of food energy to coastal waters, algae and seagrasses contribute even more primary production to the marine food web and have important ecological roles within mangrove and coral reef communities (Koltes *et al.* 1998). For example, Rodriguez & Stoner (1990) estimated that the total algal biomass for a mangrove ecosystem in Puerto Rico was similar to the total annual leaf litterfall from *Rhizophora mangle* into the surrounding waters. Since algae epiphytic on mangroves turns over its biomass 4-5 times per year, the input of algal biomass greatly exceeds that from mangroves. Seagrass beds associated with mangrove stands can also have high production rates, although Littler *et al.* (1985) reported that the contribution of seagrasses was less than 17% of the total productivity of submerged macrophytes (seaweeds and seagrasses) at Twin Cays, Belize. These intertidal and subtidal primary producers contribute to both the grazing and detrital food chains, provide habitat for numerous invertebrate and vertebrate animals, and are involved in other ecological functions such as nitrogen fixation. Their distributions are determined by both physical/chemical and biological factors.

Microscopic Algae

Microscopic algae are found in marine habitats wherever sufficient light and nutrients are available for photosynthesis. Two common groups in mangrove systems are the dinoflagellates and diatoms. Both of these groups are represented in the phytoplankton, algae in the water column at the mercy of water currents. Members of the phytoplankton are fed upon by zooplankton and sessile filter feeders such as sponges and ascidians; however, the density of these unicellular and colonial algae is seldom high enough to be a major contributor to the food web. On the other hand, production of endobiotic algae such as zooxanthellae found associated with reef-building corals and other invertebrates can exceed that of all other primary producers in tropical coastal ecosystems. Plant nutrients are hypothesized to contribute to both the low productivity of phytoplankton communities and high rate of production of zooxanthellae. Tropical marine waters generally have low concentrations of inorganic nitrogen and phosphorous, chemicals that are necessary for the growth and reproduction of photosynthetic organisms. The sparsity of these compounds explains why tropical marine waters maintain such low densities of phytoplankton compared to temperate marine waters. Zooxanthellae are able to maintain high production and growth rates as a result of nutrient cycling within coral tissues and the efficient extraction of nutrients from the water that is constantly flowing over the surface of corals.

Within mangrove stands, epibenthic microscopic algae can be found on prop roots, pneumatophores, peat banks, mudflats and on virtually every other substrate in the intertidal and subtidal. In sheltered areas, diatoms can produce macroscopic gelatinous mats with high rates of production (Littler *et al.* 1985). Certain species of benthic dinoflagellates produce toxins that can be concentrated through the food chain and cause ciguatera in humans. While ciguatera is relatively rare in Belize, species (*e.g.*, *Prorocentrum lima)* that are suspected of producing ciguatera toxin have been reported from Belizean mangrove communities (Faust 1991). Increases in ciguatera-causing algae in other areas of the world have been associated with natural and human disturbance of reef systems (Hallegraeff 1993).

Seaweed Communities

Different intertidal and subtidal substrates often support distinctive communities of macrophytes (Littler *et al.* 1985, Taylor *et al.* 1986). Typical substrates of the mangrove intertidal and shallow subtidal are prop roots, pneumatophores, peat banks, and mudflats. The bottom in subtidal channels and lagoons bordering mangrove stands is usually composed of deep, fine silt which grades toward coarser unconsolidated sediments associated with grassbeds and green algae with stolons and rhizoids.

In some mangrove stands the most abundant and characteristic intertidal mangrove community is often called the bostrychietum, named after its principal component, the red alga *Bostrychia* spp. (Fig. D-1), and is frequently observed on prop roots and pneumatophores. In the Caribbean, other seaweeds associated with the bostrychietum are the red algae *Catenella repens* and *Caloglossa leprieurri.* In other areas, algal communities on intertidal prop roots and pneumatophores are dominated by cyanobacteria, also called blue-green algae. These prokaryotic algae are particularly important in nutrient cycling because they are capable of fixing atmospheric nitrogen (N_2) into a form (NH_4^+) usable by other plants. Other areas are dominated by the red alga *Acanthophora spicifera*. All of these intertidal algal communities play host to a variety of invertebrates and are fed upon by amphipods (*e.g*., *Parhyale* spp.) and crabs (*e.g*., *Aratus pisonii, Mithrax* spp.) during receding and low tides. Mats of the delicate green alga *Caulerpa verticillata* often cover the intertidal peat banks under the mangrove canopy. *Caulerpa verticillata* mats host numerous marine invertebrates including sponges, brittlestars, tunicates, bivalves, snails, shrimp, crabs, holothurians, polychaete worms, sipunculid worms, and serpulid worms. The umbrella-like green alga *Acetabularia* spp. is a frequent component of this community.

Shallow subtidal mangrove peat banks frequently have well-developed seaweed communities of fleshy algae (*e.g*., *Caulerpa* spp.*, Dictyota* spp.*, Lobophora* spp.*, Spyridia* spp.) and/or calcified algae (*e.g*., *Halimeda* spp.*, Jania* spp.*, Neogoniolithum* spp.). Littler *et al*. (1985) found that species richness and biomass differed for wave-exposed and sheltered sites at Twin Cays, Belize, related to sea urchin herbivory and wave turbulence. In areas with abundant herbivorous sea urchins, fleshy algae such as *Acanthophora* spp.*, Spyridia* spp.*,* and *Caulerpa* spp. dominate on hanging roots of the red mangrove, whereas calcified algae such as *Halimeda* spp. and *Lithophyllum* spp. are more common on attached roots (Taylor *et al*. 1986). Apparently, the hanging root dominants are 6-20 times more susceptible to herbivory than the calcified algae and are removed from attached roots by urchins that move from the peats up the roots. In areas with no or low urchin densities, fleshy algae will out compete calcareous algae on both hanging and attached roots.

In shallow subtidal areas enriched by guano from islands with bird rookeries, entangled mats of the hair-like green alga *Chaetomorpha linum* can be found. These mats can reach diameters of a meter or more and are generally not attached to the substrate. Other indicators of nutrient-rich waters are the sheet-like green algae *Entomorpha* spp. and *Ulva* spp.*,* which are found attached to shell and coral fragments or free-floating in sheltered bays. On most mud and sand bottoms seaweeds are relatively rare; the dominant species are green algae with well-developed basal systems (*e.g*., stolons, rhizoids) for anchoring in unconsolidated sediments.

Seagrass Communities

Marine algae are plants that lack true roots, vascular tissue (xylem and phloem), and flowers. The seagrasses, however, are angiosperms or flowering plants with true stems, leaves, and roots with vascular tissue. There are only a handful of species of marine vascular plants, whereas there are numerous species of marine algae, a pattern of diversity which is the reverse of that found on land, where angiosperms are the dominant plant group in terms of species diversity, abundance, and biomass production.

In Belize, as in the rest of the Caribbean, the dominant seagrass is *Thalassia testudinum,* or turtle grass. Manatee grass *(Syringodium filiforme)* often grows with turtle grass. These two species form extensive beds that are highly productive and serve as important habitat for numerous species of invertebrates and fish. Other species found in Belize include *Halophila decipiens, Halophila engelmannii,* and *Halodule beaudettei.* Tropical seagrasses usually grow on sandy sediments to which the plants are anchored by an extensive system of belowground rhizomes and roots. Several species of marine algae grow in the sediment among the turtle-grass beds in mangrove channels. The most common of these are species of the green algal genera *Caulerpa, Halimeda, Rhipocephalus, Avrainvillea, id Penicillus.* These algae generally have extensive systems of stolons and/or rhizoids to anchor them to the unconsolidated substrate. Other algae, such as the brown alga *Lobophora variegata,* form dense layers of unattached plants that roll with the currents and surge between seagrass shoots.

Shoot density, biomass, growth, and production of turtle grass have been studied at Twin Cays, Belize, by J. Ott (University of Vienna), who compared seagrass beds in mangrove tidal channels with beds in the surrounding shallow, open lagoon and in the backreef areas. Shoot density (number of shoots per m^2) in the lagoon (approx. 1,200 shoots m^{-2}) is over twice as great as shoot density in the mangrove channel (approx. 450 shoots m^{-2}). However, individual turtle-grass plants from the mangrove channel are much larger than those of the lagoon or backreef. Consequently, total turtle-grass biomass (g m^{-2}) is higher in the mangrove channels (approx. 425 g m^{-2}) than in the lagoon (approx. 350 g m^{-2}). Although turtle grass plants in the mangrove channels grow much faster than those in the back reef and lagoon, the productivity (g m^{-2} yr^{-1}) is similar in all three habitats because of the higher density of turtle grass in the lagoon and back reef.

Sea urchins such as *Lytechinus variegatus* and herbivorous fish such as the bucktooth parrotfish *(Sparisoma radians)* graze on living and detrital turtle grass in shallow mangrove channels. The sea urchin population in mangrove channels is maintained by immigration of juveniles from the shallow waters surrounding the mangroves. Sea urchin density decreases with depth and distance from the mangroves; they are rarely found in the turtle-grass beds adjacent to patch reefs or shoals. In these other habitats, sea urchin abundance and distribution appears to be limited by reef-based predators. Manatees also graze on seagrasses. The path of their feeding can be tracked by following the uprooted turtle-grass fragments floating on the surface of mangrove channels.

Like subtidal mangrove prop roots, blades of *T. testudinum* serve as substrate for an incredibly diverse array of microscopic and macroscopic epibionts that give the leaves a fuzzy appearance (Fig. D-2). Common epiphytes include green and red filamentous algal genera (*e.g., Cladophora, Ceramium, Polysyphonia, Champia*) as well as calcareous algae. Epibiotic animals include the stinging anemone *Bunodeopsis antillarium,* the bivalve *Spirorbis spp.,* numerous bryozoans, hydroids, sponges, ascidians, and setpulid worms.

Seagrass beds are important nursery grounds for juvenile shrimp and fishes of commercial importance, such as prawns, snapper, grouper, and barracuda. The juvenile fish are dependent on the plants, their epiphytes, or the benthos associated with the seagrass beds for food and refuge. *Thalassia testudinum* beds also act as a refuge habitat for seaweeds as grazing rates are considerably lower than in back reef and fore reef habitats (Lewis & Wainwright 1985*).* In mangrove channels, the prop roots provide additional shelter, and the high accumulation of organic detritus supports a rich benthic fauna Together, mangroves, microalgae, seaweeds and seagrass beds form the basis for some of the richest fisheries in the world.

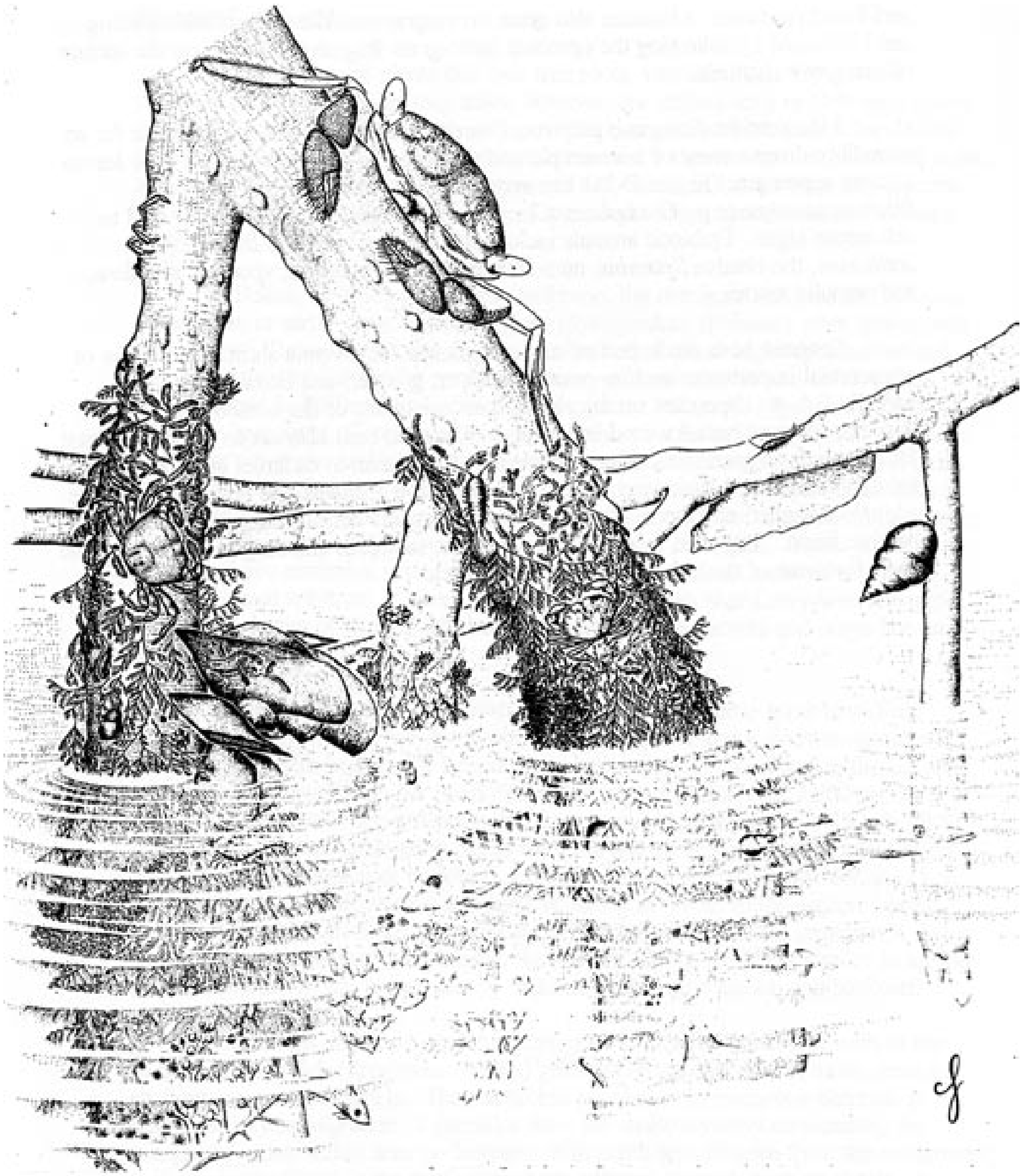


Figure D- 1. The intertidal zone on *Rhizophora mangle* prop roots provides substrate for a characteristic assemblage of marine algae.

