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Mangrove Forests

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The distribution of mangrove forests in the southeastern United States is limited to the Florida Peninsula (Fig. 1). These forests consist of the woody facultative halophytes, the red [*Rhizophora mangle* L. (Rhizophoraceae)], black [*Avicennia germinans* L. Stearn (Avicenniaceae)], and white [*Laguncularia racemosa* L. Gaertn.f. (Combretaceae)] mangroves. The buttonwood mangrove, *Conocarpus erectus* L., is also included in the mangrove flora of Florida but does not meet the "true or strict" mangrove definition proposed by Tomlinson (1986). There is an extralimital occurrence of black mangroves along the northern Gulf of Mexico; however, they are locally restricted in areal coverage, which is believed to be controlled by cold winter temperatures (Sherrod and McMillan 1985). The largest areas of mangrove forests are found along the coastal margin south of latitude 28°00′ N, 90% of which are located in the four southernmost counties of the Florida Peninsula, that is, Dade, Monroe, Collier, and Lee Counties (National Wetlands Inventory 1982, cited in Lewis et al. 1985).

THE PHYSICAL ENVIRONMENT

Physiography

Mangrove growth is typically limited to estuarine ecosystems and in more inland areas that are subject to episodes of saline intrusion as happens, for example, during hurricane-driven tidal surges (e.g., see Chapter 6 in this volume). Fringing mangrove forest growth occurs in most bays, lagoons, coves, and tidal portions of creeks and rivers from Volusia County south on the east coast, and northward to Levy County on the Gulf Coast. Mangrove forests form hydric communities, which are periodically inundated by rainfall, tides, and annual fluctuations in sea level (Wanless 1982). Red mangrove fringe forests are inundated on most, if not all, high tides. The height and periodicity of water level fluctuation, wave energy, and

FIGURE 1. Mangrove forest communities along the coast of the Florida Peninsula (Küchler 1964; Type 105).

interstitial, or pore water, salinity all contribute to structure and species composition of mangrove communities. These hydrological parameters, in addition to local topography, influence the development of several types of mangrove communities in south Florida, five of which are described below.

The geomorphological settings for mangrove forest growth along the Florida Peninsula are diverse. Thom (1984) has defined five generalized environmental settings for mangrove growth, three of which can be observed in Florida. A combination of his Type 1 River-dominated and Type 2 Tide-dominated coastal systems can be found along both coasts. The Type 3 Wave-dominated barrier-lagoon system dominates the central east coast of Florida (Indian River lagoon) and certain locations along the west coast (Charlotte Harbor, Sarasota Bay, and Boca Ciega Bay). Coincident with the progressive decrease in freshwater runoff, and the rise in soil salinity, red mangroves have invaded former freshwater tributaries of the Taylor Slough drainage basin (Everglades) and have been observed 3–8 km inland of the northern border of the Gulf coastal lagoons (i.e., inland of the Buttonwood Embankment) (Craighead 1971, Schomer and Drew 1982). The Florida Keys represent a coralline fossil barrier island system that supports a diverse pattern of fringe, overwash, and dwarf mangrove forests.

Hydrology/Climate

The hydrologic environment of mangrove communities is highly variable, though all species are limited to areas that are at least periodically inundated by brackish or saline water. The most notable hydrologic phenomenon that affects mangrove distribution is the predictable annual rise in sea level that occurs to varying levels around the Florida Peninsula. The most significant rise occurs during the fall along the Atlantic Coast, during the spring and late summer, and periodically the fall, along the Gulf Coast (Wanless 1982, see also Provost 1974, 1976). When tides are superimposed on the sea-level rise, a significant and prolonged inundation occurs. These events limit growth of terrestrial species in mangrove stands at higher elevations (elevations less than 0.6 m NGVD) and allow tidal invasion of much of the forest. This tidal invasion brings with it a wide variety of aquatic organisms (Harrington and Harrington 1961, Gilmore 1987).

Rainfall and overland sheetflow also greatly influence the flooding of mangrove forests, particularly those in association with alluvial basins or sloughs (e.g., Taylor Slough–Everglades). The warm-temperate south Florida climate can be divided into cool–dry (November–April) and warm–wet (May–October) seasons with 80% of the rain typically falling in the warm–wet season (see Chapter 6 in this volume for a more detailed account of south Florida precipitation patterns). Overland sheetflow through the Taylor Slough has recently been impacted by extensive water management activities and does not necessarily follow the natural seasonal hydrological cycle outlined above. Under natural conditions, this sheetflow has the potential to significantly impact estuarine salinity patterns and therefore mangrove forest communities (Schomer and Drew 1982). However, sheetflow associated with precipitation is no longer predictable due to anthropogenic impacts on water flow throughout the lower half of the Florida Peninsula, including Tampa Bay and the Indian River lagoon. These impacts are discussed in detail in Chapter 6 and as they may affect mangrove ecosystems are treated in the section entitled Resource Use and Management Effects.

Water salinities at most estuarine mangrove forest sites around Florida are polyhaline with means between 18 and 30 parts per thousand (ppt). However, there are sites within Florida Bay and the Indian River lagoon that commonly reach hypersaline levels, that is, generally to 40 ppt. In addition, there are mangrove fringe communities and oligohaline sites in Taylor Slough of the Everglades, and along various rivers and smaller tributaries south from Tampa Bay and Taylor Creek of the Indian River lagoon.

Well-developed mangrove forests principally occur south of 28°00′ N, where coastal air temperatures are subtropical. Mean winter coastal air temperatures south of this latitude are generally above 17°C. They remain higher at a higher latitude on the east coast primarily due to the nearshore position of the warm Florida Current. During severe winters, hypothermal mortalities of red and white mangroves have been observed in the Cedar Key/Sea Horse Key area (Lugo and Patterson-Zucca 1977), Tampa Bay, and the northern half of the Indian River lagoon (Gilmore et al. 1978, Estevez and Mosura 1982) while black mangroves receive damage further north at latitudes of 29°00′ N or greater (Sherrod and McMillan 1985).

Geology

The coastal surface geological formations of the lower Florida Peninsula are marine sedimentary sequences with occasional freshwater limestones and are all of Pleistocene origin. These are the Miami and Key Largo limestones of southeast Florida, Ft. Thompson and Anastasia formations of west-central Florida, and the Anastasia formation of east-central Florida. Mangroves associate with sediment deposits over these shallow formations, preferring low-energy shorelines where fine sediments, muds, and clays will settle (Odum et al. 1982, Thom 1984). Mangrove forest communities contribute a significant detrital mass to these sediments, thus producing fine anoxic and acidic sediments that are typically high in organic materials. Mangrove growth is not limited to these substrates as bare rock and inorganic sands may also support growth under low wave and current energy conditions (Odum et al. 1982). Whereas red mangroves are capable of producing large deposits of peat (Cohen and Spackman 1974), the occurrence of peat is not ubiquitous around the coast for reasons that are not known.

VEGETATION

Historical Maritime Mangrove Forest Coverage

The area extent of mangrove forest coverage in Florida has been estimated to be approximately 202,000 ha (National Wetlands Inventory 1982, cited in Lewis et al. 1985). Whereas there has been a substantial reduction in the total area coincident with the historical development of Florida, no one has attempted to estimate the predevelopment historical coverage. From an ecological perspective, however, the loss of total area may not be as important as other environmental changes that have been and are taking place in this biological community. The two principal changes are related to the alteration in the freshwater hydroperiod by land drainage and runoff water diversion, and the selective legal protection of the more popular species and habitats (Snedaker 1989).