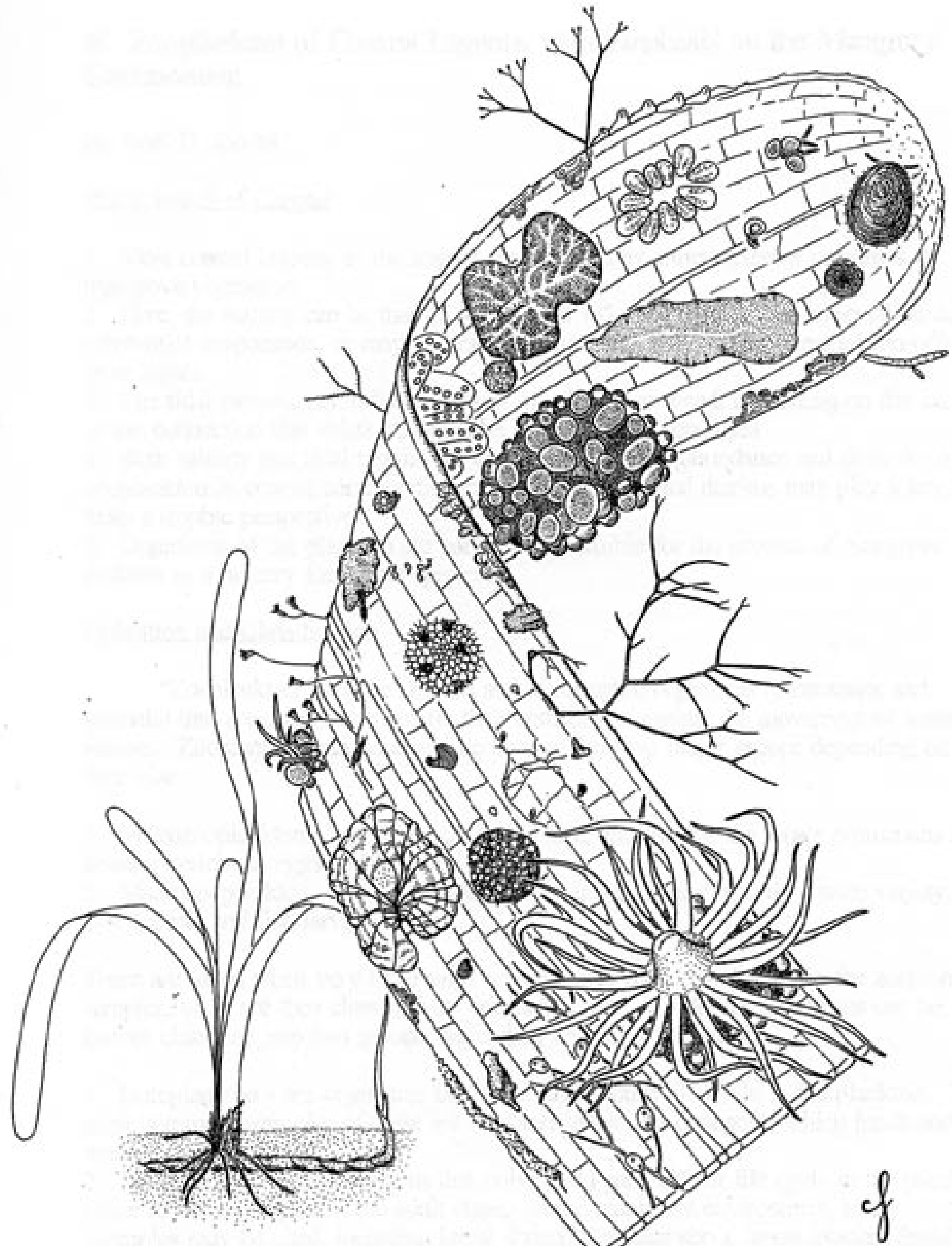


Figure D-2. Numerous species of organisms occur as epibionts on the blades of Turtle Grass, *Thalassia testudinum*.

E. Zooplankton of Coastal Lagoons with Emphasis on the Mangrove Environment

By Noel D. Jacobs

Major Points of Chapter

1. Most coastal lagoons in the tropics are bounded by either seagrass meadows or mangrove vegetation.
2. The salinity can be that of ocean water (32-35‰), or may be hypersaline due to substantial evaporation or may be brackish if the lagoon receives terrestrial run-offs and river inputs.
3. The tidal movements in these lagoons may be pronounced, depending on the extent of the connection that exists between the lagoon and the open sea.
4. Both salinity and tidal regime affect the abundance and diversity of the zooplankton in coastal communities; however, accumulated detritus may play a key role from a trophic perspective.
5. Organisms of the plankton are partially responsible for the success of mangrove systems as a nursery for higher species.

Definition and Classification

Zooplankton may be defined as heterotrophic organisms (protozoans and animals) that are unable to maintain their distribution against the movement of water masses. Zooplankton can generally be divided into two major groups depending on their size:

1. Microzooplankton - are 20 to 200 µm in size, and include the larger protozoans and small invertebrate eggs and larvae.
2. Macrozooplankton - are larger that 200 µm in length and include a wide variety of invertebrate and fish larvae.

There are times when very large salps and medusae may be collected in the zooplankton samples; these are then classified as "megaplankton." Planktonic organisms can be further classified into two groups, depending on their life history:

1. Holoplankton - are organisms that spend their entire life cycle in the plankton. The most common examples of these are crustaceans such as copepods, which hatch and mature in the plankton.
2. Meroplankton - are organisms that only spend part of their life cycle in the plankton, either as larvae or part of the adult stage. In the mangrove environment, many examples may be cited, including larval shrimp *(Penaeus* spp.), larval lobster *(Panulirus* spp.), larval fish (*e.g., Lutjanus* spp.), as well as a series of other meroplanktonic invertebrates.

Function, Diversity, and Abundance

In an aquatic environment, phytoplanktonic organisms are the primary producers and, thus, represent the base of the food chain. The energy present at this level is transferred to other organisms higher in the system by a specific group of herbivores, the zooplankters, which represents the second trophic level and is an indispensable energy-bridge in most aquatic food chains. By applying this concept to the mangrove system, one can appreciate that the attractive nature of this system as a nursery for many commercial species is determined to a considerable extent by the abundance and diversity of the planktonic populations found therein.

Copepods (Calanoida and Cyclopoida) form 50-80% of the zooplankters, followed by the cladocerans (mostly *Daphnia* spp.), amphipods, isopods, mysids, ostracods, fish eggs and larvae, and other crustacean larvae such as phyllosomas, megalopas, and zoeas. Even though the species diversity of the zooplankton generally tends to decrease as we move from immediate coastal water bodies to more inland ones, the diversity in mangrove environments is relatively high (between 2- 3 when calculated by Shannon-Weiner's Diversity Index; the highest being 5 for the most diverse aquatic communities). The planktonic organisms that are abundant in these environments must possess special adaptation capabilities so as to resist seasonal changes in temperature and salinity, increased concentrations of suspended solids during the rainy season, and a possible influx of pollutants of terrestrial origin.

Because mangrove environments are subject to drastic changes in salinity, their zooplanktonic communities tend to consist mainly of euryhaline species, some of which may be characteristic of these environments. Mangrove systems are normally shallow and have high concentrations of organic matter. This fact can be highlighted by the presence of organisms in the zooplankton that are typical of shallow coastal habitats. Three of the most common examples include individuals of the orders Cumacea, Cladocera, and Tanaidacea. Gastropods may also appear in zooplankton samples collected from coastal lagoons. These are more abundant in areas where significant mixing takes place (such as the major inlet of mangrove lagoons), reflecting their filter feeding habits. There are certain zooplankton species that are typically oceanic and are not likely to be present in coastal lagoons and are thus absent from mangrove environments. These include sergestids (such as *Lucifer* spp.,) and chaetognaths (arrowworms), mostly from the genus *Sagitta*. Their presence in a mangrove environment may indicate unfavorable alterations to their oceanic habitat, or that hydrological processes only temporarily introduced them.

Generally, zooplankton abundance and diversity vary seasonally. In mangrove habitats, this is more pronounced due to the effects of tidal movements, pluvial inputs and terrestrial run-offs. Larvae of hydrozoans (cnidarians) can be used to demonstrate this concept. It is known that hydrozoan larvae are abundant during spring and summer in most tropical lagoons, probably as a result of the spring plankton bloom. Studies conducted in Mexico have shown statistically significant differences in the densities of hydrozoan larvae collected in a coastal lagoon during the period March - August of a given year, and those collected from October - February. Other planktonic organisms such as shrimp larvae also vary seasonally, which may be due to factors other than those mentioned above. The influences of temperature, salinity and biological determinants, coupled with the effects of water dynamics, result in a patchy horizontal and variable vertical distribution of zooplankton populations.

Planktonic Animals as Indicators of Environmental Pollution

Because of their location in low-relief areas on the coast, mangrove habitats are vulnerable recipients of toxic and other hazardous substances from land-based sources. Human population increases, compounded by the development of resorts, new communities and industries, create an increasing threat to coastal habitats. Generally, potential problems include sedimentation resulting from dredging and shoreline landfill, sewage effluents, inorganic deposits from aquacultural operations and pesticide residues from agricultural production. The by-products of these activities can result in reduced diversity, altered ecosystem structure, and reduced plankton stability with violent fluctuations in standing stocks of a few species. This can be interpreted further as a reduction in the useful potential of the mangrove system as a nursery and spawning ground for many important species. None of these changes is desirable; some are clearly undesirable.

Conscious of the vulnerability of coastal ecosystems to pollution, scientists and decision-makers have been trying to identify new ways of detecting pollutants in these systems from an early stage before irreversible or catastrophic events occur. With this in mind, the concept of bioindicators was developed. The use of planktonic organisms as bioindicators has received quite a bit of attention over the last decade.

If we view the pollutants-mangrove system interaction from a Belize point of view, we can appreciate that the major land-based sources of pollution in the country are: inorganic deposits from aquacultural operations, pesticide residues from agricultural production, and sedimentation as a result of dredging and shoreline land fill. The selection of key species that can act as indicators of changes in the mangrove system as a result of these activities requires a previous knowledge of the temporal, seasonal and bathymetric distribution of the species in the area of interest. Species that are typical of coastal lagoons, such as those of the orders Tanaidacea, Cumacea and Cladocera, may be viable options. It is obvious that temporary inhabitants of these habitats will not serve as dependable indicators.

Changes in the zooplankton community structure are common signs of alterations to the environment. For example, if a medium to long-term study were to be conducted in southern Belize in the Placencia Lagoon in the vicinity of several shrimp farms, there are two scenarios that may arise. 1) Eutrophication as a result of inorganic deposits will have a direct negative effect on fish eggs and larvae, and on larval shrimp, but will favour cladocerans and gastropods. This will result in these organisms being dominant in the lagoon, when the normally dominant groups in this type of environment are Tanaidacea, Cumacea and Cladocera. From this, we gather that eutrophication has caused a reduction in the number of individuals of the Tanaidacea and Cumacea orders, an increase in the number of gastropods, and thus a modification of the species hierarchy in the community. 2) The second scenario contemplates the effect of pesticide residues from nearby banana farms that may be acting in conceit with eutrophication. The anticipated change in the zooplankton community is a massive bloom of cladocerans, but a reduction of the other groups. Cladocerans are known to resist levels of pesticide residues that are toxic to most of the other aquatic organisms. A change in the community such as this, tells us that the polluting effects of the pesticides have exceeded those of eutrophication, and this can be justified by the absence of gastropods as a dominant species in this scenario.

The major critique of using planktonic organisms as indicators has been that they do not indicate cause-and-effect; that is, they cannot be used to identify the specific polluting agent that is causing the effects observed. This is partially true but is also debatable. The important point is: they are much faster at indicating changes in the environment compared to other methods commonly used. For example, histopathological observations are of much use when studying the effects of pollutants on aquatic organisms. However, the observable pathological conditions, which may develop in an organism, are the end result of a series of interactive events between the polluting agent and the organism. Therefore, they represent changes that occurred in the environment sometime in the distant past and not at the moment of the observation. Planktonic organisms tend to be more sensitive in this respect.

The importance of zooplankton in coastal lagoons and specifically in mangrove habitats has been highlighted. It is clear that besides their key role in the trophic structure of these systems, their potential use in marine pollution studies is an area worth exploring. Alterations to zooplankton community structure may provide a new option as an environmental monitoring tool in coastal habitats.

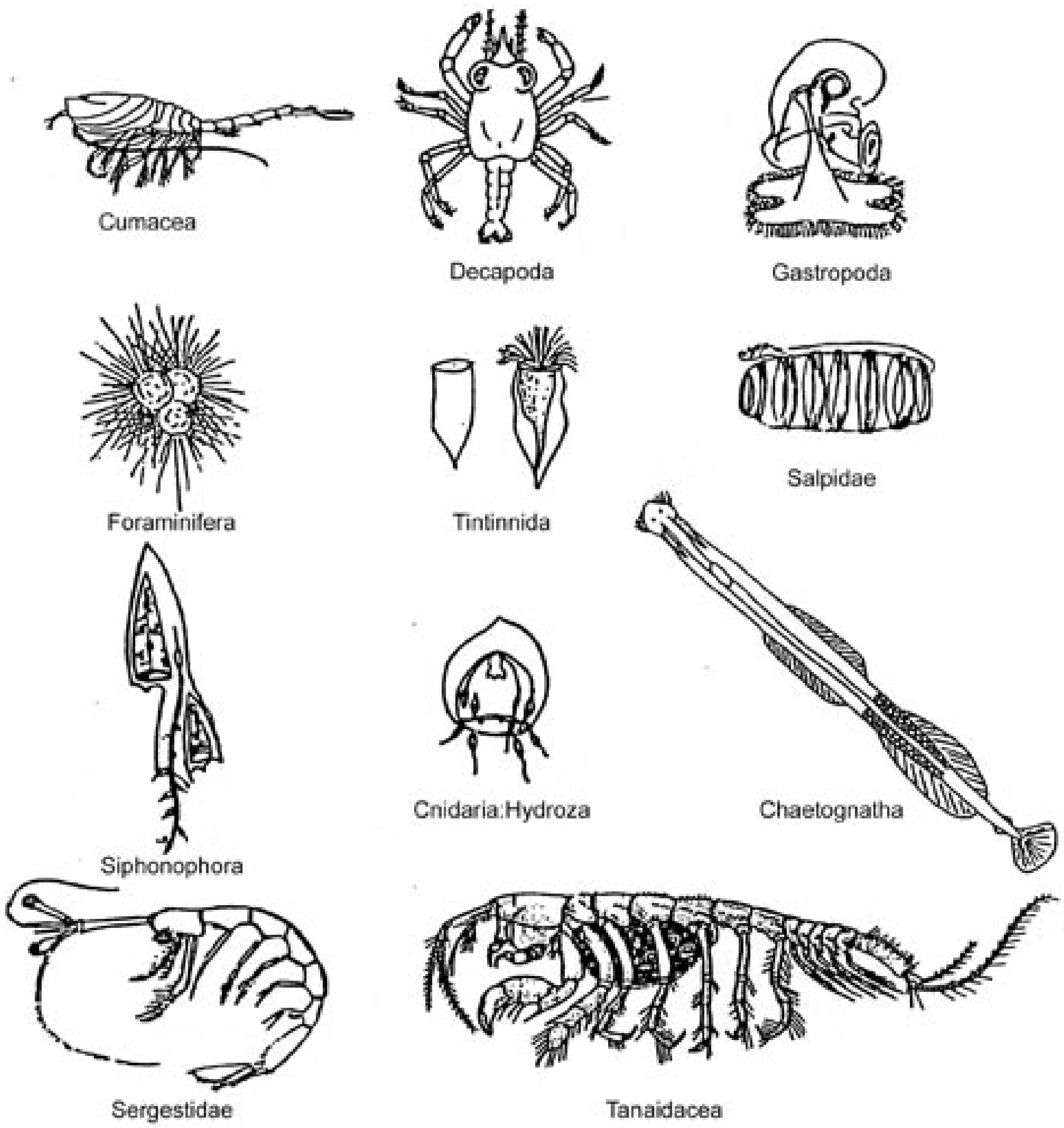


Figure E-1. Types of zooplankton found in coastal lagoons and specifically in mangrove habitats

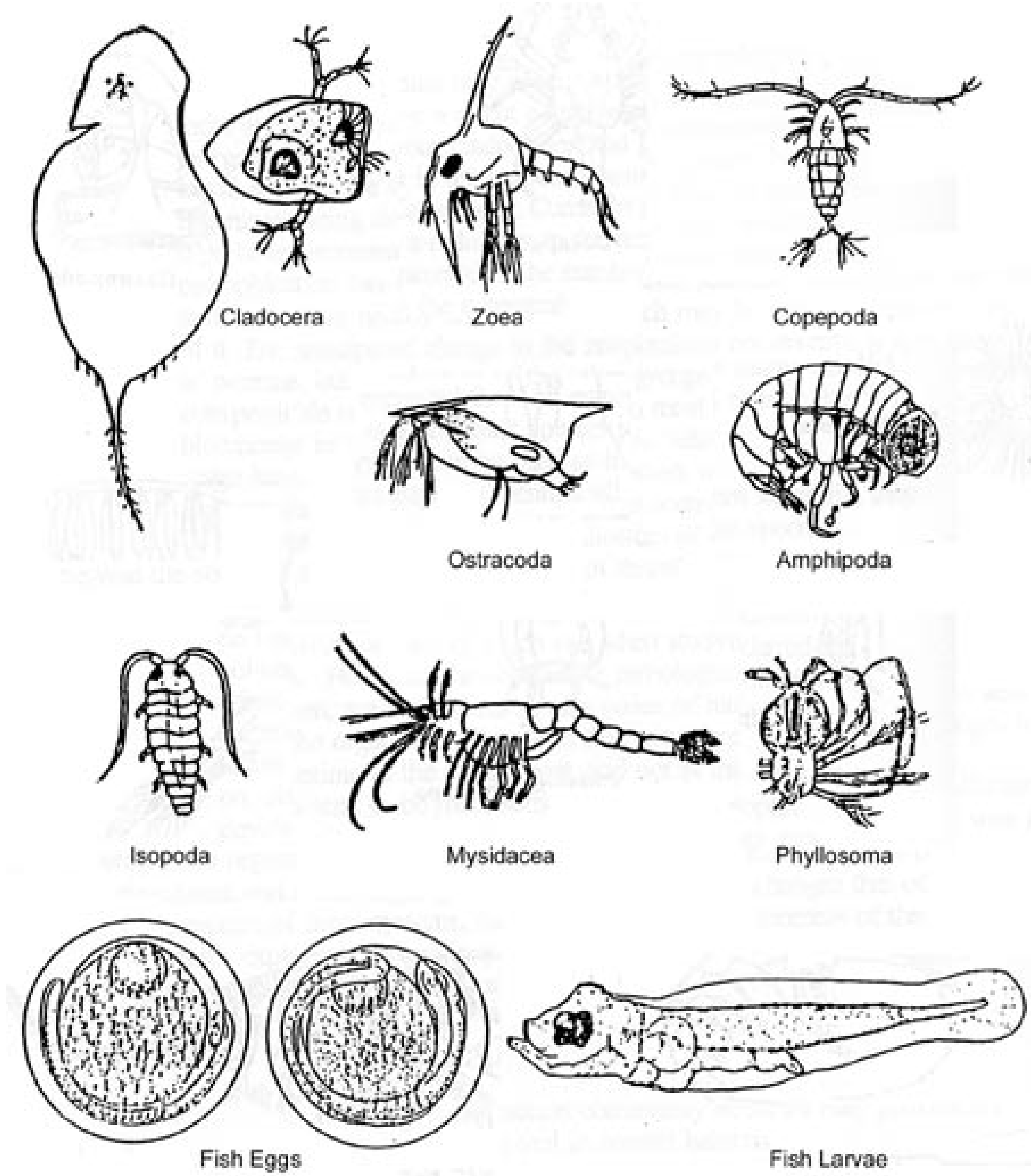


Figure E-1, continued. Types of zooplankton found in coastal lagoons and specifically in mangrove habitats

F. Biological Adaptations to Environmental Extremes in Mangrove Flora

By Karen McKee

Major Points of Chapter

1. The mangrove habitat is comprised of an array of environmental conditions that requires specialized adaptations for survival, growth, and reproduction.
2. It is typically the extremes, rather than the average, of physical and chemical factors that determine species distributions.
3. In the mangrove habitat, the dominant abiotic factors that limit plant growth include flooding intensity, hypersalinity, temperature extremes, high or low irradiance, and nutrient deficiencies.
4. Actively growing tissues (*e.g.,* seedlings) are generally the most vulnerable to environmental extremes.
5. Resistance to abiotic stresses may be attained by mangroves via two types of strategies: avoidance and/or tolerance. Generally, the most successful strategies are those that allow avoidance of stress.
6. Mangrove species exhibit a variety of strategies for stress resistance.

Mangroves represent a taxonomically diverse group of trees and shrubs, yet are all adapted to growth in the intertidal zone (Tomlinson 1986; Mendelssohn & McKee 2000). Tidal action results in physical and chemical gradients across the intertidal zone where the degree of soil waterlogging, salinity, and nutrient availability may vary substantially (McKee 1993). It is the variation in these factors that affects the growth of mangroves across the intertidal zone (Ball 1988). Solar radiation also varies spatially across mangrove forest with degree of canopy development and relative occurrence of light gaps (opening in the canopy). Incident light, in turn, affects soil temperature and salinity (through evapotranspiration). Spatial and temporal variation in freshwater input also influences mangroves.

Although mangroves exhibit species-specific adaptations to the conditions found in the intertidal habitat, extremes in abiotic factors can generate stressful conditions that reduce the mangrove's capacity for growth, reproduction, and survival (Ball 1988). In addition to adaptation (a genetically determined characteristic that enhances the ability of an organism to cope with its environment), mangroves may also exhibit some degree of acclimation (a phenotypic response to environmental change) to environmental extremes.

The effect of environmental extremes and the ability of the mangroves to resist these stresses vary with stage in their life cycle. The seedling phase is the most critical for survival and spread of a population and is also the most vulnerable to environmental extremes. The juvenile or sapling phase is the most capable of acclimation. In the adult phase, environmental factors affect assimilative process and are reflected in the frequency of flowering, fruit set, and propagule development.

Salinity

Plants are typically divided into two groups depending on their salinity adaptation: halophytes, which grow and complete their life cycle in habitats with a high salt content and non-halophytes, which grow in a non-saline habitat. Mangroves are facultative halophytes (can grow in either salt- or freshwater) (Ball 1988). Some reports indicate that a few mangroves are obligate halophytes. However, many mangrove species can be grown quite successfully in freshwater in the greenhouse. Mangroves are dominant in saline environments primarily because these conditions exclude nonhalophytic species that would otherwise out compete mangroves in a freshwater habitat. There are two major effects of salinity on plants:

1. A water deficit: The presence of salts in the soil solution makes it more difficult for a plant to take up water because the concentration of water external to the roots is decreased relative to the inside of the root. The relative concentrations are important because water only moves from a region of high concentration to one of low concentration. If water uptake is reduced because of a high salt content in the soil, the plant can suffer from dehydration.
2. A toxic ion effect: Two dominant ions in seawater are sodium (Na^+) and chloride (Cl^-). Both can have direct toxic effects on plants by inhibiting enzyme activity, interfering with protein synthesis, and by altering respiration rates.

Mangroves exhibit a number of strategies for or tolerance of salinity stress:

Avoidance strategies

1. exclusion of salts by the plant roots
2. excretion of salts from salt glands in the leaves
3. dilution of salts by increased water content in tissues (succulence)
4. elimination of salt-saturated organs

Tolerance strategies

1. compartmentalization of salts in the vacuole–removes toxic ions from metabolically active portions of the cell
2. synthesis of organic (compatible) solutes–to balance inorganic ions in the vacuoles

Structural/anatomical modifications to a saline environment

1. stomata on lower leaf surface–decreases water loss from plan
2. thickened cuticle on leaf surface–decreases water loss
3. salt glands in leaf epidermis

Flooding

Mangroves experience varying depths and durations of flooding by the tides. There are two major impacts of flooding on plants: oxygen deficiency in the root zone and accumulation of soil phytotoxins (McKee *et al*. 1988; McKee 1993). In a well-drained (upland) soil, the roots of plants grow in an aerobic environment since the soil pores are filled with air. When a soil becomes flooded, the soil pores are filled with water. The respiratory activities of roots and soil microorganisms quickly use up the oxygen in the flooded soil. Because the diffusion of oxygen in water is 10,000 times slower than in air, this oxygen is not replaced quickly. Thus, mangrove soils are typically anaerobic (without oxygen). The lack of oxygen can have a number of effects on plants, but primarily it reduces root respiration and the production of energy for nutrient uptake, transport processes, and anabolic metabolism (synthesis) (McKee & Mendelssohn 1987; McKee 1996). In the absence of oxygen, soil, microorganisms switch to other electron acceptors to support the breakdown of carbohydrates. These reactions yield a variety of potentially toxic compounds. In marine soils, however, the most toxic compound produced is hydrogen sulfide. Hydrogen sulfide's toxicity is equal to that of hydrogen cyanide, and very small quantities of this phytotoxin can completely inhibit aerobic respiration of plants and animals. Mangrove soils contain levels of hydrogen sulfide that exceed (by orders of magnitude) concentrations known to inhibit respiratory enzymes (McKee *et al.* 1988).

Avoidance strategy:

1. aerenchyma (air-space tissue) development in roots. Mangrove roots contain abundant air spaces which allow transport of oxygen from the aerial portions of the plants to the root tips—allowing continuation of aerobic respiration, reduction in the amount of living cells requiring oxygen, and removal of toxic volatile compounds from the roots (Scholander *et al.* 1955).
2. aerial roots. Mangroves exhibit a high degree of development of aerial roots that act in transport of oxygen from the atmosphere to belowground roots growing in the anaerobic soil. Prop roots (red mangrove) and pneumatophores (black and white mangrove) are important in providing an extensive system of air pathways to the belowground root system (Scholander *et al*. 1955; Gill & Tomlinson 1977).
3. lenticels. These openings in the secondary tissue covering the stems and aerial roots allow oxygen entry aboveground (Scholander *et al.* 1955; Gill & Tomlinson 1977).
4. development of an oxidized rhizosphere (root zone). Leakage of oxygen from the plant roots creates a buffer zone in which toxic, reduced compounds such as hydrogen sulfide can be oxidized (rendered harmless) (McKee *et al*. 1988).

Tolerance strategy:

Switch to anaerobic pathways of respiration. Plants, including mangroves, possess metabolic pathways that can function in the absence of oxygen (McKee & Mendelsshoh 1987) This mechanism is useful in the short-term, but because it generates a fraction of the energy yield of aerobic respiration it is not a successful long-term strategy for flood resistance.

Irradiance (Light)

Plants require light to provide energy for photosynthesis. Light is probably the most important and one of the most variable components of the plant environment. An alteration in light intensity, whether a deficit or excess, will result in a disruption of plant metabolic processes. Solar radiation also affects plant temperature and developmental processes.

Excess: Plants can reflect, absorb, or transmit solar radiation incident on their leaves. The degree of damage depends on the wavelength of radiation, leaf structure, and leaf orientation. Typically, leaves can reflect 70% of infrared radiation, 6-12% of visible light, but only 3% of ultraviolet (UV) light. Some effects of excess light include: 1) photoinhibition – excess light causes the formation of reactive molecules that destroy photosynthetic reaction centers, 2) photodestruction of chlorophyll, and 3) inactivation of nucleic acids and proteins. Strategies to avoid radiation damage include: 1) increase in reflective properties of leaves (coloration, cuticle, hairs), 2) increased content of pigments other than chlorophyll, 3) heliotropism – reorientation of leaves to minimize light interception, and 4) synthesis of compounds that absorb UV radiation (*e.g.*, tannins) (Lovelock *et al.* 1992).

Deficit: Low light levels lead primarily to starvation as carbohydrates are used as substrate for respiration first, then other sources of energy are tapped. Low light levels occur under a closed canopy where light intensity may be two orders of magnitude lower than in areas exposed to direct sunlight. Plant strategies to cope with light deficit include: 1) increased leaf area to maximize light interception, 2) increased chlorophyll content to increase light absorption, and 3) phyllotaxy – arrangement of leaves along the stem to maximize light interception and avoid shading of lower leaves.

Temperature

Plants, in general, are poikilotherms; that is, they attain the temperature of the ambient environment. Because of this, they must have some form of tolerance to temperature stress. Temperature extremes may: 1) limit physiological process through enzyme denaturation or membrane damage, or 2) cause death of part of or whole plant, eliminating it from a particular niche or reducing its competitive vigor. Some symptoms of high-temperature injury are: 1) chlorotic mottling of leaves, fruits, etc., 2) appearance of necrotic lesions, particularly on stems and hypocotyls (part of seedling below attachment of cotyledons), and 3) death. Plant organs usually suffer heat damage at temperatures between 40° and 55°C. Heat sensitivity is also correlated with the stage of growth; that is, actively growing tissues (seedlings, flowers) are more susceptible to heat than mature tissues.

Avoidance strategies: Plants avoid heat damage by several means:

1. heliotropism—leaves oriented to minimize interception of incident radiation
2. reflectance properties of the leaf may deflect incident radiationd
3. issipation of heat by evaporative cooling of transpiration
4. growth in cool habitats (water, shade)

Tolerance strategies: Plant tissues may experience high temperatures, but exhibit protoplasmic tolerance (which is genetically determined and varies among species). Some examples of tolerance strategies include the following:

1. presence of heat-stable proteins that resist changes in response to temperature extremes
2. ability to rapidly synthesize proteins to replace those denatured by heat
3. synthesis of substances that protect proteins from damage
4. carbohydrate reserves that provide extra substrate to support temperature-induced increases in respiration rates

G. Adaptations to Environmental Change in Marine Fauna

By Richard Blanquet and Walter I. Hatch

Major Points of Chapter

1. Water in liquid form is indispensable to life on Earth.
   a. Although it is a chemically simple molecule, water possesses several unique characteristics that are important both physiologically and ecologically.
   b. Of special importance are its solvent, characteristics, light-absorbing and heat-related properties.
2. In biological systems, water can move into and out of organisms across cell membranes.
   a. Water will move from regions of high water concentration to regions of lower water concentration (osmosis).
   b. Solutes may move passively from high to low concentration (diffusion) or by biological processes (active transport).
3. The levels of dissolved solutes (salinity) as well as temperature and light are extremely important in determining the distribution of aquatic organisms.
4. Mangroves and estuarine environments are characterized by rapid changes and/or extremes in salinity, temperature, and even light.
5. Organisms differ in their abilities to tolerate such fluctuations and will succumb if the change exceeds or falls below a given level.
   a. These levels are called an organism's lethal limits.
   b. Lethal limits differ for different species and will often change within a given species over its lifetime, seasonally, or with respect to an organism's past history.
6. Physiological and behavioral changes which enable organisms to adjust to environmental changes are referred to as adaptations.
7. Adaptations may take the form of conformity and tolerance of change in internal conditions or active regulation of internal conditions.
   a. Species that allow their body temperature or internal salt concentration to change in proportion to changes in ambient conditions are called conformers.
   b. Species that maintain a constant internal environment despite changes in external conditions are called regulators.
8. Marine invertebrates are essentially thermal and osmotic conformers though they may quantitatively regulate the specific types of solutes or ions that are present in their tissues.
9. Marine vertebrates such as fish, amphibians, and reptiles are essentially thermal conformers but maintain a fairly constant internal osmotic concentration despite fluctuations in external salinity.
10. Marine vertebrates such as birds and mammals are excellent regulators of both temperature and osmotic concentration.