Changes in the freshwater hydroperiod mainly affect the salinity balance, which may rise when freshwater flow is reduced or become lower in areas normally exposed to increased freshwater discharge, such as from land drainage canals. In nonconfined areas of a moderate salinity increase, the area of mangrove vegetation has expanded (Reark 1975). Elsewhere, changes in the local salinity regime have favored the development of dwarf mangrove vegetation (cf. Egler 1952) or have been associated with invasive colonization by certain halophytic exotics, such as Australian pine (*Casuarina equisetifolia*) and Brazilian pepper (*Schinus terebin-*

thifolius). In general, the attainment of maximum structural development and productivity of mangroves, in the absence of damaging hurricanes, is closely related to the availability of freshwater runoff and the terrigenous nutrients that are entrained in it (Pool et al. 1977).

As a result of the environmental political movement during the late 1960s and early 1970s, and the classic mangrove research of Odum (1969a) and Heald (1969), mangroves were placed under the protective jurisdiction of government agencies. However, the laws as presently administered, give selective protection to one species (the red mangrove) and one vegetation type (the fringe forest), which have been heavily popularized in the media and in educational materials. The other mangrove species and habitat types are being lost at a disproportionate rate with unknown consequences for the functional diversity of the coastal zone.

Plant Communities

Traditionally, the low species-richness mangrove vegetation type has been described and interpreted on the basis of the zonation of species (cf. Chapman 1976). This approach was based on the observed tendency for the species to segregate in monospecific zones, which was interpreted as reflecting a successional pattern (Davis 1940, Egler 1952). In Florida, however, the classical zonation pattern is not commonly observed except in local areas of relatively well-defined topographic gradients. The large expanses of mangrove vegetation in coastal floodplains and basin environments, for example, seldom exhibit an aggregation or zonation of species. In 1973, Snedaker and Lugo (see also Lugo and Snedaker 1974) developed a spatial classification system that has subsequently been shown to have a statistically valid basis (Pool et al. 1977, Twilley 1985, Snedaker 1989). That classification system is based on gross differences in topography, surficial hydrology, and the related salinity regime. It is used here as the basis for the discussion of mangrove habitats, or forest types, in Florida. The accompanying data summaries are adapted from Snedaker (1989) based on the published works of Pool et al. (1977) and Twilley et al. (1986) (Table 1).

TABLE 1 Characteristics of Mangrove Forest Type of Southern Florida[a]

	Mangrove Types				
Characteristics	Fringe Forest	Overwash Forest	Riverine Forest	Basin Forest	Dwarf Forest
Forest height (m)	7.65	6.37	12.64	12.14	<1.0
Mean stand diameter (cm)	8.31	11.12	19.37	10.53	1.75
Complexity Index[b]					
Trees	26.44	13.17	38.77	18.41	1.5
Saplings	1.54	2.17	22.76	4.09	—
Litter production (mg/ha/yr)	9.00	9.00	12.98	6.61	1.86

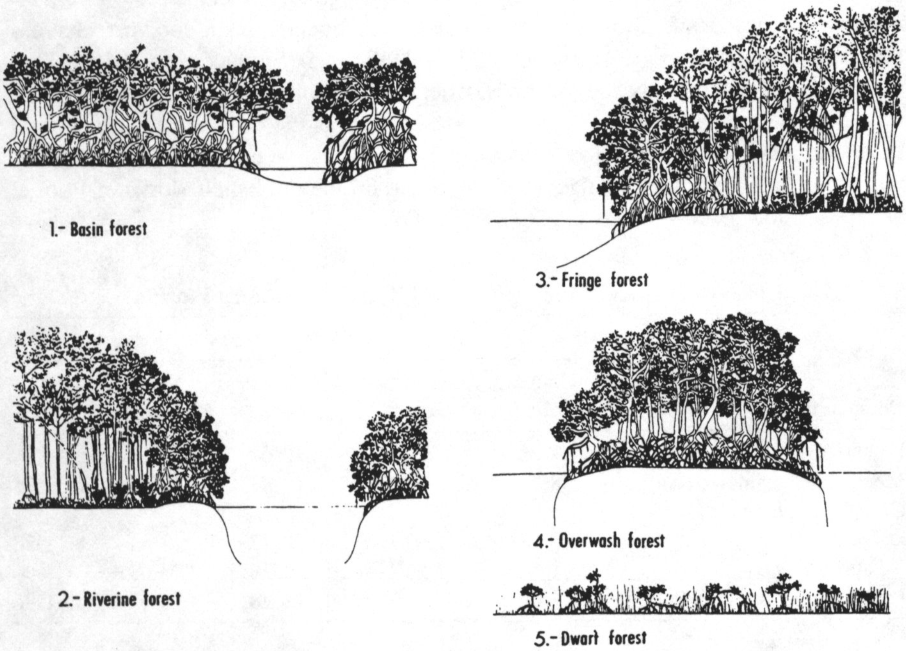
[a] Data are averages.

[b] Complexity Index utilizes tree height, density, and number of species as independent variables and the sum of present contribution of individual species (Poole et al. 1977).

Mangrove Fringe Forests Mangrove fringe forests, almost by definition, occur along sheltered coastlines with exposure to open water as found along the shorelines of lagoons and bays (Figs. 2 and 3A, C). In this situation, the canopy foliage forms a vertical wall in response to the full sunlight. The fringe forest type is almost exclusively dominated by the red mangrove, although in areas where there is a rising topographic gradient, the other species may assume sequential dominance along the gradient. It is this single pattern that formed the interpretive model for mangrove species zonation and the even more speculative argument that the zonation pattern recapitulated plan succession (cf. Davis 1940, Snedaker 1982).

The principal characteristics of this forest type are related to the pattern of tidal inundation whereby water flows in on rising tides and out on falling tides. This means that buoyant materials such as leaves, twigs, and propagules are exported from the habitat on each outgoing tide. In the contiguous shallow water, leaves decompose and become nutritionally enriched and are consumed by a variety of marine–estuarine animal life forms. Because of the unsupported presumption that whole leaves or bulk detritus are the most important organic contributions to nearshore foodwebs (cf. Odum 1969a, b), the fringe forest (and the dominant red mangrove trees) receive the highest level of government protection. In Florida, at the present time, even horticultural pruning or trimming of red mangroves can evoke a severe legal penalty.

Also related to the pattern of tidal inundations (700+ per year) is the common occurrence of a shoreline berm and/or an interior wrack line. The suspension and


1.- Basin forest

2.- Riverine forest

3.- Fringe forest

4.- Overwash forest

5.- Dwarf forest

FIGURE 2. Mangrove forest community types. (From Snedaker and Lugo 1973.)

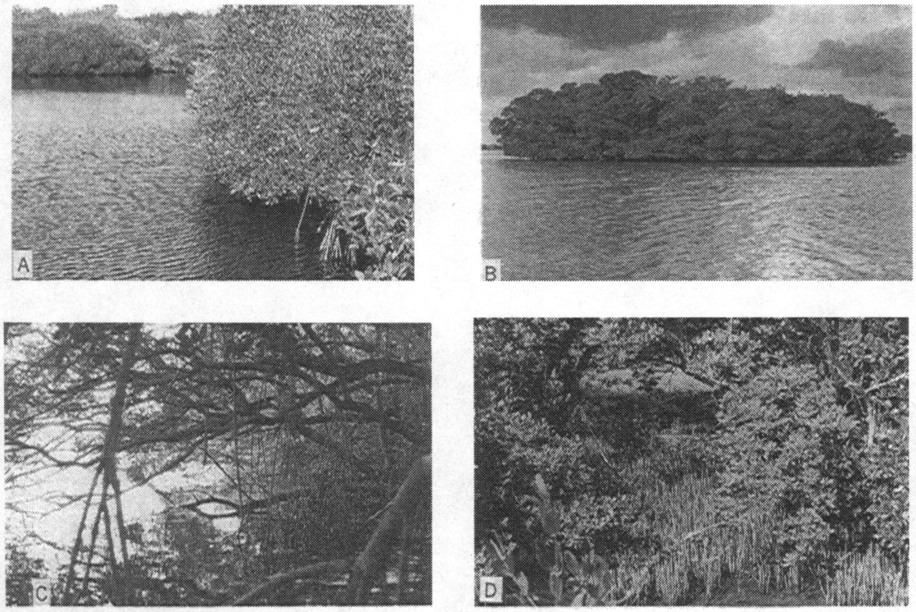


FIGURE 3. Examples of mangrove forest community types: (A) fringe forest, red mangrove (*Rhizophora mangle*); (B) overwash *Rhizophora* island; (C) detail of red mangrove fringe forest with subcanopy and prop roots; and (D) semi-open canopy of black mangrove (*Avicennia germinans*) basin forest.

transport of materials in moving water are functions of the current or flow velocity. When the direction of water changes, as during a reversal of the tides, suspended materials tend to settle out in a characteristic zone of deposition. Also, during storm events, loose debris including human-made flotsam and jetsam, are carried into this habitat where it accumulates in a wrack line.

Overwash Mangrove Islands In just about all ecological aspects, the overwash mangrove island type is equivalent to the fringe forest mainly because of the relatively high frequency of tidal inundation (Figs. 2 and 3B). The principal difference, however, lies in the fact that tidal waters completely overwash the island on almost every tidal cycle. Although tidal overwash also occurs on the retreating or falling tides, the water is not necessarily the same parcel that entered due to the mixing and exchange that take place on the inland water side of the island. Likewise, in the case of strong littoral circulation, the overwash approximates a unidirectional flow. Also, the presence of a berm or wrack line is seldom observed. An interesting aspect of overwash islands, or mangrove-dominated islands in general, is the high incidence of bird rookeries. Presumably, this is mainly due to the island effect, which provides a water barrier to potential terrestrially based predators and scavengers, such as rats, feral cats, and raccoons.

Although the overwash tidal flux pattern is different in comparison to the fringe forest, many structural and functional characteristics of the mangrove overwash islands are not statistically different from that of the mangrove fringe forests. Some of the similarities are illustrated in Table 1. Note that the litter production values from both forest types have been pooled to form a single estimate [see Twilley et al. (1986) for the statistical rationale].

Riverine Mangrove Forests In those areas of Florida which still retain some natural pattern of freshwater river or stream discharge into the coastal zone, mangroves occupy the seasonal floodplain (Figs. 2 and 4B). Their presence is due

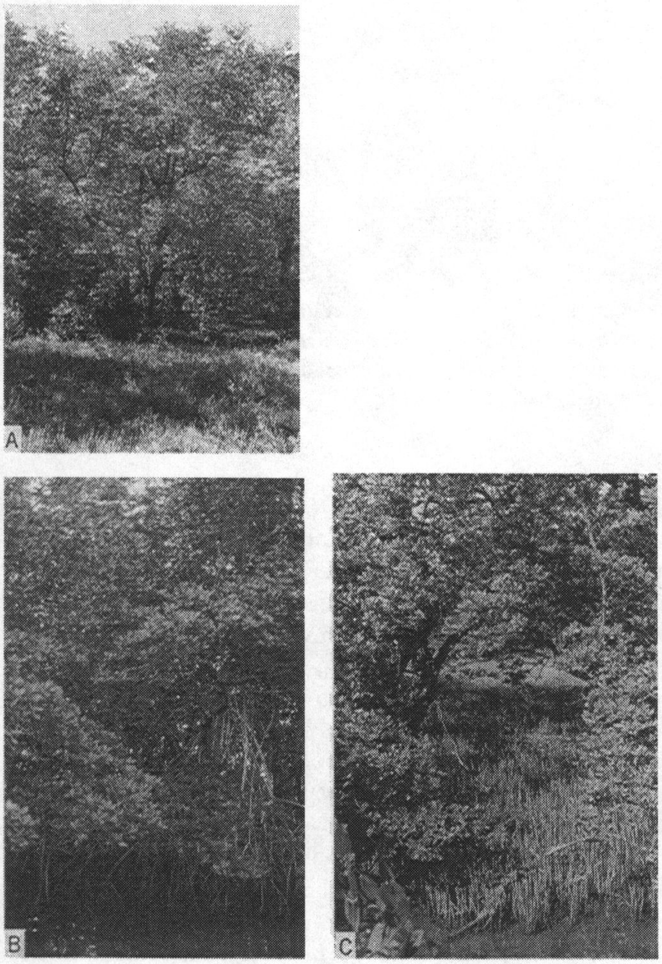


FIGURE 4. Examples of mangrove forest community types: (A) basin forest meadow of salt wort (*Batis maritima*) and glass wort (*Salicornia virginiae*) with stand of black mangrove (*Avicennia germinans*); (B) riverine forest stand of large red mangrove (*Rhizophora mangle*) (> 10 m height); and (C) pneumatophores of black mangrove in tidal basin forest.

exclusively to the salinity of the contiguous marine environment that dominates during the low-water period of the year. Although the salinity drops during the high-water season in the fall, the salinity regime is adequate to both exclude glycophytic competitors and accelerate the productivity of the dominant mangrove vegetation. Riverine mangrove forests in Florida, as well as elsewhere in the world where there is abundant fresh water, represent the most productive forest type (Pool et al. 1977).

The high productivity is attributable to the reduced salinity, or chlorinity, and the fact that freshwater runoff from land also carries with it mineral nutrients that are required for plant growth. The period of reduced salinity coincides with the higher availability of mineral nutrients, and the late-summer, early-fall season of higher sea level in Florida (sea level is not necessarily higher in other parts of the world; see Wanless 1982). Comparative data for riverine mangrove forests illustrate both how they differ from the other forest types and their relatively higher productivity.

In terms of the relationship to secondary marine productivity via the detrital food web, the riverine (as well as the basin forest type) may be equally important. This is due to the fact that during the low water season, organic detritus in this forest decomposes in situ, forming fine particulates and a suite of soluble organic chemicals that are exported during the season of flooding.

The basin mangrove forest type is probably the most common type (in south Florida) and the one that is also the most commonly destroyed for ''development'' objectives. This type exists in more-inland topographic depressions, which are not tidally flushed by all high tides (Figs. 2, 3D, and 4A, C). Depending on the specific location, relative to tidal activity and freshwater runoff, this habitat type may experience seasonal periods of hypersaline soil water, which, if severe, can limit mangrove growth or induce mortality (Cintron et al. 1978). In such extreme situations, the basin environment may contain areas of varying size of succulent herbaceous halophytes or exist as a barren, tidal, salt flat. Normally, forested mangrove basins are dominated by the black mangrove but may also contain various proportions of exotic trees such as Australian pine and Brazilian pepper.