The Unique Properties of Water

Water, in liquid form, is essential to the evolution and existence of life on Earth. About 71% of Earth's surface is covered with seawater to an average depth of 3.5 km. Thus, the oceans are the largest repositories for living organisms. The bodies of living organisms are composed mostly of water (50-95%) in which medium most biochemical reactions occur. It is necessary, therefore, to address some of water's physical and chemical properties to help us understand the ecology and physiology of aquatic organisms.

Chemically, water is a simple molecule containing two atoms of hydrogen (H) bonded to one atom of oxygen (O) whose formula is expressed as H_2O. The hydrogen atoms are asymmetrically joined to the oxygen so that the two H atoms are at one end of the molecule while the O molecule is at the other. This creates a differential charge distribution—positive at one end and negative at the other. Water is, therefore, referred to as a polar compound. The negative end of one water molecule can attract the positive end of another forming weak chemical bonds called hydrogen bonds. If water were not polar, its molecules would be only weakly attracted to one another, and it would be a gas at room temperature!

The attraction between molecules is referred to as cohesion and gives water its characteristic viscosity or resistance to flow. The viscosity of water is relatively low compared to other common liquids and decreases with increasing temperature. Cohesion of water molecules at the water's surface, or surface tension, creates a molecular film that can support small organisms like insects and enable them to walk across the surface.

While water is a simple molecule chemically, its atomic structure gives it many unique properties that are essential for life.

Light-absorbing properties:

1. Water efficiently absorbs light at the extreme ends of the sun's radiant energy spectrum.
2. At one end, infrared wavelengths are rapidly absorbed within the first few meters of the water surface, limiting direct warming effects to the upper layers.
3. At the other end, ultraviolet (UV) wavelengths are also rapidly absorbed, which protects aquatic organisms from these potentially damaging rays.
4. Water also efficiently absorbs light in the visible spectrum including photosynthetically active wavelengths. Within a few hundred meters of the surface, there is insufficient light for any net photosynthetic activity. This light attenuation is an important factor in the distribution of aquatic plants.

Heat-related Properties:

1. Water has the highest rate of heat conduction of all common liquids.
2. The density of liquids (mass/unit volume) is temperature-dependent. Unlike other liquids, water's highest density does not occur at its freezing point (0°C) but at 4°C. Therefore, as water cools to 4°C in natural waters, it sinks, creating water movement and circulation. Also of importance is the fact that ice at 0°C is less dense than water at the same temperature and will, therefore, form an insulating layer at the surface retarding cooling of underlying water. This prevents many small bodies of water from freezing solid to the bottom that is of obvious consequence to the aquatic residents.
3. Water has a high heat capacity, that is, the quantity of heat required to raise the temperature of 1 g of a substance 1°C. This means that larger bodies of water must absorb large amounts of heat to effect a change in temperature. Because of this property, aquatic organisms do not experience rapid temperature changes, which is characteristic of terrestrial environments. Also, because of the large amounts of heat absorbed, large bodies of water exert a moderating effect on the climate of land masses adjacent to them.
4. Water has a high heat of vaporization, defined as the quantity of heat lost or gained per unit mass of a substance changing from a liquid to a gas, or vice versa, without an increase in temperature. This means that water has a high boiling point (100°C) and is a liquid over most of

the biotic temperature range. This property accounts for the cooling effect of evaporative water loss (sweating, panting) used for thermoregulation in terrestrial, and a few intertidal, animals.

Solubility-related Properties:

1. Being a polar molecule, water can dissolve more kinds of solute molecules than any other common liquid. The amount of a given substance that can be dissolved in a given amount of water is directly proportional to the water temperature. Seawater is a complex mixture of many inorganic and organic salts; the total amount is referred to as salinity. For seawater, this averages about 35 g per 1,000 g of water (often cited as parts per thousand, represented as ‰). About 99.9% of the salts are inorganic, mainly sodium chloride (NaCl); but, they also include the nitrates and phosphates essential for aquatic plant growth. The remainder of the solutes in seawater is organic, and many are important to aquatic organisms. The intracellular and extracellular water of organisms also contains an assortment of solute molecules, variable in both concentration and type.
2. The salt content of seawater decreases its freezing point to about -1.9°C. As seawater freezes, the ice formed excludes the dissolved salts and makes the remaining liquid more concentrated. This also occurs in body water and has important consequences for survival.
3. The respiratory gases, oxygen and carbon dioxide, are also soluble in water. The amount of a given gas that can be dissolved in a given amount of water decreases with an increase in the temperature and salinity of the water. Thus, tropical marine species live in environments that contain less oxygen (per unit volume of water) than Arctic marine or freshwater species. Dissolved carbon dioxide can be used as a raw material for photosynthesis, which may also affect the pH of aquatic environments, and thus affect photosynthetic rates of aquatic plants.

Organismal Adaption to Environmental Change

Organisms are normally subjected to a range of environmental changes, such as temperature and salinity, over their lifetimes. To survive and reproduce, organisms must be able to respond effectively or adapt to these changes. Adaptation is a general term referring to any alteration or response of an organism that favors survival in a changed environment. The functional basis for such adaptive responses is a basic concern for environmental physiologists and ecologists not only with respect to understanding basic biological function but also to help predict the effects of environmental alteration by human activity on these organisms. The vastness and dynamic nature of marine environments from the constancy of the abyssal depths to the rapid changes associated with estuarine or intertidal environments offers a wide range of adaptive responses. Among the most studied environmental changes are temperature, salinity, and light.

Different species exist within differing ranges of environmental change. The upper and lower values that a species can survive are termed its lethal or tolerance limits. Environmental changes that bring organisms close to their lethal limits elicit changes referred to as resistance adaptations. Arctic fish, which normally live at -10°C, often have upper lethal limits close to 10°C, whereas for tropical fish, 10°C is well below their lower lethal limits!

Over their lifetimes, organisms rarely exhibit fixed lethal limits. For instance, temperate species adapted to winter conditions can survive lower temperatures that would prove fatal to summer-adapted forms of the same species. The causes of heat and cold death are not well understood, but probably relate, in part, to a disruption in normal integrative biochemical reactions and pathways.

Many environmental changes are not extreme and are well within an organism's ability to tolerate. Adaptive responses to these changes are called capacity adaptations. Species that allow internal conditions to change in proportion to environmental changes are called conformers. Those that maintain constant internal conditions are called regulators. Many species may respond as conformers to one environmental change but as regulators to another.

Mangrove, estuarine, and intertidal environments often exhibit large fluctuations in temperature and salinity. We will limit consideration to these variables, although oxygen levels, pH, and nutrient levels are also important considerations.

Effects of Temperature

Marine mammals and birds that maintain constant internal temperatures despite environmental fluctuations are called homeotherms. On the other hand, fishes, reptiles, and invertebrates do not maintain constant body temperatures and are referred to as poikilotherms.

Temperature affects the rate of metabolic processes. Oxygen consumption is usually measured as a reflection of this effect. An increase of 10°C usually results in a change in oxygen consumption between 1.5 and 3 times the original rate. The relationship between temperature and metabolic rate may cause serious problems for organisms that cannot adapt. For instance, winter temperatures may severely suppress activity in some poikilotherms. Summer temperatures may increase metabolic rates to levels that cannot be sustained by available oxygen or nutrient levels. If temperature changes are gradual, however, most species can adjust their metabolic rates to favorable levels.

Effects of Salinity

Organisms need to maintain adequate levels of inorganic salts (ions) in their body fluids for proper metabolic function. Not only must total salt levels be maintained, but qualitatively the types of ions must also be adjusted. Since cells are permeable to water and numerous ions, external changes in these will result in passage of salts or water into or out of cells in response to the concentration gradient experienced. These movements may result in unacceptable volume changes or cell rupture.

Many organisms can allow internal salt concentrations to fluctuate within limits and are called osmoconformers. These almost invariably qualitatively change the types of ions present and are called ionic regulators. Many planktonic animals exchange lighter ammonium ions for the heavier sodium ion, thus, increasing their buoyancy.

Marine fish are osmoregulators. This is normally accomplished through active salt transport through the gills and a varying urine production. Freshwater fish maintain higher internal concentrations than their environments and are called hyperregulators. Marine fish normally have lower levels of salts than seawater and are called hypoosmoregulators.

Marine vertebrates such as fish, amphibians, and reptiles are essentially thermal conformers, but many have evolved both behavioral (ectotherm) and physiological mechanisms (heterotherm) for elevating their body temperature. Although these organisms cannot maintain a constant body temperature, they all maintain a fairly constant internal osmotic concentration despite fluctuations in external salinity.

Marine vertebrates such as birds and mammals are excellent regulators of both temperature and osmotic concentration. Their waterproof skin and air-breathing ability eliminate many of the problems of salt and water balance faced by organisms in more intimate contact with the water. Their lack of gills and insulation such as feathers, fur, or blubber help prevent heat loss to the water and help make maintaining a constant elevated body temperature feasible.

H. Role of Mangrove Environment in the Life History of Marine Fishes

By Will Heyman

Major Points of Chapter:

1. The life history strategy of many marine organisms includes an obligate period of dispersal in the plankton – ending in a period within mangroves.
2. Mangroves provide two distinct services for fishes: a) the prop roots constitute a protected habitat for larvae and early juveniles, and b) mangrove leaves form the basis of the detrital food web on which many fish depend.
3. There is a seasonal utilization of mangrove habitat divided into spatial and temporal niche spaces. Breeding events are followed by pelagic periods, recruitment events, and then blooms in predators, both zooplankton and nekton.
4. Ocean currents can control delivery of planktonic organisms into mangroves.
5. Mangroves form a crucial link in the life history of most of the commercially important reef organisms, and are thus economically linked to fishing and tourism industries.

Introduction: The life cycle of Marine Organisms

The life cycle of most marine fish includes an obligate period within mangrove ecosystems. Marine fish generally reproduce together, releasing large numbers of offspring, with little parental investment. These "spawning aggregations" result in mass spawning events, with fertilized eggs being released into the water. Within 24 hours, these floating eggs divide from a single cell and differentiate into tiny swimming larvae, which inhabit marine plankton. They follow ocean currents and eventually, if they encounter suitable habitat, will metamorphose into their juvenile forms within mangrove and seagrass habitats in a process called recruitment. The mangrove and seagrass habitats provide two important things for the juveniles: food and shelter. As juveniles grow into young adults they often continue to forage in mangrove and seagrass communities, until final migration back to open reef environments, where they will spawn and renew the cycle. The maintenance of marine biodiversity and the organisms of reef environments depend on the health of all the intact communities required in the life cycle of each organism and the connections between them.

Tropical Oceans are Deserts

Why are temperate oceans, and those oceans on western continental slopes green and dark while tropical areas, like the waters of the Caribbean Sea seaward of Belize, are turquoise blue and transparent? The darker waters are rich with phytoplankton, which blooms in response to the presence of sunlight and available nutrients derived from upwelling waters or coastal rivers. On the Caribbean coast, however, there is no major source of nutrient input to the system and so the waters are considered largely oligotrophic, or nutrient-poor.

But Caribbean coral reefs are some of the most diverse ecosystems on earth. Where do the nutrients come from? Nutrients that support tropical marine and coastal environments are derived largely on site from the primary productivity of seagrasses, mangroves, and coral reefs. Rapid nutrient recycling into higher trophic levels ensures that organic materials are maintained in living biomass around reefs, seagrass, and mangroves, while the surrounding seawater appears largely like a desert, nearly devoid of nutrients.

The Importance of Mangrove Communities in Food Webs

Mangrove prop root communities are complex ecosystems surrounding the roots of red mangroves. Mangrove leaves, wood, propagules, flowers, bracts, and other organic materials fall continuously to the intertidal forest floor. These leaves and other litter cannot be digested by herbivores and are thus unavailable nutrient sources for higher trophic levels. When bacteria and fungi metabolize the leaf litter, however, it releases nutrients via a pathway that has been called the detrital food loop. The detritus is eaten by shrimp, mullet, and myriad smaller organisms within the mangrove prop root community and thus passed into the food web.

The Gray Snapper: An Example of the Connections Between Mangrove. Seagrass. and Coral-Reef Communities

The gray snapper, *Lutjanus griseus,* is one example of a species that depends on the intact links between these three communities to complete its life cycle. It spawns on the ocean side of reefs. The postlarvae then move out into the seagrass beds to feed and seek protection. Once the juveniles are at least 70 mm in length, they inhabit the mangrove prop-root community and migrate out into the seagrass beds every night to feed. When they become adults, they return to the coral reefs to live and reproduce. Shrimp, blue crabs, lobsters, and mullet are other examples of organisms that move to different habitats during their life cycle. The life histories of such species help illustrate the importance of maintaining the complex interactions between mangrove, seagrass, and coral reef communities.

Reef Fish Spawning Aggregations

Most commercially important reef fish species migrate great distances, and aggregate for spawning at specific times and locations. In Belize, 14 such aggregations have been recently located and documented by a group of national and international scientists and fishermen in Belize (Heyman *et al.* 2001). Recent findings suggest that these aggregation sites are all located at reef promontories**,** protruding edges of reefs that jut into deep water on the windward side of the barrier reef and atolls. It has been further documented that as many as 26 species (including most of the snappers and groupers) spawn at such sites, at various times of year, and at various times of the month. Thus, these sites are predictable in time and space. Using a combination of tools, including the knowledge of patriarch fishermen, aerial photographs, and satellite imagery, the location of potentially important spawning sites can be predicted. Careful underwater observation can help to document and monitor these sites, and determine their importance as spawning sites.

Since most of the reproductive output from any given species occurs at the brief time of the spawning aggregations, these times and places are crucially important in the life cycle of these species. Since the sites are multi-species spawning sites, the areas are crucially important in the life history of the entire reef ecosystem. Multi-species spawning aggregation sites are now considered important conservation targets, for inclusion in marine reserves. In Belize, spawning aggregation sites are included in reserves at Gladden Spit, Half Moon Cay, and Glover's Reef. Though several of these sites are known for the Turneffe Atoll, they have not been well documented, and none is presently included within a marine reserve.