Due to the large areal extent of basin mangrove forests, particularly in south Florida, they probably contribute the largest absolute quantity of organic detritus to Florida's nearshore waters. The majority of the organic matter is exported in a very fine particulate or dissolved form and is usually associated with dark, tannin-stained water. Whereas the tidal export of whole leaves has been considered traditionally to be the most important function of mangroves, recent research (Camilleri and Ribi 1986, Alongi 1987) suggests that the dissolved materials have equally important roles in the structure and functioning of estuaries. This consideration indicates that a mosaic or diversity of mangrove forest types and related functions has greater ecological importance than any single forest type or organic matter export pattern.

Dwarf Mangrove Forests Dwarf mangrove forest vegetation occurs in marginal environments where nutrients, freshwater inflow, and tidal activity are limiting.

The largest single tract of dwarf mangroves is in the saline Everglades of southeast Florida (Egler 1952), although the habitat type appears elsewhere in Florida where vegetative growth is perpetually limiting, particularly in relatively dry inland transition areas. All species of mangroves can exist in the dwarf form and the most unique characteristic is the fact that they have a maximum height at maturity of only about 1 m (Table 1). This characteristic distinguishes the dwarf form from mangroves exposed to transitory stress, which have variable heights. Although there is no evidence that adequately explains the mangrove dwarfing phenomenon, similar research on the tall and short forms of *Spartina alterniflora* (Gallagher et al. 1988) suggests that there may be some genetic control. Another unusual feature is that despite the small stature and low unit-area biomass, leaf litter production by dwarf mangroves is disproportionately high.

Mangrove Community Succession As stated earlier in the comments on mangrove species zonation, the traditional concepts of plant succession are seldom applicable to the mangrove ecosystem in either the long or short term. During the Holocene period of sea-level rise in Florida, coastal mangrove wetlands have either (1) retreated along an inland-moving salinity gradient, (2) been overstepped as when retreat is made impossible by high topographic relief or some other exclusionary factor, or (3) kept pace with the rise in sea level as might occur through vertical peat building or the accretion of allochthonous organic or inorganic detritus (Parkinson 1987). From the geological perspective, mangrove community replacement sequences (i.e., plant community succession) are strictly a function of mean sea level, modified of course by other factors such as local episodes of sediment accretion and deposition.

On shorter time scales, measured in terms of multiple decades, community succession (i.e., directional change in species composition or habitat type) is controlled by local geomorphological processes, mainly those of oscillating patterns of accretion and erosion. Snedaker (1982) and Lugo (1980) reviewed the ecological literature on the topic and came to the same general conclusion: that is, the mangrove ecosystem at any given time and place represents a ''succession of successions'' (Lugo 1980) in which the particular habitat type and species composition are transitory over time. As such, the state of the ecosystem simply reflects the temporary ''optimum'' conditions prevailing at that time, all of which are controlled by geomorphic processes and related hydrologic patterns.

ANIMAL COMMUNITIES

Principal Mangrove Forest Animal Communities

Mangrove forest animal communities can be divided into at least seven spatial guilds defined by principal microhabitat associations. These are dynamic spatial groups with species often moving from one guild to another during ontogeny or with changes in environmental conditions. These guilds interact with, contribute, or receive species from adjacent aquatic guilds occupying other habitats (e.g.,

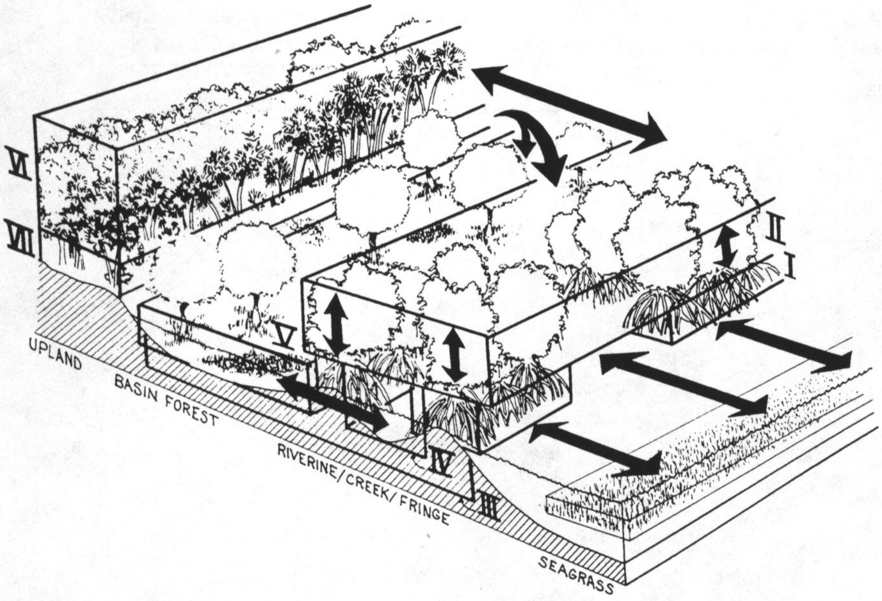


FIGURE 5. Mangrove spatial guild distribution illustrating organism communities discussed in the text and presented in Table 2.

organisms inhabiting proximate seagrass meadows) and two proximate terrestrial guilds on the adjacent uplands (organisms occupying arboreal and terrestrial microhabitats of adjacent upland forests, Fig. 5, Table 2).

Sublittoral/Littoral Mangrove Guild: Spatial Guild I The habitat of this guild consists of the aquatic prop root zone of the red mangrove (*Rhizophora mangle*). This community typically occurs in association with red mangroves forming fringe, riverine, or overwash forests. Other mangrove species may contribute depending on the topography where the swamp meets open water. However, the only other plant species consistently observed emerging from the sublittoral zone is smooth cordgrass (*Spartina alterniflora*), which is typically colonized and eventually displaced by the red mangrove.

Several physical characteristics of the fringe zone dictate the nature of the animal communities that inhabit it. The red mangrove fringe is located adjacent to open water or along coastal rivers and creeks where wind, tidal, and freshwater flow energies are relatively great, when compared to basin forests further inland. These energies may vary depending on the exposure of the estuary or river and generally the greater exposures experience higher tidal and wind energies and therefore have higher minimum dissolved oxygen levels and lower anoxic sulfide levels. These conditions are optimum for sessile filter feeders, which characterize the prop root community, although there may be distinct faunal changes within the community depending on the proximity to oceanic or to freshwater conditions.

TABLE 2 Habitat and Microhabitat Distribution of Organisms Showing an Association with Mangrove Forest Habitats of the Southeastern United States[a]

Habitat	Species
	Sublittoral/Littoral Mangrove Guild: Spatial Guild I (Red Mangrove Fringe, Riverine and Overwash Forests)
RESIDENTS—SESSILE	
Tunicates	Black tunicate, *Ascidia niger*
	Mangrove tunicate, *Ecteinascidia turbinata*
Crustaceans	Barnacle, *Balanus eburneus*
	Mangrove gribble, *Sphaeroma terebans*
Molloscs	Eastern white slipper shell, *Crepidula plana*
	Eastern oyster, *Crassostrea virginica*
	Tree oysters, *Isognomon* spp.
	Broad ribbed carditid, *Carditamera floridana*
	Mossy ark, *Arca imbricata*
	Scorched mussel, *Branchidontes exustus*
	Wood boring martesia, *Martesia striata*
RESIDENTS—MOBILE	
Molluscs	Keyhole limpet, *Diodora cayensis*
	Crown conch, *Melogena corona*
	Lightning whelk, *Busycon contrarium*
	Rock shells, *Thais* spp.
	Oyster drills, *Urosalpinx* spp.
	Pisa snails, *Pisania pusio*
	Ceriths, *Cerithidea* spp.
	Dove snails, *Anachis semiplicata*
	Turret snails, *Turritella* spp.
	Bubble snails, *Bulla striata*
	Mud snails, *Nassarius* spp.
Crustaceans	Herbst's panopeus, *Panopeus herbsti*
	Harris mud crab, *Rithropanopeus harrisi*
	Broadback mud crab, *Eurytium limosum*
	Snapping shrimp, *Synalpheus fritzmuelleri*
Teleosts	Sailfin molley, *Poecilia latipinna*
	Mosquitofish, *Gambusia affinis*
	Mangrove gambusia, *G. rhizophorae*
	Inland silverside, *Menidia beryllina*
	Hardhead silverside, *Atherinomorus stipes*
	Skilletfish, *Gobiesox strumosus*
	Florida blenny, *Chasmodes saburrae*
	Highfin blenny, *Lupinoblennius nicholsi*
	Banded blenny, *Paraclinus fasciatus*
	Fat sleeper, *Dormitator maculatus*
	Notchtongue goby, *Bathygobius curacao*
	Emerald goby, *Gobionellus smaragdus*
	Naked goby, *Gobiosoma bosc*
	Crested goby, *Lophogobius cyprinoides*
	Clown goby, *Microgobius gulosus*