The spawning behavior of reef fishes within aggregations varies considerably but always ends in spawning events whereby gametes are released in the open water and fertilization takes place in the water column. Some fishes, such as cubera and dog snappers, spawn in dramatic aggregations of thousands of individuals in schools that can reach over 30 m through the water column. The gamete cloud that is released can be so thick that underwater visibility drops to less than a 0.5 m.

Transport of Gametes

Where do eggs and larvae go after they are released at spawning aggregations? Though the timing and location of spawning aggregations are beginning to be more accurately documented, the transport fate of released gametes is far less obvious. Larvae of snappers and groupers generally stay in the plankton for about 3 weeks, before they metamorphose into juveniles. It is generally believed that surface ocean currents transport the eggs, which float for 24 hours, until the larvae are able to swim. In their first few days, larvae are motile, but cannot swim far or fast, and do not begin to eat until about 4 or 5 days after hatching, when their mouth parts are developed. As the larvae mature, their swimming ability increases dramatically such that Pacific fish larvae are believed to be able to swim as far as 5 km during a single day. So, where do these young fish go? It is generally believed, as stated above, the young juvenile fishes wind up in shallow mangrove prop root communities, but this is poorly documented and not well understood.

Ocean and Nearshore Currents

Though the oceans appear on maps as large areas of blue, there are complex movements and dynamics within these systems. Ocean currents can transport the larvae and eggs of many species, from the site of their spawning, towards the eventual site of their recruitment. Currents can be studied using a variety of modern tools including some instruments that are used in the water, and others that are categorized as remote sensing. Current meters can be either Lagrangian (moving with the current) or Eulerian (stationary meters that can measure currents moving by). These instruments can be complex, computer assisted and expensive electronic tools. Alternately, very simple tools, such as current drogues, can provide meaningful data at low cost. Remotely sensed data that can be useful in tracking ocean currents include measures of sea surface temperature, sea surface height, and chlorophyll content.

The currents of the Caribbean Sea are dominated by the existence of circulating current gyres that spin in circles as they move westward across the Caribbean Sea. Most gyres in the northern part of the basin are anticyclonic eddies, spinning clockwise, while those in the southern Caribbean are cyclonic eddies, spinning counterclockwise. These gyres move slowly across the ocean basin until they collide with the Belize Barrier Reef and Atolls. Currents around the reefs are driven by the presence and absence of these gyres. Though the gyres are stochastic in space and time, there is some repeatability to their movements and models of these currents are helping scientists and managers to understand the dynamics of circulation around the reefs. New multidisciplinary studies of larval release, transport, and recruitment require collaboration between biologists and physical oceanographers.

Sting of Pearls – Networks of Marine Protected Areas

In order to withstand the growing pressures on tropical marine environments, scientists suggest the use of mutually replenishing marine reserve networks. Some consider these reserves like a “String of Pearls” where each pearl is a marine reserve, and the string is the ocean currents that link them together. Clearly, multi-species spawning aggregation sites should be included within these networks. Other areas that are linked to these spawning aggregations by ocean currents and provide habitat for larval and early juvenile stages are equally important to protect the entire life cycle of reef organisms. Studies of ocean currents and examination of the larval and early juvenile usage of mangrove habitats may in turn lead to identification of priority areas for nursery conservation. A resilient network of marine reserves along the MesoAmerican Barrier Reef, in habitats that are important for the critical life stages of marine organisms, might help to conserve this biologically diverse, economically important, and visually stunning marine and coastal ecosystem.

PART II: FIELD ACTIVITIES

Field Activity: Mangroves and Mangrove Associates

Objective: Participants will learn to distinguish among the three mangrove species present in Belize based on vegetative and reproductive characteristics. They will also become familiar with the common mangrove associates.

Summary: Participants will examine leaves, stems/trunks, aerial roots, flowers, flints, and propagules of *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), and *Laguncularia racemosa* (white mangrove). They will also examine and record vascular plant species that are associated with mangrove species.

Materials: Clipboard
Data sheets
Pencil
Plastic bags

Procedure: Break the large group into three smaller groups of equal size. Each small group will spend approximately 45 minutes at each of the three stations. Collect samples of flowers and leaves at each site for detailed examination in the laboratory session.

Station 1. Red-mangrove stand. At this station you will examine the vegetative and reproductive parts of *Rhizophora mangle*. What other vascular plant species are present?

Leaves

Sketch or trace the shape of a leaf:

What is the leaf arrangement (alternate or opposite)?

Are there hairs, glands, or other structures on the blade or petiole?

Stems/Trunk

Describe: color
texture
shape

<u>Aerial Roots</u>

Describe type (prop, drop, pneumatophores, etc.):

Sketch the aerial root system:

(Laboratory)

Flowers

Sketch a red-mangrove flower:

How many petals?
How many sepals?
How many stamen?

Fruit/Propagule

Sketch a red-mangrove fruit and propagule:

Seedlings

Indicate the cotyledons, hypocotyl, and epicotyl.

Station 2. Black-mangrove stand. At this station you will examine the vegetative and reproductive parts of *Avicennia germinans*. What other vascular plant species are present?

Leaves

Sketch or trace the shape of a leaf

What is the leaf arrangement (alternate or opposite)?

Are there hairs, glands, or other structures on the blade or petiole?

Aerial Roots

Describe: color
texture
shape

Describe type (prop, drop, pneumatophores, etc.):

Sketch the aerial root system:

(Laboratory)

Flowers

Sketch a black-mangrove flower:

How many petals?
How many sepals?
How many stamen?

Fruit/Propagules

Sketch a black-mangrove fruit and propagule:

Seedlings

Indicate the cotyledons, hypocotyl, and epicotyl.

Station 3. White-mangrove stand. At this station you will examine the vegetative and reproductive parts of *Laguncularia racemosa*. What other vascular plant species are present?

Leaves

Sketch or trace the shape of a leaf

What is the leaf arrangement (alternate or opposite)?

Are there hairs, glands, or other structures on the blade or petiole?

Stems/Trunk

Describe: color
texture
shape

Aerial Roots
Describe type (prop, drop, pneumatophores, etc.):

Sketch the aerial root system:

(Laboratory)

Flowers

Sketch a white-mangrove flower:

How many petals?
How many sepals?
How many stamen?

Fruit/Propagule

Sketch a white-mangrove fruit and propagule:

Seedlings

Indicate the cotyledons, hypocotyl, and epicotyl.

Field Activity: Mangrove Forest Structure

Objective: Participants will examine the structure and function of a mangrove forest ecosystem on Calabash Cay. They will become familiar with attributes of vegetative structure.

Summary: Participants will establish three 10 x 10 m plots in a flinging red mangrove forest which will be used to monitor long-term productivity of the mangrove forests at Calabash. They will measure tree height and dbh of all trees in the plots, and they will map the position of each tree. They will also establish five 1 x 1 m subplots within each plot to measure seedling density, productivity, and survival.

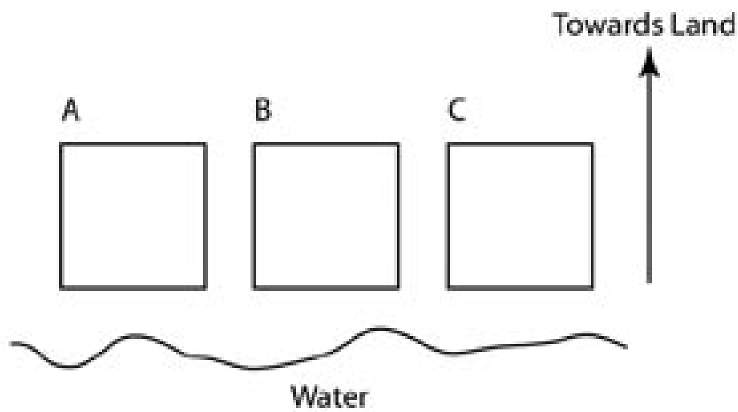
Materials: Clipboard, data sheets, pencil
1 m long tape measure
10 m long tape measure
Telescoping rod
Flagging
Calculator
Al nails
Al tags and wires
Sighting compass
PVC stakes
Tree-marking paint
Nylon twine
Hammer

Procedures: Divide the large group into three smaller groups. The small groups will visit three separate plots, where they will set up the plots according to CARICOMP protocol.

Plots A, B, C

The following methods are consistent with standardized protocol in the CARICOMP Manual (1994).

Establish the three plots in a red mangrove forest fringing the coast or a lagoon. Leave 3 m - 5 m between plots. During the course of this exercise, avoid walking inside the plots as much as possible. The array for the plots should be as follows:



To begin each plot, mark a tree to be the left side corner closest to the water. Each team should use a different color of flagging. Measure out 10 m, parallel to the shore, to the second corner. Mark with flagging. Use a compass to set the second side (from the second corner to the third). Complete the square in a similar way.

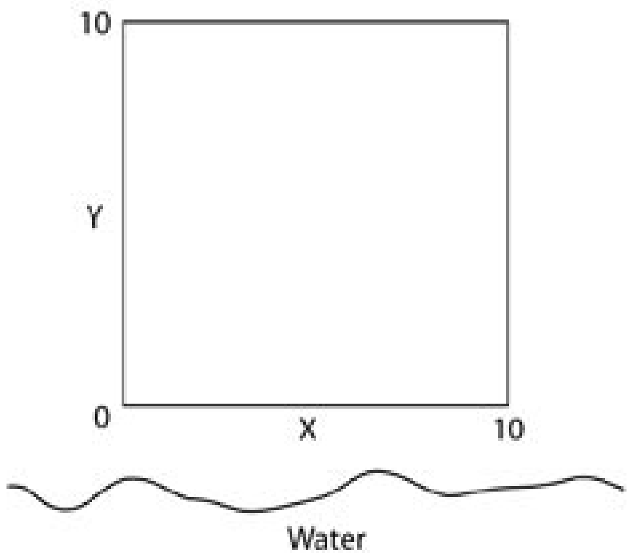
Subplots: Within each plot, randomly place five 1 x 1 m subplots. Mark the corners of each subplot with PVC stakes and delineate plots with flagging. In each subplot, label, identify, measure, and map all seedlings and saplings (<2.5 cm dbh). Label each plant with an Al tag attached loosely with a wire. Measure total height of each plant within each subplot Map these plants using XY plotting techniques. Record coordinates. The 0 point in each subplot should be at the left side corner closest to the water. The X axis should be parallel to the water, and the Y axis should be perpendicular to the water. Note that the reason for establishing these subplots first is to prevent damage to seedlings and saplings on the forest floor. Carefully avoid walking in the subplots while doing all the subsequent work in the plots!

Label Trees: In each plot, use aluminum nails and Al tags to label and to number all trees with trunk diameter >2.5 cm. Red mangrove trees sometimes have more than one trunk arising from common buttress roots. Note that prop roots that grow do~ from high branches should be ignored when deciding where to measure circumference. Consider each stem > 2.5 cm as a separate tree.

Diameter: Measure the circumference of each tree immediately above the buttress roots. Paint a ring around the trunk at the point of measurement. One year from now when these trees will be remeasured, the measuring tape can be placed on top of this ring. Diameter will be calculated later as: dbh = c/π.

Height: Measure the height of each marked red mangrove tree as: a) height above sediment surface of the highest buttressing prop roots; b) length of trunk from top of highest buttressing prop roots to main area of branching; c) total height from sediment surface to highest leaves in the canopy. For black and white mangroves, measure: a) total height from sediment surface to highest leaves; and b) the length of trunk from sediment surface to area of main branching.

Mapping: Use XY plotting techniques to map all the trees within each plot and record coordinates for each tree. The 0 point in each plot should be at the left side corner closest to the water. The X axis should be parallel to the water, and the Y axis should be perpendicular to the water.



Data Sheet: Forest Structure - Plot A

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure - Plot A, cont.

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure - Plot B

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure - Plot B, cont.

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure - Plot C

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure - Plot C, cont.

Position		Tree No.	Species	Circumference	Diameter	Basal Area	Height		
X	Y						Prop roots	Trunk length	Tree height

Data Sheet: Forest Structure Seedling/Sapling Subplots

Plot (A, B, or C)	Subplot No.	Position		Sapling or Seedling No.	DBH if needed	Species	Height (cm) from the sediment surface	Live (Y/N)
		X	Y					

Data Sheet: Forest Structure Seedling/Sapling Subplots

Plot (A, B, or C)	Subplot No.	Position		Sapling or Seedling No.	DBH if needed	Species	Height (cm) from the sediment surface	Live (Y/N)
		X	Y					

Data Sheet: Forest Structure Seedling/Sapling Subplots

Plot (A, B, or C)	Subplot No.	Position		Sapling or Seedling No.	DBH if needed	Species	Height (cm) from the sediment surface	Live (Y/N)
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Data Sheet: Forest Structure Seedling/Sapling Subplots

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		X	Y					

Data Sheet: Forest Structure Seedling/Sapling Subplots

Plot (A, B, or C)	Subplot No.	Position		Sapling or Seedling No.	DBH if needed	Species	Height (cm) from the sediment surface	Live (Y/N)
		X	Y					

Field Activity: Mangrove Arboreal Communities

Objective:	Participants will examine the supratidal zone in a mangrove forest. They will become familiar with the common arboreal occupants of this zone, and they will determine the impact of herbivores on the mangrove canopy
Summary:	Participants will visit sampling sites at Turneffe. They will characterize and record the components of supratidal communities in different types of mangrove stands and measure the herbivore damage to mangrove leaves and wood.
Materials:	Clipboard, data sheets, pencil Sharpie® Collecting bags Specimen trays Centimeter rule Pocket knife Field guides to birds and insects Cool box
Procedures:	Divide the large group into three smaller groups of equal size. Each small group will spend approximately 45 minutes at each of three stations. Collect insects and other arthropods from the canopy. Collect samples of leaves and twigs from red mangrove to measure herbivory. Place samples in collecting bags, label (name, date, location, description of site, etc.), and store in a cool box. During the evening lab session, we will examine these specimens and quantify herbivory.

Station 1. Faunal diversity in the supratidal zone. At this station you will examine the species composition of the fauna associated with arboreal habitats along a gradient from a low intertidal red-mangrove fringe along a channel to a high intertidal black-mangrove stand on the landward side of a mangrove forest.

Observe and list species in the following taxa:

Vertebrates:

Birds: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Reptiles: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Invertebrates:

Snails: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Crabs: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Insects: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Others: ______________________ ______________________

______________________ ______________________

______________________ ______________________

______________________ ______________________

Station 2. The cow-horn orchid/ant/red-mangrove community along Orchid Creek at Calabash. At this station, you will examine the interactions among an epiphytic orchid (*Schomburgkia tibicinis*), an ant (*Azteca instabilis*), and red mangrove.

1. Locate a red-mangrove tree with an epiphytic orchid. In what part of the trees is the orchid located?

2. Sketch the orchid, including the pseudobulb, leaves, peduncle, and flowers. How many pseudobulbs are there in this orchid clump?

3. Examine an orchid's peduncle and flowers. Look for extrafloral nectaries (EFNs). Compare the density of EFNs on the peduncle, leaves, flowers, and pseudobulbs. Describe:

4. Collect a pseudobulb. Are there any openings into the pseudobulb? Dissect and sketch:

5. Look for ants on the orchid. Where are they located? What are they doing? What kind of ants are they? Where do they live?

6. Place a herbivorous insect *(e.g,* moth larva) on the orchid where the ants will encounter it Describe the ants behavior towards the insect.

7. Place a herbivorous insect on several other parts of the orchid. Does the response of the ants to the herbivore vary with its location? How would you explain what you observe?

8. Do you think the orchid benefits or harms the mangrove? How?

9. Do you think the ants benefit or harm the orchid? the mangrove? How?

Station 3. Insects in the mangrove canopy. At this station you will collect samples of leaves and twigs from red mangrove to compare the level of damage by herbivores that feed on leaves (folivores) to the level of damage by those that feed on twigs (xylovores).

Herbivory will be assessed as the proportion of leaf area lost from the canopy of red mangrove. The proportion of leaf area lost to folivores can be estimated directly by measuring the amount of damaged or missing leaf tissue relative to the total leaf area. Because stem borers cause indirect loss of leaf area by killing the twigs to which the leaves are attached, we must convert the number of twigs killed by xylovores to the amount of leaf area lost from the canopy as a result of this types of herbivoiy. Conversion of these twig data to proportion of leaf area lost from the canopy requires estimation of the numbers of live and dead twigs per tree.

1. Select 3 red-mangrove trees.
    a. Count the number of twigs on one primary branch.
    b. Count the number of primary branches per tree.
    c. Estimate the number of twigs (total and dead) per tree. (*e.g,* twigs per 1° branch x 1° branches per tree = total twigs per tree).

Tree	Twigs per 1° branch		1° branch per tree	Total live twigs per tree	Total dead twigs per tree
	Live	Dead			
1					
2					
3					

2. Collect a 50-twig sample of dead twigs.
    a. Gather solitary dead twigs, rather than twigs from a dead branch, from the red-mangrove canopy.
    b. Store samples in large collecting bags. Label.
    c. Take sample back to lab where we will determine cause of death of each twig and calculate the proportion of twigs killed by stem borers.

3. Collect a 20-twig sample of live twigs.
    a. Haphazardly select twigs from all over the canopy.
    b. Do not remove leaves from twigs.
    c. Label and store in bags in a cool box.
    d. Take sample back to lab where we will measure proportion of leaf area lost to folivores.

4. Compare proportion of leaf area missing from the canopy by leaf-feeding herbivores with that removed by stem-boring herbivores.

a. Calculate mean proportion leaf area lost from the canopy due to leaf feeders.

b. Calculate mean proportion of leaf area lost from the canopy due to stem borers.

5. Calculate the cumulative herbivory by both feeding guilds.

(Laboratory)

1. **Twig herbivory Data.** Dissect each twig in the twig samples. *Cause of death:* Record "N" if no stem borer, name of species of borer if known "Unknown" if species is not known. *Inquiline:* Record presence and identity of any inquilinous organisms using hollow twigs. Collect and preserve all stem borers and hollow-twig inquilines in 70% ethanol.

Twig #	Cause of death	Inquiline	Twig #	Cause of death	Inquiline
1			26		
2			27		
3			28		
4			29		
5			30		
6			31		
7			32		
8			33		
9			34		
10			35		
11			36		
12			37		
13			38		
14			39		
15			40		
16			41		
17			42		
18			43		
19			44		
20			45		
21			46		
22			47		
23			48		
24			49		
25			50		

2. Leaf Herbivory Data. Remove leaves from the 20 live twig and place them in a large container. Blindly select a subset of 50 leaves. Measure the proportion of leaf area missing or damaged from each leaf

a. Place grid overlay over a leaf.
b. Count the number of squares that are completely or partially occupied by the leaf.
c. Count the number of squares that are completely or partially occupied by missing or damaged leaf tissue.
d. Calculate proportion of each leaf area missing or damaged:

$$\frac{\text{Number of squares with leaf damage}}{\text{Number of squares occupied by leaf}} = \text{Proportion of leaf area missing or damaged}$$

Leaf #	b	c	d	Twig #	b	c	d
1				26			
2				27			
3				28			
4				29			
5				30			
6				31			
7				32			
8				33			
9				34			
10				35			
11				36			
12				37			
13				38			
14				39			
15				40			
16				41			
17				42			
18				43			
19				44			
20				45			
21				46			
22				47			
23				48			
24				49			
25				50			

Field Activity: Mangrove Intertidal and Subtidal Habitats — Algal and Seagrass Communities

Objective: Participants will examine intertidal and subtidal plant communities at three sites. They will become familiar with common macrophytes and associated animals of different mangrove-associated habitats, including prop roots, mangrove peats, seagrass communities, and soft-sediment bottoms. Participants will also sample and examine periphyton and planktonic algae.

Summary: Students will snorkel along the edge of mangrove stands at two sites to examine the intertidal and subtidal algal communities associated with red-mangrove prop roots, peat banks, and adjacent subtidal habitats. Students will also snorkel in a turtle- grass bed in a shallow, open lagoon. They will compare species composition and cover of macrophytes in the different habitats and will speculate on reasons for the observed distribution patterns. Light levels, salinity, temperature, and nutrient concentrations will be determined for each site to help explain differences in species composition. Students will also identify animals associated with macrophyte communities, particularly herbivores (e.g, amphipods, sea urchins, crabs) and epibionts. Phytoplankton samples will be taken at all three stations.

Materials:
- Snorkel gear
- Plastic collecting bags
- Pocket knife or paint scraper
- Flexible measuring tapes
- Floating collecting buckets and sample trays
- Phytoplankton nets
- Sample bottles for plankton and water samples
- Thermometer
- Radiometer
- Underwater writing slates, pencil, field guides
- Lugol's phytoplankton preservative
- Transect line and 0.5 m^2 quadrat

Procedures: Break the large group into three smaller groups. Each small group will spend approximately 45 minutes at each of three stations. After studying intertidal and subtidal communities, each team will collect water samples for salinity and nutrient analyses back at the lab. Light measurements and phytoplankton sampling will be conducted at the end of the field activity.

Station 1. Intertidal and subtidal algal communities associated with a mangrove stand. At this station you will examine the intertidal and subtidal algal communities on red-mangrove prop roots and peats along a mangrove stand.

As a group we will identify common species of algae and animals. Record the common species below. (It may help you to remember them if you sketch them.)

Algae	Animal

Working in groups of two, locate a root with a diversity of algae. Note whether it is hanging or attached. Identify as many different algae and associated animals as you can, recording their positions along the root relative to the water level and estimating their percent cover. You will do this by gently laying a flexible measuring tape along the root, holding one end at the top of the root and letting the other sink towards the bottom. Also note the water level on the tape. To estimate percent cover of each species~ divide the number of occurrences by the length of the root. Enter your data below.

How long is the root? _____ cm   Water level on the tape _____ cm

Position on tape	Algae	Invertebrates

After examining the root, identify algae on neighboring peats and soft sediments. Record the data below.

Substrate	Height above/below water (+/- cm)	Algae	Invertebrates

Collect samples of the most common species of algae for examination in the lab. Also measure the water temperature and collect water samples for nutrient analyses.

Summary Table for Station 1

Root #	Hanging or Grounded	Algal species	Vertical range	% cover	Associated fauna
1.					
2.					
3.					
4.					

Temperature: _____ °C   Salinity: _____‰

Photon irradiance: ______ µmoles/m^2/sec

NH_3-N: _____mg/l NO_3^- -N: ______ mg/l PO_4^{3-} ______mg/1

Station 2. Intertidal and subtidal algal communities associated with a mangrove stand. As with Station 1 you will examine the intertidal and subtidal algal communities on red-mangrove prop roots and peats along a mangrove stand.

As a group we will identify common species of algae and animals. Record the common species below. (It may help you to remember them if you sketch them.)

Algae	Animal

Working in groups of two, locate a root with a diversity of algae. Note whether it is hanging or attached. Identify as many different algae and associated animals as you can, recording their positions along the root relative to the water level and estimating their percent cover. You will do this by gently laying a flexible measuring tape along the root, holding one end at the top of the root and letting the other sink towards the bottom. Also note the water level on the tape. To estimate percent cover of each species~ divide the number of occurrences by the length of the root. Enter your data below.

How long is the root? _____ cm Water level on the tape _____ cm

Position on tape	Algae	Invertebrates

After examining the root, identify algae on neighboring peats and soft sediments. Record the data below.

Substrate	Height above/below water (+/- cm)	Algae	Invertebrates

Collect samples of the most common species of algae for examination in the lab. Also measure the water temperature and collect water samples for nutrient analyses.

Summary Table for Station 2

Root #	Hanging or Grounded	Algal species	Vertical range	% cover	Associated fauna
1.					
2.					
3.					
4.					

Temperature: _____ °C Salinity: _____‰

Photon irradiance: ______ µmoles/m^2/sec

NH_3-N: _____mg/l NO_3^- -N: ______ mg/l PO_4^{3-} ______mg/1

Station 3. Seagrass communities. At this station you will examine the distribution and abundance of organisms associated with a turtle-grass community. A 0.5 m transect line has been laid from the shore out into the lagoon across a turtle-grass bed. Swim along the transect and make observations at regular intervals (every 5 meters unless instructed otherwise). You will be using a 0.5 m2 quadrat to determine the density and diversity of organisms along the transect. Record data below.

Quadrat #	Bottom type	Macrophyte species	Density #/0.5 m^2	Epifauna species	Density #/0.5 m^2

Quadrat #	Bottom type	Macrophyte species	Density #/0.5 m^2	Epifauna species	Density #/0.5 m^2

Collect plankton and water samples for analyses in the laboratory.

Temperature: _____ °C Salinity: _____‰

Photon irradiance: ______ μmoles/m^2/sec

NH_3-N: _____mg/l NO_3^- -N: ______ mg/l PO_4^{3-} ______mg/1

(Laboratory)

Phytoplankton and Periphyton Samples.

Examine the surface of macrophytes under a dissecting microscope and preserved phytoplankton samples under a compound microscope. Try to identify the major groups present using the keys in the lab. Sketch common epibiont and phytoplankters below.

Phylum	Genus	Sketch of organism

Field Activity: The Zooplankton Community of Calabash Caye, Belize

Objective: Identify and compare the zooplankton community of a reef habitat, a mangrove channel and a mangrove lagoon, in the vicinity of Calabash Caye.

Materials: Conical plankton net, 63 cm diameter, 300 - 333 µm mesh
75 ft of 3/8” thick nylon rope
10 plastic jars of 500 ml capacity
200 ml of 5% seawater Formalin
Stempel pipette (or a 3 ml syringe)
2 petri-dishes for each work-group
Microscopes
Deionized water
Key to zooplankton identification
Masking tape and markers

Sampling sites: The three sites to be sampled are (1) the patch-reef habitat in front (to the east) of Calabash Caye, (2) the mangrove channel located north of Calabash Caye, and (3) the mangrove lagoon behind (west of) Calabash Caye.

Procedure: Triplicate zooplankton samples will be collected from each of the three sites. The conical net will be towed from a small boat for 5 minutes, with the boat traveling at a speed enough to avoid the sinking of the net, but not too fast, otherwise the net will be drawn out of the water. The normal speed should be between 1 to 2.5 knots. The samples will be collected from the first 80 cm of the water column, and therefore the net should be maintained at this depth. After 5 minutes of towing the cod-end will be removed and the samples collected will be transferred to plastic jars, and fixed with seawater Formalin. The samples collected will be identified with the assistance of a stereoscopic microscope and a taxonomical key to the identification of zooplankton, during the wet-lab session. Taxonomic richness and diversity will be determined

Wet-lab (Diversity Determinations)

Work Group:	Net:	Mesh:	Date:
Tow depth:	Tow time:		

Number of Individuals

Taxa	Reef habitat	Mangrove channel	Mangrove lagoon
Amphipoda			
Chaetognatha			
Cephalopoda			
Cladocera			
Cladocera			
Cumacea			
Decapoda			
Foraminifera			
Gastropoda			
Hydrozoa			
Isopoda			
Ostracoda			
Polychaeta			
Pteropoda			
Sergestidae			
Siphonophora			
Stomatopoda			
Tanaidacea			
Tintinnada			
Thaliacea			
Fish eggs			
Fish larvae			
Undetermined			

Wet-Lab, Continued

Data Analysis

	Reef habitat	Mangrove channel	Mangrove lagoon
No. of groups			
No. of individuals			
Diversity Index			

Note: Do diversity calculations on a separate sheet with the following formula.

$$H=\log N - [1/N \sum(n_i \log n_i)]$$

Where: H = Shannon-Wiener's Diversity Index
N = Total number of individuals
n_i =Number of individuals in the i^{th} group

Interpretations

1. Which community is the most diverse?

2. Which taxonomic group appeared to be the most

3. Is there a notable trend in the diversity values as we move from one community to another?

4. What possible explanations may be given for the differences observed in each community?

Field Activity: Environmental Extremes and Adaptive Strategies in Mangroves

Objective: Participants will examine environmental characteristics along a transect across a mangrove forest. They will also become familiar with mangrove structural/anatomical characteristics that confer resistance to the abiotic stress factors present in the mangrove habitat.

Summary: Participants will conduct measurements of salinity, temperature, light intensity, and flooding intensity at three sample sites representing different environmental extremes. They will also record differences in structural and/or anatomical characteristics observed among the three mangrove species and across sites.

Materials: **Field**

Thermometers (temperature)
Quantum irradiance meter (light intensity)
Collecting bags
Clipboard, data sheets, pencil
Pocket knife
Centimeter rule
Calipers
Meter tape
Protractor
Sample bottles

Lab

Refractometer (salinity)
pH meter
Leaf area meter
Microscopes
Hach kits (nitrates and phosphates)

Procedures: Divide the large group in three smaller groups of equal size. Each small group will spend approximately 45 minutes at each of the three stations.

Collect some of the plant material from each station for more detailed observations of the anatomical structure in the laboratory (another hour or so).

Station 1. Fringe forest
Station 2. Interior forest
Station 3. Dwarf forest

At each station, you will measure temperature, light levels, water depth, tree height and dbh (diameter at breast height) and collect water samples for measurement of salinity, nutrients, pH, and sulfide. You will also collect leaves, twigs, and roots for examination of morphology and anatomy in the laboratory.

1. Measure:
    a) Temperature of air, water, and soil (5 cm depth)
    b) Light levels: direct and reflected light (expressed as a percentage of a reference)
    c) Water depth at high and low tide
    d) Height and dbh of 5 representative trees (of the species dominating the canopy)

2. Collect pore-water with the sipper device provided. Collect a reference seawater sample from the end of the pier. Place collected water in the sample bottles provided and label. Return to lab and measure salinity with the refractometer ,pH with the pH meter, and nitrate and phosphate with the Hach kits. Sulfide will be assessed by a ranking procedure: open the bottle briefly and smell. Rank the odor of the sample as follows: 0 = no detectable odor of sulfide, 1 = weak odor, 2 = strong odor.