TABLE 2 ***(Continued)***

Habitat	Species
	Sublittoral/Littoral Mangrove Guild: Spatial Guild I (Red Mangrove Fringe, Riverine and Overwash Forests) (Continued)
TRANSIENTS	
Molluscs	Squid, *Loligo* spp.
Crustaceans	Spiny lobster, *Panulirus argus*
	Pink shrimp, *Panaeus duorarum*
	Grass shrimp, *Palaemonetes* spp.
	Great land crab, *Cardisoma guanhumi*
	Fiddler crabs, *Uca* spp.
	Swimming crabs, *Callinectes* spp.
Teleosts	Snook, *Centropomus undecimalis*
	Jewfish, *Epinephelus itajara*
	Tripletail, *Lobotes surinamensis*
	Leatherjacket, *Oligoplites saurus*
	Gray snapper, *Lutjanus griseus*
	Dog snapper, *L. jocu*
	Sailor's choice, *Haemulon parra*
	Bluestriped grunt, *H. sciurus*
	Sheepshead, *Archosargus probatocephalus*
	Striped mojarra, *Eugerres plumieri*
	Yellowfin majarra, *Gerres cinereus*
	Irish pompano, *Diapterus auratus*
	Black drum, *Pogonias cromis*
	Red drum, *Sciaenops ocellata*
	Sergeant major, *Abudefduf saxatilis*
	Checkered puffer, *Sphoeroides testudineus*
	Mangrove Arboreal Canopy Guild: Spatial Guild II
RESIDENTS	
Molluscs	Angulate periwinkle, *Littorina angulifera*
	Latterhorn snail, *Cerithidea scalariformis*
	Coffeebean snail, *Melampus coffeus*
Crustaceans	Sea roach, *Ligia exotica*
	Mangrove crab, *Goniopsis cruentata*
	Mangrove crab, *Aratus pisonii*
	Mangrove crab, *Sesarma curacaoense*
	Gibbes' pachygrapsus, *Pachygrapsus transversus*
Insects	Moths, *Ecdytolopha* spp.
	Mangrove skipper, *Phocides pigmalion*
	Hairy green caterpillar, *Alaroda slossoniae*
	Red-stripped yellow processionary caterpillar, *Automeris io*
	Puss moth, *Megalopyge opercularis*
	Mangrove scolytid beetles, *Poecilips rhizophorae*
Reptiles	Mangrove snake, *Nerodia fasciata compressicauda*
Birds	Greenbacked heron, *Butorides striatus*
	Belted kingfisher, *Megaceryle alcyon*

TABLE 2 (*Continued*)

Habitat	Species
Mangrove Arboreal Canopy Guild: Spatial Guild II (Continued)	
RESIDENTS (*Continued*)	
Birds (*Continued*)	Cuban yellow warbler, *Dendroica petechia gundlachi*
	Florida prairie warbler, *D. discolor paludicola*
	Black-whiskered vireo, *Vireo altiloquus*
	Gray kingbird, *Tyrannus dominicensis*
	Mangrove cuckoo, *Coccyzus minor*
	White-crowned pigeon, *Columba leucocephala*
	Southern crested flycatcher, *Myiarchus crinitus crinitus*
	Florida cardinal, *Cardinalis cardinalis floridana*
TRANSIENTS/DIURNAL MIGRANTS	
Birds	Anhinga, *Anhinga anhinga*
	Double-crested cormorant, *Phalacrocorax auritus*
	Brown pelican, *Pelecanus occidentalis*
	Wading birds, 19 species: Areidae, Ciconiidae, and Threskiornithidae
	Osprey, *Pandion haliaetus*
TRANSIENTS/SEASONAL MIGRANTS	
Birds	Warblers, Emberizidae
	Vireos, Vireonidae
	Loggerhead kingbird, *Tyrannus caudifasciatus*
	Stripe-headed tanager, *Spindalis zena*
Mangrove Benthic and Infauna Community: Spatial Guild III	
RESIDENTS	
Crustaceans	Broadback mud crab, *Eurytium limosum*
	Harris mud crab, *Rithropanopeus harrisii*
	Fiddler crabs, *Uca* spp.
	Giant land crab, *Cardisoma guanhumi*
	Crayfish, *Procambarus alleni*
	Pink shrimp, *Penaeus duorarum*
	Glass shrimp, *Palaemonetes* spp.
Insects	Salt marsh mosquito, *Aedes taeniorhynchus*
	Salt marsh mosquito, *A. solicitans*
	Sand flies, *Culicoides* spp.
	Rivulus, *Rivulus marmoratus*
Mangrove Tidal Creek and Ditch Community: Spatial Guild IV	
Molluscs	Lightning whelk, *Busycon contrarium*
	Squid, *Loligo* spp.
Crustaceans	Pink shrimp, *Penaeus duorarum*
	Glass shrimp, *Palaemonetes* spp.
	Swimming crabs, *Callinectes* spp.
Elasmobranchs	Bull shark, *Carcharhinus leucas*
	Atlantic stingray, *Dasyatis sabina*

TABLE 2 (*Continued*)

Habitat	Species
	Mangrove Tidal Creek and Ditch Community: Spatial Guild IV (Continued)
Teleosts	Gulf killifish, *Fundulus grandis*
	Striped mullet, *Mugil cephalus*
	Tarpon, *Megalops atlanticus*
	Ladyfish, *Elops saurus*
	Snook, *Centropomus undecimalis*
	Jewfish, *Epinephelus itajara*
	Gray snapper, *Lutjanus griseus*
	Red drum, *Sciaenops ocellatus*
Reptiles	Soft shelled turtles, *Tionyx* spp.
	Mangrove diamondback terrapin, *Malaclemys terrapin rhizophorarum*
	Green turtles, *Chelonia mydas mydas*
	Mangrove water snake, *Nerodia fasciata compressicauda*
	Florida crocodile, *Crocodylus acutus*
	American alligator, *Alligator mississippiensis*
Birds	Anhinga, *Anhinga anhinga*
	Cormorants, *Phalacrocorax* spp.
	Brown pelican, *Pelecanus occidentalis*
	Surface and diving birds, 29 species: Anaidae and Rallidae
Mammals	Manatee, *Trichechus manatus latirostris*
	River otter, *Lutra canadensis*
	Bottlenosed dolphin, *Tursiops truncatus*
	Mangrove Basin Forest Community: Spatial Guild V
RESIDENTS	
Crustaceans	Glass shrimp, *Palaemonetes* spp.
	Fiddler crabs, *Uca* spp.
Insects	Salt marsh mosquito, *Aedes taeniorhynchus*
	Salt marsh mosquito, *A. solicitans*
	Corixids
Fish	Sheepshead minnow, *Cyprinodon variegatus*
	Mosquitofish, *Gambusia affinis*
	Sailfin molly, *Poecilia latipinna*
	Marsh killifish, *Fundulus confluentus*
TRANSIENTS	
Birds	Egrets and herons: Areidae, Ciconiidae, Threskiornithidae
Reptiles	Mangrove diamondback terrapin, *Malaclemys terrapin rhizophorarum*
	Mangrove water snake, *Nerodia fasciata compressicauda*
Mammals	White-tailed deer, *Odocoilus virginiana*
	Raccoon, *Procyon lotor*
	Bobcat, *Felix rufus*
	Gray fox, *Urocyon cinereoargenteus*

[a] See Fig. 2 for the same microhabitats and associated guilds.

The animal communities associating with the sublittoral red mangrove zone can be divided into several categories for convenience of discussion. There are two major temporal association categories defined by the degree of time spent by the organism in mangrove prop root habitation. Thus organisms can be classified as either residents when they occupy the prop root microhabitat for the majority of their life history, or transients when they utilize the prop root zone only periodically, seasonally, or for a portion of ontogeny. Residential organisms may either be sessile or mobile. The reproductive strategies of sessile organisms most often involve a broadcast of eggs or larvae into the water column where they are dispersed, either throughout the estuary or occasionally out to sea. This ensures species dispersal and colonization of viable mangrove habitat elsewhere. Sessile residents are often filter or mucous feeding organisms taking advantage of food movement associated with the tidal and wind energy exposures of the red mangrove fringe. These organisms may occur in small colonies or as individuals. The most notable representatives are filter feeding bryozoans, ascidians [black tunicate (*Ascidia nigra*) and the mangrove tunicate (*Ecteinascidia turbinata*)], barnacles (*Balanus eburneus*), the gastropod (*Crepidula plana*) and pelecypod molluscs (oysters *Crassostrea virginica*/*Isognomon* spp.), broad ribbed cardita (*Carditamera floridana*), ark (*Arca imbricata*), scorched mussel (*Branchidontes exustus*), wood boring crustaceans (isopod *Sphaeroma terebrans*), and wood boring martesia (*Martesia striata*), which may occur at various levels along the prop roots from the sublittoral into the littoral zone depending on the species requirements (Fig. 6). Sessile organisms often compete for limited space on mangrove prop roots and may also be limited by small variations in hydrology, water quality, and food availability (MacNae 1968, Courtenay 1975, Estevez 1978, Mook 1986).

Mobile residents of the mangrove prop root zone consist of a diverse group of invertebrates and vertebrates, which are often capable of spending their entire life histories among the mangrove roots (Hobbs 1942, Goodbody 1961, MacNae 1968, Rutzler 1969, Coomaus 1969, Kolehmainer 1973, Kolehmainer and Hildner 1975, Sasekumar 1974, Courtenay 1975, Yoshioka 1975, Estevez 1978, Sutherland 1980, Kohlmeyer and Bebout 1986, Mook 1986). However, in contrast to the sessile species, the mobile fauna may move to immediately adjacent habitats and not require gamete, embryo, or larval movement as the only means of dispersal. A variety of polycheates, molluscs, crustaceans, and fishes occur in this category. The mobile molluscs are all gastropods, which either consume detrital material or scrape periphyton and microscopic algae [e.g., keyhole limpet (*Diodora cayensis*)] or are predators on other molluscs and invertebrate phyla. Examples of predators, scavengers, and detrital feeders commonly associated with the mangrove prop root zone are the crown conch (*Melongena corona*), lightning whelk (*Busycon contrarium*), rock shells (*Thais* spp.), oyster drills (*Urosalpinx* spp.), pisa snails (*Pisania pusio*), ceriths (*Cerithidea* spp), dove snails (*Anachis semiplicata*), turret snails (*Turritella* spp.), bubble snails (*Bulla striata*), and the mud snails (*Nassarius* spp.). Mobile resident mangrove prop root crustaceans consist of fewer species, mostly amphipods and the predaceous xanthid crabs (*Panopeus herbsti*). Most resident fishes are small, often cryptic and planktivorous, usually feeding on cope-

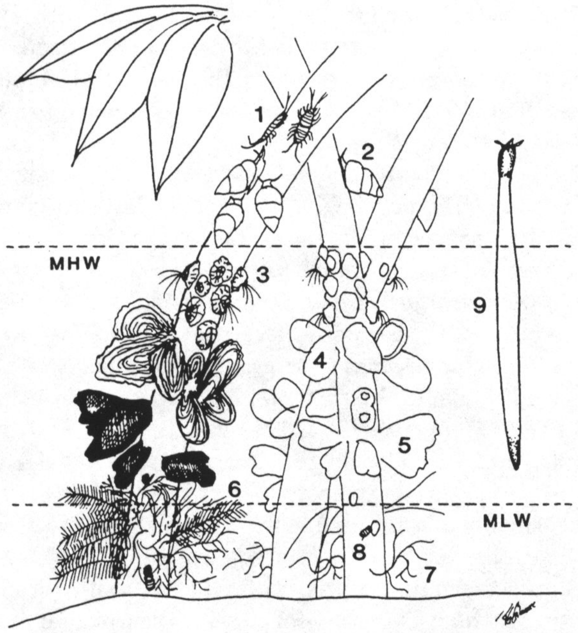


FIGURE 6. Vertical zonation of organisms associated with red mangrove prop roots with an illustration of the seed of *Rhizophora mangle*: 1, *Ligia exotica*; 2, *Littorina angulifera*; 3, *Balanus ebureus*; 4, *Crassostrea virginica*; 5, *Phallusia nigra*; 6, *Caluerpa* spp.; 7, *Acanthophora* spp.; 8, *Sphaeroma terebans*; 9, propagule of *Rhizophora mangle*.

pods, amphipods, insects, and a wide variety of invertebrate larvae. Some, however, are herbivorous or omnivorous, feeding on attached algae and diatoms, such as the sailfin molly (*Poecilia latipinna*) and the combtooth blennies (Blenniidae). The Guild I resident ichthyofauna includes the gobiesocid skilletfish (*Gobiesox strumosus*); the poeciliid livebearers—mosquitofish (*Gambusia holbrooki*), mangrove gambusia (*Gambusia rhizophorae*), and sailfin molly (*Poecilia latipinna*); the atherinid silversides—inland silverside (*Menidia beryllina*) and hardhead silverside (*Atherinomorus stipes*); the combtooth blennies—the Florida blenny (*Chasmodes saburrae*), highfin blenny (*Lupinoblennius nicholsi*), and the clinid (*Paraclinus fasciatus*); the gobioid fishes—the fat sleeper (*Dormitator maculatus*), notchtongue goby (*Bathygobius curacao*), emerald goby (*Gobionellus smaragdus*), naked goby (*Gobiosoma bosc*), crested goby (*Lophogobius cyprinoides*), and clown goby (*Microgobius gulosus*) (Odum and Heald 1972, Odum et al. 1982, Thayer et al. 1984).