3. Select a representative terminal twig on the five trees measured above. Locate the penapical leaf pair and measure their orientation relative to the twig with the protractor. Collect these twigs and place in the plastic bags. Return samples to the lab and measure leaf area, width, and length of all leaves on a twig with the leaf area meter. Compare the color of the leaves collected at this site with that from the other two stations. Note any chlorotic mottling. Cut a thin cross-section of a leaf and mount on a slide. Sketch the cross-section and identify the following layers or structures: cuticle, upper epidermis, hypodermis (if present), palisade and spongy mesophyll, lower epidermis, salt glands (if present), hairs (if present), stomata.

Examine the twigs and observe the leaf scar arrangement Measure the internodal distance with a centimeter rule.

4. Collect aerial roots and attached belowground roots from dwarf R. mangle (Station 3) and *A. germinans* (Station 2) and place in plastic bags. Return to lab and sketch the entire root system, noting the location of lenticels (openings in the periderm of the aerial roots). Cut a cross-section of a belowground root and observe under the microscope. Sketch and label the epidermis, cortex, stele, and aerenchyma.

	Station/Forest Type		
Environmental	Station 1/Fringe	Station 2/Interior	Station 3/Dwarf
Temperature (°C)			
Air			
Water			
Soil			
Light levels (mE)			
Reference			
Direct			
Reflected			
Water depth (cm)			
High tide			
Low tide			
Pore-water			
Salinity (‰)			
Sulfide (rank)			
pH			
Phosphate			
Nitrate			
Plant			
Dominant canopy sp.			
Canopy structure			
Seedling or sapling?			
dbh (cm)			
Individual leaf			
Orientation (°)			
Width (cm)			
Length (cm)			
Area (cm^2)			
Color/chlorosis			
Leaf area/twig (cm^2)			
Twig			
Leaf scar arrangement			
Internodal distance			

Station/Forest Type

Station #	Station 1/Fringe	Station 2/Interior	Station 3/Dwarf
Root system (sketch)			
Cross-section (sketch)			

Field Activity: Water Quality and Response of the Mangrove Jellyfish *Cassiopea* to Varying Salinity

Objective: Participants will measure water quality of water in a mangrove system and in a coral-reef system

Summary: Participants will compare pH, salinity, temperature, dissolved oxygen, nitrates, and phosphates of the water in the mangrove with water in seagrass and coral-reef communities. They will also observe and record the morphological and physiological adaptations of the mangrove jellyfish *Cassiopea* to its mangrove environment. These animals are normally found resting "upside-down" in shallow, sometimes stagnant, water. Dining the hot/dry times of the year water temperatures may reach 33° C and become hypersaline due to evaporation. After heavy rainfall, on the other hand, runoff may produce hyposaline conditions.

Materials: **Field**

Aquaria
Thermometers (3)
Refractometer
Clipboard, data sheets, pencil
Graduated cylinder
Watch
Sample bottles
Markers
Plastic bags
Snorkel gear
Cool boxes (3)
Gloves
Quadrat

Lab

Microscopes
Hach 2000
Hach reagents (ammonia, nitrate, phosphate)
Hach cuvettes
25 ml graduated cylinder

Procedure: The large group will be broken up into three small groups. Each small group will spend approximately 45 minutes at each of the three stations.

Station 1. The response of the mangrove jellyfish Cassiopea to varying salinity. At this station, participants will observe and record the physiological responses of Cassiopea to differences in salinity.

1. Collect 6 *Cassiopea* and place them in a small aquarium filled with normal seawater. Record temperature and salinity. Count the number of times a selected animal pulsates in a one-minute time period to determine the pulsation rate. To calculate the mean pulsation rate, average the counts for animals 1, 2, and 3 and record. This will serve as your control value.

	Animal l	Animal 2	Animal 3
Temperature			
Salinity			
Pulsation rate			

Mean pulsation rate = ______ (Control)

2. Place two of the animals in 75% seawater, two in 50% seawater, and two in 25% seawater. Allow the animals to settle and record an initial pulsation rate at ($time_0$). Wait fifteen minutes and again record pulsation rate at ($time_{15}$).

3. Return each animal to normal seawater and again record pulsation rates after another fifteen-minute interval at ($time_{30}$).

Time	*Cassiopea*	Salinity (% seawater)		
		75%	50%	25%
$time_0$	1			
	2			
	mean			
$time_{15}$	1			
	2			
	Mean			
$time_{30}$	1			
	2			
	Mean			

How do the pulsation rates at $time_0$, $time_{15}$, and $time_{30}$ compare with the control value?

CAUTION: JELLYFISH POSSESS NEMATOCYSTS WHICH MAY CAUSE SKIN IRRITATION. AVOID SKIN CONTACT; HANDLE ANIMALS WITH GLOVES.

Station 2. Mangrove water quality; Cassiopea behavior and population density. At this station, students will measure pH salinity, temperature, dissolved oxygen, nitrates, and phosphates of the water at different sites in the mangrove. They will also observe normal populations of Cassiopea while snorkeling. [Work from a boat.]

1. Collect water samples at three points along a transect across a small mangrove lagoon. Take all samples from a depth of 0.5 m. Label bottles and store in cool box for analysis during the evening lab. Measure temperature at 0.5 m at each site.

	Site 1	Site 2	Site 3
Temperature			
pH			
Salinity			
Dissolved O_2			
Nitrates			
Phosphates			

Describe each site (e.g, depth, turbidity, SAVs, wave energy, etc.):

Site 1: ____________________

Site 2: ____________________

Site 3: ____________________

2. Estimate the population density of Cassiopea (number/rn^2) at the three sites. Place a 0.25 m^2 quadrat on the bottom. Count the number of *Cassiopea* that occur completely or in part within the quadrat. Do not count animals that just touch the outside edge of the quadrat. Repeat three times.

Quadrat	Number of Cassiopea		
	Site 1	Site 2	Site 3
1			
2			
3			
Mean			

Note the slow contraction of the bells of each individual. Can you offer an explanation for their “upside-down” orientation and constant bell contraction?

What color are these jellyfish? To what is this color due? What is the ecological significance of this symbiosis? Collect a few specimens for observation during the evening wet lab session; keep them cool and shaded.

Station 3. Water quality in mangrove, seagrass, and coral-reef communities. At this station, students measure pH salinity, temperature, dissolved oxygen, nitrates, and phosphates of the water at three sites from mangrove, to seagrass, to a coral reef.

1. Collect water samples at three points along a transect that extends from a windward mangrove stand, across a seagrass bed, to patch reefs. Take all samples from a depth of 0.5 m. Label bottles and store in cool box for analysis during the evening lab. Measure temperature at 0.5 m at each site.

	Site 1	Site 2	Site 3
Temperature			
pH			
Salinity			
Dissolved O_2			
Nitrates			
Phosphates			
Turbidity			

Describe each site (*e.g.*, depth, turbidity, SAVs, wave energy, etc.):

Site 1: ____

Site 2: ____

Site 3: ____

As you move along the transect, count the number of *Cassiopea* that you observe. Discuss reasons why the mangrove community is the “preferred” habitat of this animal.

Field Activity: Diversity of Macrofauna in Mangrove, Seagrass, and Coral-Reef Communities

Objective: Participants will compare the obvious complexity of coral macrofaunal communities with seagrass and subtidal mangrove communities

Summary: Participants will snorkel along transects from the mangroves across seagrass beds to the extensive patch reefs around the cays. Each participant will make an inventory of the species observed an attempt to compare diversity and dominant species in each community.

Materials: Clipboard, data sheets, pencil
Field guides
Collecting bags
Marking pen
Cool box
Snorkel gear

Procedure: Break the large group into three smaller groups of equal size. Each small group will spend approximately 45 minutes at each of three stations.

Complete the following tables and compare mangrove, seagrass, and patch-reef communities for species richness and abundance of organisms. Collect samples of macroalgae and seagrass from the mangrove, seagrass, and patch-reef sites for detailed microscopic examination in the laboratory.

Station 1. Mangrove community.
Station 2. Seagrass community.
Station 3. Coral-reef community.

1. List fishes, invertebrates, corals, and algae observed in each of the communities:

		Mangrove	Seagrass	Patch Reef
Fishes	1.			
	2.			
	3.			
	4.			
	5.			
	6.			
	7.			
	8.			
Inverte-brates	1.			
	2.			
	3.			
	4.			
	5.			
	6.			
	7.			
	8.			
Corals	1.			
	2.			
	3.			
	4.			
	5.			
	6.			
	7.			
	8.			
Algae	1.			
	2.			
	3.			
	4.			
	5.			
	6.			
	7.			
	8.			

2. Rank the three most commonly observed species for each community type:

Community Type	Species Group	Rank		
		1	2	3
Mangrove	Fishes			
	Corals			
	Invertebrates			
	Algae			
Seagrass	Fishes			
	Corals			
	Invertebrates			
	Algae			
Patch reef	Fishes			
	Corals			
	Invertebrates			
	Algae			

3. Collect samples of seagrass and macroalgae from each site for microscopic examination during the evening lab session. Label collections (name, date, location) and store them in a cool box.

Field Activity: Larvae Transport from Fish Spawning Aggregation Sites

Objective: Participants will conduct drift studies to determine the probable planktonic pathway between fish spawning aggregation sites, and inshore mangrove environments.

Summary: Participants will utilize simple current drogues and handheld GPS systems to map the transport pathways and speeds of currents as they move away from known spawning aggregation sites east of Calabash Caye and Blackbird Caye.

Materials: Clipboard, data sheets, and pencil
Current drogues
Handheld Garmin GPS
Nautical Charts
Handheld calculator

Procedures: Participants will be divided into 3 groups and rotate through each of 3 stations.

1. Participants will learn the basic functions of a handheld Garmin 12 GPS unit.
2. Participants will use nautical charts to learn how to plot positions.
3. Participants will conduct field studies from an outboard skiff, using current drogues and a handheld GPS to calculate the speed and direction of surface currents at spawning aggregation sites. Finally, participants will plot the data, gathered in the field, on the nautical charts, and hypothesize about transport velocities and routes.

Station 1: Nautical Charts

1. Using the nautical charts provided, determine north, the scale of the map (note that one minute of latitude is equal to 60 nautical miles). What are the two coordinate systems? What is the position of Calabash Caye (using Latitude and Longitude with degrees, minutes, and seconds)?

2. What is Universal Transverse Mercator? What are its advantages and disadvantages?

3. What is the water depth between Turneffe Atoll and Lighthouse Reef Atoll? What is the depth within the Turneffe? What is the depth east of Lighthouse Reef Atoll?

4. Map two spawning aggregation sites on the nautical chart – Blackbird Caye, and Calabash Caye:

Station 2: Handheld Garmin GPS

1. Participants will familiarize themselves with the various menus on the GPS. Please be sure that the datum is set at NAD 27 Central, the units are metric, the coordinate system to Lat Long (degrees, minutes, seconds) and be sure that the language is English.

2. Compare the satellite reception standing on the open beach versus that under shade of dense trees or inside a building. What is the maximum accuracy that you can attain?

3. Learn how to mark a waypoint. Record the number (name), time, and location of the waypoint. Repeat this process at a different location (at least 50 meters away from the first).

4. Use the Distance Function to calculate the bearing and distance using a simple map with a north arrow, scale bar and vector indicating the relationship between the two points. Roughly map the relationship between these two points below or on a separate sheet.

Station 3: Field Observations of Surface Currents Using Drogues.

1. Participants should familiarize themselves with the use of the current drogues before heading into the field.

2. Do fish larvae float or sink after spawning? Why? Are currents consistent at all water depths? Which currents are transporting larvae, those currents at the surface, or those at 30 m depth?

3. Using the GPS as a compass, or the compass on the boat, estimate the speed and direction of the wind. Be sure to use the appropriate convention - state which direction the wind is coming from.

4. Using a current drogue, measure the speed and direction of the currents at the spawning site – Calabash Caye or Blackbird Caye. Do this by installing the drogue in the water at the spawn site and leaving for several minutes so that the drogue can begin to move with the current. Take a GPS position (be sure to note down the number in your notebook) to mark the position of installation. Let the drogue drift with the prevailing current and take position every 15 minutes or so, allowing the drogue to drift as long as possible, given the available time. Repeat the process several times as time allows.

4. Back in the laboratory, record your data on the overall data sheet being collected by the entire class. Plot the speed and direction of the currents from your data as a vector, with the length of the vector indicating the speed, and the direction of the vector consistent with that bearing obtained using the distance function on the GPS. Note that you will have to calculate the speed from the formula: *Rate = Distance x Time*. Current speeds are reported in cm/second so you will have to make appropriate conversions. You will obtain the starting and stopping time for the vector from the start and stop positions in the GPS, and subtract to obtain the number of minutes. The Distance and Bearing between the starting and stopping points will be evaluated using the distance function on the GPS. All of the data for the class should be plotted on a single graphic to indicate the variation in the speed and direction of the currents at the spawning site.

5. Measure the speed and direction of the current within the Blackbird Caye Channel. Repeat the measurement on flooding and ebbing tides. We are trying to determine if the currents within the channel are more controlled by tidal forces, or by wind driven surface currents. What is your educated guess?

6. From what you have learned in this exercise, write a paragraph with a conceptual hypothesis about the transport fate of fish larvae spawned at the Blackbird Caye and Calabash Caye sites, and how this transport might be affected by offshore processes and winds, and what the likely destination of larvae would be.

Field Activity: The Value of Mangrove Swamps as Nurseries

Objective: Participants will learn to appreciate the role of mangroves as nurseries for many commercial and sports fishes in Belize.

Summary: Participants will examine the waters among mangrove prop roots for immature stages of larger fish and invertebrates. They will examine adjacent systems to locate these same species. To appreciate how the flow of energy from the swamps helps to support adjacent communities, they will examine the composition and export of leaf litter from the mangrove.

Materials: Clipboard, data sheets, pencil
Snorkel gear
Field guides
Quadrat frames
Collecting bags
Specimen trays
Plankton net

Procedures: Break the large group into three smaller groups. Each group will spend approximately 45 minutes at each of three stations in the mangrove channel, a reef area, and in the mangrove forest. Participants will look for sizes and abundances in fishes in the various habitats.

Station 1. Mangrove as a nursery. At this site, you will swim along a mangrove channel to look for juvenile fish and invertebrate species in the water column. Compare the number and size of individuals of the same species with those living in the adjacent reef system.

1. Swim a 50 m transect along the mangrove channel, looking carefully for juvenile fish and invertebrates.

2. List species of fish that you see and the number of each of these species, along with the approximate mean size for these fish. If you can't identify to the species level, family level or common names are OK.

Fish species	# of fish	Mean Length (mm)	Food preference

3. As you are swimming, look for tiny invertebrates in the water column along the roots. Do you see any mysids, copepods, or shrimp? Are they under closed canopy or in light gaps? What do they eat? Which organisms prey on these?