Transient representatives of Guild I are typically represented by developmental stages of animals that occur elsewhere as adults. Juveniles of a variety of crustaceans and fishes spend a portion of their larval, postlarval, or juvenile developmental periods within the prop root habitat. Many of these species are structure associates both as juveniles and adults, but the adult stage is often found on reef structures either in an estuary or on the adjacent continental shelf. The spiny lobster (*Panulirus argus*) moves to the prop root habitat from proximate seagrass beds before it migrates to offshore reef formations (Witham et al. 1968, Olsen and Koblic 1975, Olsen et al. 1975, Little 1977). The most notable fish examples are the centropomid—snook (*Centropomus undecimalis*); serranid—jewfish (*Epinephelus itajara*) and lobotid-tripletail (*Lobotes surinamensis*) [which mimics mangrove leaves as a juvenile (Breder 1944)]; carangid—leatherjacker (*Oligoplites saurus*); lutjanids—gray snapper (*Lutjanus griseus*) and dog snapper (*L. jocu*); haemulids—sailor's choice (*Haemulon parra*) and bluestriped grunt (*H. sciurus*); sparid—sheepshead (*Archosargus probatocephalus*) and gerreids (*Eugerres plumieri*) and (*Gerres cinereus*); sciaenids—black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellata*); pomacentrid—sergeant major (*Abudefduf saxatilis*); and tetraodontid—checkered puffer (*Sphoeroides testudineus*) (Austin and Austin 1971, Odum and Heald 1972, Odum et al. 1982, Thayer et al. 1987, Kenyon Lindeman, personal communication). Juveniles of these species associate with the prop root structure offered by the red mangrove both to seek prey and to seek refuge from predation. The checkered puffer is found in this microhabitat also as an adult. The tripletail, snook, gray snapper, red drum, and jewfish may occur over vegetated or structured bottoms adjacent to the prop roots as adults but typically cannot occupy the limited space within the prop root matrix when mature as they reach a large size (Gilmore et al. 1983).

The Mangrove Arboreal Canopy Guild: Spatial Guild II This guild also consists of resident and transient species. Some are amphibious often with a larval development period in totally aquatic conditions while others never contact the water.

Resident members of this guild consist of a few molluscs, a variety of crustaceans, many insects, a reptile, and a few nesting birds (Warner 1967, Heald 1969, Simberloff and Wilson 1969, Simberloff 1976, Onuf et al. 1977, Owre 1978, Beever et al. 1979). Common members of the molluscan fauna are the angulate periwinkle (*Littorina angulifera*), ladder horn snail (*Cerithidea scalariformis*), and coffee-bean snail (*Melampus coffeus*). These molluscs may migrate from the water's surface well up into the canopy, grazing on surface diatoms, periphyton, or mangrove leaves. They also may migrate down onto the sediments below the trees when the mud surface is exposed between tides or seasonal inundations. The behavior of the omnivorous mangrove crabs is similar to canopy molluscs as they usually avoid submergence yet have a broad vertical range. The principal species are *Goniopsis cruentata*, *Aratus pisonii*, *Pachygrapsus transversus*, and *Sesarma* spp. *Aratus pisonii* may consume living mangrove leaves along with canopy insects (Warner 1967, Diaz and Conde 1989, Wilson 1989). Another important canopy crustacean is the isopod *Ligea exotica*, a detritivore, scavenger, and consumer of smaller arboreal arthropods. A wide variety of insects inhabit the mangrove canopy, foraging on other insects and products of the mangrove, e.g., the dethreutid moth (*Ecdytolopha* sp.), mangrove skipper (*Phocides pigmalion*), hairy green caterpillar (*Alarodia slossoniae*), red-striped yellow processionary caterpillar (*Automeris io*), puss moth (*Megalopyge opercularis*), and the mangrove scolytid beetles (*Poecilips rhizophorae*) (Onuf et al. 1977). The mangrove salt marsh snake (*Nerodia fasciata compressicauda*) is a mangrove resident that has been observed to inhabit the mangrove canopy both during the day and at night possibly in an inquiescent resting mode or hunting arboreal crustaceans and insects (Ashton and Ashton 1981, R. G. Gilmore, personal observation). However, the principal foods of this amphibious species are small fishes that inhabit the tide pools of the mangrove forest (Hebrand 1981). Insectivorous and euryphagous arboreal birds commonly occur in the insect-rich mangrove canopy both as migrants (Lack and Lack 1972) and residents. The most notable among the residents are the Cuban yellow warbler (*Dendroica petechia gundlachi*), black-whiskered vireo (*Vireo altiloquus*), Florida prairie warbler (*Dendroica discolor paludicola*), gray kingbird (*Tyrannus dominicensis*), and the mangrove cuckoo (*Coccyzus minor*). The white-crowned pigeon (*Columba leucocephala*) is a herbivorous arboreal pigeon that consumes fruits and seeds of a variety of plants, including the black mangrove, and nests in mangroves (Owre 1978). Two other passerine birds that nest and feed within the mangrove canopy are the southern crested flycatcher (*Myiarchus crinitus crinitus*) and the Florida cardinal (*Cardinalis cardinalis floridana*). The flycatcher is principally insectivorous while the cardinal is omnivorous, feeding on a variety of plant materials in addition to a copious consumption of insects.

The most notable transients in the mangrove canopy Guild II are the migratory birds, which fall into two broad categories of migration: (1) those that roost or nest in mangrove forests and make diurnal feeding forays into other habitats and (2) those that make seasonal appearances in the mangrove swamp during or as a result of long-distance migrations. There are several species that commonly nest on mangrove islands or in mangrove thickets but typically feed either in open estuaries, ponds, on flooded salterns of adjacent halophyte prairies, along tidal creeks, on freshwater streams, or on freshwater glades. The most conspicuous groups are the surface/diving birds (29 species: Pelecanidae, Anaidae, Phalacrocoracidae, and Rallidae) and wading birds (19 species: Areidae, Ciconiidae, and Threskiornithidae). Many of these species consume molluscs, crustaceans, and fishes that also associate with the mangrove forest ecosystem (Allen 1942, Kahl 1964, Kushlan and Kushlan 1975, Kushlan 1976, 1978, 1979, 1981, Odum et al. 1982) and are therefore responsible for considerable biological transport of secondary and tertiary productivity. Many of the surface/diving and wading birds may nest in the mangrove canopy (Kushlan and White 1977, Maxwell and Kale 1977, Ogden et al. 1978). The second migratory category is typified by major spatial movements over several hundred or thousand kilometers with typically only a seasonal occurrence in the mangrove forest. Some of the previously listed surface/diving bird and wading bird groups may also occur in this migratory category when they migrate from summer breeding and feeding areas further north to overwintering grounds in the mangrove forest. Mangrove forest populations of ospreys (Accipitridae), vultures (Cathartidae), warblers (Emberizidae), and vireos (Vireonidae) may increase substantially seasonally due to ephemeral passage through mangrove swamps from more northern latitudes. Southern visitors, the Bahama pintail (*Anas bahamensis*), masked duck (*Oxyura dominica*), Caribbean coot (*Fu-*

lica caribea), loggerhead kingbird (*Tyrannus caudifasciatus*), thick-billed vireo (*Vireo crassirostris*), and stripe-headed tanager (*Spindalis zena*), are more apt to associate with mangrove ecosystems but they are typically rare. Both northern and southern short-term visitors generally show little impact on the mangrove ecosystem.

The Mangrove Benthic and Infauna Community: Spatial Guild III The benthic community of mangrove swamps is generally considered impoverished compared to adjacent open water or seagrass communities principally due to the influence of relatively harsh environmental conditions, yet it is highly productive, particularly when considering bacterial populations (Alongi 1987). All the principal organisms in this community can be considered mangrove swamp residents. Because of their typical association with specific sites and generally limited mobility, many Guild III organisms are spatially zoned between the water's edge and the terrestrial upland, that is, from tidal creek and red mangrove fringe through the basin forest habitat.