4. Collect a plankton-tow sample of water near the roots. How does the density of organisms in this sample compare with the reef sample?

5. Look at the bottom. Do you see any leaf litter? What species of mangrove is most common? Are the leaves intact or broken? Describe the leaves found on the bottom. Are there signs of herbivory? What is eating the leaves? Can you see what appears like decomposition? What source probably has a larger contribution to the food chain ~ herbivory, or the detrital food loop?

6. Pick up some red-mangrove leaf litter from the bottom; feel the surface. What is on the surface of the leaf?

7. Draw a diagram for a food chain that includes spawning aggregations, seagrasses, and mangrove systems and their connections.

Station 2. Fish populations in reef communities. At this site, you will swim around a reef area to look for the juvenile fish and invertebrates.

1. Swim a 50 m transect across a patch-reef area. Count and visually estimate the lengths of all the fish that you see and record these in the table below, along with their food preferences.

Fish species	# of fish	Mean Length (mm)	Food preference

2. As you are swimming look for tiny invertebrates in the water column. How does this compare with the mangrove community of water-column invertebrates?

3. Collect a plankton-tow sample. How does the density of organisms in this sample compare with the mangrove sample?

4. Look on the bottom for red-mangrove leaf litter. Can you find any recognizable leaves?

5. Are there more predators in the mangrove or in the coral reef?

Field Activity: Hurricane Hattie Damage at Soldier Cay

Objective: Participants will survey a small mangrove island of known damage by a major hurricane to determine how this island has changed following the storm.

Summary: Participants will examine the flora and the physical and vegetative structure of Soldier Cay. They will compare the current status of the island with accounts made in 1960 (pre-Hurricane Hattie) and in 1962 (post-Hurricane Hattie).

Materials: Clipboard, data sheets, pencil

Collecting bags

Specimen trays

Measuring tapes

Corer

Clinometer

Telescoping rod

Compass

Field guide to Caribbean plants

Procedure: The large group will be broken up into three smaller groups of equal size. Each small group will spend approximately 45 minutes at each of the three stations.

Station 1. The effects of Hurricane Hattie on human habitation and activities at Soldier Cay.

At this station, you will explore Soldier Cay and look for evidence of human habitation and activities that existed there before 1961. (Note: Refer to the text and maps in Stoddart (1962, 1965) publications, included in the appendix of the Mangrove Ecology Field Manual, for descriptions of the island in 1960 and 1962.)

As a reference point; try to find the location of the “house posts” indicated on the 1962 map.

Prior to 1961, the central portion of the island was a coconut plantation. Look for evidence of coconut cultivation.

Examine and describe the substrate of the vegetated portion of Soldier Cay at three intervals along an east-to-west transect:

Site 1 (Leeward)	
Site 2 (Middle)	
Site 3 (Windward)	

Based on your observations, is this island presently suitable for cultivation?

Station 2. The effects of Hurricane Hattie on the physiography of Soldier Cay. At this station, you will examine the current physiography of Soldier Cay and compare it to maps made in 1960 (pre-Hurricane Hattie) and in 1962 (post-Hurricane Hattie) by D. R. Stoddart.

Measure the current size of Soldier Cay. (Note: In 1960, it was 145 yards long with a maximum width of 55 yards.)

Maximum length	
Maximum width	
Maximum elevation	

On the east side of the island beginning near the north end and extending southward, examine the platform on which Soldier Cay stands. Describe the intertidal and subtidal areas that immediately border the seaward side of the cay, including the rock pavement; detached loose boulders, and tidal elevation.

What is the origin of the substrate in this area?

How did the large blocks of rubble get in their current positions?

At the landward edge of the platform, locate the storm or “shingle” ridge. Examine the composition of the rubble in the ridge. Why is this called a shingle ridge? Has more than one ridge formed? If so, what does this indicate?

Station 3. Changes in the vegetation of Soldier Cay since Hurricane Hattie. At this station, you will examine the flora and vegetative structure of Soldier Cay and compare its current status with floristic surveys made in 1960 (pre-Hurricane Hattie) and in 1962 (post-Hurricane Hattie) by D.R Stoddart.

Walk a transect across Soldier Cay. Measure the height of the vegetation at 10 m intervals along a transect across the island. Record the number of strata in the canopy and the plant species where height measurements are made. Use Stoddart's 1962 map of Soldier Cay to mark the location and direction of the transect.

Interval	Vegetation height	Number of strata	Species
1.			
2.			
3.			
4.			
5.			
6.			
7.			
8.			
9.			
10.			

Examine each plant species encountered along the transect. List the species. If you find a plant that you do not know, collect a small sample of it. If possible, collect a portion with flowers.

1.	11.
2.	12.
3.	13.
4.	14.
5.	15.
6.	16.
7.	17.
8.	18.
9.	19.
10.	20.

Look for remains of fallen trees. Record the species, location, and direction of any tree fall that you find.

How do the flora and vegetative structure of Soldier Cay compare with Stoddart's descriptions of the island before and after Hurricane Hattie?

Glossary

Abiotic: non-living; part of physical environment

Abundance: the number of individuals of a species in a particular area; a component of biological diversity

Active transport: movement of a substance into an organism or into a cell against a concentration gradient; requiring the expenditure of energy

Adaptation: a genetically determined characteristic that enhances the ability of an organism to cope with its environment; any alteration or response of an organism that favors survival in a changed environment.

Aerenchyma: air-space tissue

Aerial Roots: specialized roots in mangrove plants that are exposed to the air, at least during low tide

Aerobic: refers to the presence of oxygen

Algae: an evolutionarily diverse group of non-vascular plants that lack structural complexity, that do not develop as embryos with covering provided by parent; and that lack reproductive structures with sterile tissues (all cells are potentially fertile)

Anaerobic: refers to the absence of oxygen

Angiosperm: flowering plants with true stems, leaves, and roots with vascular tissue

Arboreal Community: an assemblage of organisms associated with the above-ground parts of a tree

Avicennia germinans: black mangrove

Basal Area: the amount of area covered by tree stems, expressed in terms of square meters per hectare

Benthos: organisms associated with the bottom or bed of a body of water

Biodiversity: biological diversity; refers to the number of species in an ecosystem and the relative abundance of the different species

Biomass: the weight per unit area of living material

Biotic: the living components of an organism’s environment

Canopy: the leaf part of a plant

Ciguatera: poisoning caused by eating shellfish that have been exposed to toxin- producing species of dinoflagellates (outbreaks of these species are known as red tides)

Community: the organisms that inhabit a particular area with potentially interacting populations

Conformer: species that allow their body temperature or internal salt concentration to change in proportion to changes in ambient conditions

Conocarpus erectus: buttonwoods, an important mangrove associate

Coppicing: resprouting from tree stumps

Detrital-based Ecosystem: primary producers □□– detritus □□ detritivores □□consumers (predators)

Detritivores: organisms that feed on detritus

Detritus: dead organic material

Diffusion: the movement of molecules of a substance from a region of higher concentration to a region of lower concentration

Disturbance: alteration of a habitat by some agent of change, natural or unnatural

Diversity: biological diversity

Ecology: the study of interactions between organisms and their environment; seeks to explain abundance and distribution of organisms

Ecosystem: a biological community and its physical environment

Ectotherm: body temperature determined by environmental conditions rather than physiological conditions

Endosymbiont: an organism that lives inside the cells of its host organism

Endotherm: an animal whose body temperature is maintained by its own heat production

Endozoan: an animal that lives inside another organism

Epibiont: an organism that uses another living organism as substrate

Epifauna: animals that use another living organism as substrate

Epiphyte: a plant that uses another living organism as substrate

Eulerian: stationary meters that can measure currents moving by. These instruments can be complex, computer assisted and expensive electronic tools

Gyre: circulating currents that spin in circles as they move westward across the Caribbean Sea. Most gyres in the northern part of the basin are anticyclonic eddies, spinning clockwise, while those in the southern Caribbean are cyclonic eddies, spinning counterclockwise.

Heterotherm: physiological mechanism for elevating body temperature

Homeotherm: marine mammals and birds that maintain constant internal temperatures despite environmental fluctuations

Hydrochory: dispersal by water; a major means which mangrove spreads seeds, fruit, and/or propagules

Instar: stage between molts in the life cycle of an insect

Internode: the space on a twig between two nodes

Interstitial Water: water in the soil

Intertidal Zone: the littoral region between the mean high tide and mean low tide; exposed at low tide, submerged at high tide

Invertebrates: animals that lack a backbone

Lagrangean: current meter which moves with the current

Laguncularia racemosa: white mangrove

Larva: an immature stage of an animal that undergoes metamorphosis

Lenticel: a pore in the stems or aerial roots of mangroves through which gases are exchanged

Light Gap: a patch in a forest characterized by different environmental conditions than the habitat surrounding it (e.g., higher light intensity, lower humidity, higher soil temperature), formed by removal of part of the canopy overhead by some disturbance

Mangal: the mangrove environment

Mangrove: an assemblage of tropical trees and shrubs that grows in the intertidal zone; a non-taxonomic term used to describe a diverse group of plants that are all adapted to a wet, saline habitat. Mangrove may typically refer to an individual species. Terms such as mangrove community, mangrove ecosystem, mangrove forest, mangrove swamp, and mangal are used interchangeably to describe the entire mangrove community.

Mangrove Associates: plants that live in the mangal but lack one or more of the properties of a true or strict mangrove

Mangrove Peat: the organic substrate produced by mangrove roots and other organic material in a mangrove forest

Mature-phase Species: species that can maintain and replace themselves in an environment

Medusae: these occur in two classes (Hydrozoa and Scyphozoa) and seven orders, and refer mainly to the 'bell' or 'umbrella' form of these organisms. The term 'medusae' is usually used when referring to the orders of the above two classes of Cnidarians, for example, the orders Limnomedusae, Narcomedusae, Trachymedusae, Cubomedusae, etc. The typical medusa consists of a swimming bell or umbrella with the mouth at the center of the concave subumbrellar surface; marginal tentacles and other appended parts are usually present The umbrella may be shallow or deep, ranging in shape from subspherical to an almost flat saucer, exhibiting a tetraradiate symmetry; a body plan of four identical quadrants is usually present.

Meiofauna: tiny benthic animals less than 1 mm in size

Meristem: regions in a plant where cells are actively dividing or have the potential to divide

Monospecific: vegetated or inhabited by one species

Mutualism: a relationship between two or more species in which all receive some benefit

Node: the point on a stem where a leaf and its axillary bud are formed

Osmoconformer: an organism that can allow its internal salt concentration to fluctuate within limits

Osmoregulator: an organism that maintains a constant internal salt concentration

Osmosis: the movement of water or other solvent across a semipermeable membrane from a region of low solute concentration to a region of high solute concentration

Periphyton: organisms that live attached to underwater substrates

Petals: floral parts interior to the sepals and exterior to the pistil and anthers

Petiole: the stalk portion of a leaf that attaches the leaf blade to the stem at the node

Phloem: vascular tissue in a plant that transports sugar and other organic compounds throughout a plant

Phytoplankton: microscopic plants floating in the water column

Pioneer-phase Species: species that are able to invade and colonize disturbed areas during early stages of succession

Plankton: microscopic organisms floating in the water column, not associated with the substrate

Pneumatophores: vertical extensions from cable roots in black and white mangrove

Poikilotherm: an animal that does not maintain a constant body temperature

Population: all members of a species that live in a common area

Pore-water Salinity: salinity of the water in the soil

Predators: secondary consumers; living prey is consumed in whole or in part

Primary Consumers: herbivores

Primary Productivity: the rate at which inorganic material and energy are converted to organic material

Propagule: mangrove dispersal unit; seedling

Prop Root: aerial roots of red mangrove

Radicle: embryonic root

Range: the geographic area in which a species occurs

Recruitment: process where floating fish eggs divide from a single cell and differentiate into tiny swimming larvae, which inhabit marine plankton. They follow ocean currents and eventually, if they encounter suitable habitat, will metamorphose into their juvenile forms within mangrove and seagrass habitats

Redox Potential: a measurement of the oxidized vs. reduced chemical elements of the soil; the more negative the potential, the more reducing the soil conditions

Regulators: species that maintain a constant internal environment despite changes in external conditions

Rhizoid: nonvascular anchoring root-like structure in a plant

Rhizophora mangle: red mangrove

Rhizosphere: the soil area immediately around the roots

Rookery: a colony of birds or the place where a colony of birds lives

Salinity: refers here to the concentration of salt in the water

Salp: barrel-shaped pelagic tunicates belonging to the classes Thaliacea and Larvacea. These, in turn, belong to the family Salpidae, the order Salpida, and genus Salpa; however, there are other genera such as Thalia, Transtedtia, Thetys. These organisms may be solitary or joined in chainlike colonies. Each individual consists of a permanent, barrel-shaped, cylindrical, prismatic or spindle-shaped structure opened at both ends; transparent, with complete or incomplete hoop-like muscle rings; polymorphic with sometimes quite different solitary and aggregate forms.

Salt Exclusion: ability of a mangrove to exclude salt at the root surface, (e.g., red mangrove)

Salt Excretion: ability of a mangrove to take up saltwater through its vascular tissue and secrete it out through pores on the leaf surface

Seagrass Bed: large, dense stands of seagrass, (e.g., turtle grass)

Sepals: floral parts external to petals

Sessile: an organism attached or fixed in one place

Species Richness: the number of species in a habitat

Stilt Roots: prop roots of red mangrove

Stolon: horizontal branch or runner

Substrate: the surface on which an organism lives

Subtidal Zone: region below the mean low tide mark

Succession: progressional change in the species composition of an ecosystem over time as the organisms alter the environment

Supratidal Zone: region above the mean high tide mark

Surface Tension: cohesion of water molecules at the water's surface

Symbiosis: close living arrangement between a pair of species

Tannin: a phenolic compound found in plants believed to function in antiherbivore defense and protection from ultraviolet radiation

Taxonomy: the formal guidelines for classifying organisms based on evolutionary relationships

Terrestrial Communities: communities of organisms that live on land

Transect: an ecological method particularly useful in examining zonation or gradients

Trophic Level: refers to a position in the hierarchy of the food web shared by all organisms are the same number of steps away from the primary producers

Trophic Structure: organization of energy flow through a community

True Mangroves: strict mangrove; term defined by P.B. Tomlinson; 5 criteria: restricted to tidal swamps; salt tolerance by salt exclusion or salt excretion; morphological specialization, (e.g., aerial roots and vivipary; forms pure stands; isolated from nearest terrestrial relatives at least at the generic level)

Upwelling: vertical movement of water currents that brings up nutrients from deep regions

Vascular Plants: angiosperms; plants with vascular tissue, (i.e., xylem and phloem true leaves, stems, and roots)

Viscosity: resistance to flow in a liquid

Vivipary: continuous development from flower through germinated seedling while attached to parent plant

Xylem: vascular tissue in angiosperm transports water

Xylovore: an animal that eats wood

Zonation: a distinct arrangement of species along an environmental gradient

Zooplankton: microscopic animals floating in the water column

Zooxanthellae: dinoflagellates (unicellular algae) that live as symbionts in other organisms

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