Nematodes, polychaetes, molluscs, harpacticoid copepods, isopods, amphipods, shrimp, crabs, a variety of insects, and small benthic fishes typify the benthic fauna (Hobbs 1942, Tabb and Manning 1961, Tabb et al. 1962, Hopper et al. 1973, Weinstein 1979, Alongi 1987). The molluscs *Melampus coffeus* and *Cerithidea scalariformis* graze on freshly fallen mangrove leaves, particularly in the red mangrove fringe habitat (Odum et al. 1982, Mook 1986). The mangrove crabs (*Aratus pisonii* and *Sesarma* spp.) may also visit the mud flats below the canopy during exposure periods (Odum et al. 1982, Wilson 1989), but the principal species are the aquatic xanthid mud crabs (*Eurytium limosum* and *Rithropanopeus harrisii*), the amphibious fiddler crabs (*Uca* spp.), and the giant land crab (*Cardisoma guanhumi*) (Tabb et al. 1962, Odum and Heald 1972). The fiddler crabs typically show species-specific habitation zones and changes in density relative to soil type, hydrological conditions, vegetation type, and season of the year (MacIntosh 1984). Greater densities occur in herbaceous vegetation zones, up to 205 m^{-2} than in woody mangrove zones, to 63 m^{-2} (MacIntosh 1984). They also represent a major bioperturbation of mangrove swamp and marsh soils and a major source of biomass. Another important crustacean in the benthic community is the crayfish (*Procambarus alleni*), particularly in the low salinity mangrove forests of south Florida (Hobbs 1942). Penaeid (*Penaeus* spp.) and palaemonid (*Palaemonetes* spp.) shrimp invade the mangrove benthos during inundation periods, feeding on a variety of detrital, plant, and animal materials (Odum and Heald 1972).

Several insects oviposit and feed in association with mangrove mud/sand substrates. Salt marsh mosquitos (*Aedes taeniorhynchus* and *A. solicitans*), sandflies (*Culicoides* spp.), and corixids are examples of substrate ovipositors. The corixids spend much of their life history in the swamp but may fly several kilometers as an adult (Scudder 1976) as may the *Aedes* mosquitos.

There is only one fish species that is a documented benthic burrow inhabitant in mangrove swamps of Florida, *Rivulus marmoratus*. *Rivulus* is commensal with the giant land crab (*Cardisoma guanhumi*) and lays its self-fertilized eggs on exposed mud substrate during a short terrestrial migration at which time it breaths through its skin (Huehner et al. 1985, Abel et al. 1987, Taylor 1988).

The Mangrove Tidal Creek and Ditch Community: Spatial Guild IV This guild contains a wide variety of transient and resident species. Large aquatic predators enter the mangrove community through the tidal tributary habitat, which acts as a major transport artery between the adjacent estuary or ocean and the wetland forest. This habitat is characterized by constant immersion, although the level may change greatly.

A variety of predaceous invertebrates and vertebrates often utilize the mangrove river or creek as a thoroughfare for ephemeral feeding forays. Notable examples are the lightning whelk (*Busycon contrarium*), squid (*Loligo* spp.), blue crab (*Callinectes sapidus*), and shrimp (*Penaeus* spp.). Predaceous fishes that commonly use this habitat are juvenile bull sharks (*Carcharhinus leucas*), Atlantic stingray (*Dasyatis sabina*), tarpon (*Megalops atlanticus*), ladyfish (*Elops saurus*), snook (*Centropomus undecimalis*), jewfish (*Epinephelus itajara*), gray snapper (*Lutjanus griseus*), and red drum (*Sciaenops ocellatus*) (Austin and Austin 1971, Odum and Heald 1972, Tabb et al. 1974, Gilmore et al. 1982, 1983, Lewis et al. 1985). These species usually reveal a very seasonal occurrence in the mangrove habitat with entry into the tidal creeks often as juveniles and departure as either adults or late juveniles. The principal foods of these species are crustaceans and insects, when these species are small juveniles, and fish as they reach larger sizes. However, the snook has been found to feed on fish while still at an exceptionally small size, 11.0 mm SL (Gilmore et al. 1983). Soft shelled turtles (*Trionyx* spp.), mangrove diamondback terrapins (*Malaclemys terrapin rhizophorarum*), and green turtle (*Chelonia mydas mydas*) are often observed in this habitat, as are the mangrove water snake (*Nerodia fasciata compressicauda*), Florida crocodile (*Crocodylus acutus*), and the American alligator (*Alligator mississippiensis*). Great blue herons (*Ardea herodias*), great egrets (*Casmerodius albus*), little blue herons (*Florida caerulea*), snowy egrets (*Egretta thula*), brown pelicans (*Pelecanus occidentalis*), cormorants *Phalacrocorax* spp.), and anhingas (*Anhinga anhinga*) also hunt fish and crustaceans along shoals and shallow creek shorelines while the green-backed heron (*Butorides virescens*) typically hunts from the limbs or prop roots of the mangrove fringe. The belted kingfisher (*Megaceryle alcyon*) is also a common mangrove forest inhabitant, perching on limbs in the canopy and diving on mosquitofish or mollies near the surface. Commonly observed predaceous mammals are the bottlenosed dolphin (*Tursiops truncatus*) and river otter (*Lutra canadensis*). Herbivorous manatees (*Trichechus manatus latirostris*) commonly enter tidal creeks and have been observed consuming mangrove leaves directly from the tree (R. G. Gilmore, personal observation).

The Mangrove Basin Community: Spatial Guild V The mangrove basin habitat is characterized by seasonal changes in the availability of water as this mangrove community occurs further inland of the red mangrove fringe. The basin habitat is generally separated from tidal waters by a small berm, the top of which rises to the mean high-water level below the adjacent red mangrove fringe canopy. The basin may be continuously flooded during late summer/fall sea-level rise and high rainfall periods, yet exposed for several months during the cool–dry season (Provost 1974, 1976). Basin forest of much of the Florida Peninsula may consist of homogeneous stands of red mangrove, or mixed red, black, and white forests and often a mixture of mangrove and "herbaceous salt prairie." The herbaceous salt prairie typically consists of the herbaceous halophytes, *Distichlus spicata*, *Batis maritima*, *Salicornia* spp., and *Juncus romoerianus*, typically with interspersed bare areas, salterns, and ponds that may support a periphyton mat and beds of aquatic grass (*Ruppia maritima*). These vegetation differences undoubtedly influence animal use of the basin forest; however, little work has been done to quantify these differences. During the inundation period, an aquatic fauna emerges or invades the mangrove prairie basin. During drying periods the aquatic fauna either migrates to permanent ponds, the adjacent estuary, tidal creeks, and prop root habitats, or survives as stranded eggs on the basin surface (Harrington 1959, Haeger, 1960, Harrington and Harrington 1961, Tabb et al. 1974, Gilmore et al. 1982, Gilmore 1987).

The benthic invertebrate fauna previously described for mangrove fringe habitats also occurs at various locations across the basin flats. Some of these animals may reach their largest population size and concentrations in this habitat: for example, *Uca* spp. (MacIntosh 1984), *Aedes* mosquito larvae (Haeger 1960, Provost 1967), and corixids (R. G. Gilmore, personal observation). Palaemonid shrimp are also quite abundant when the basin is inundated (Gilmore 1987).

The most abundant fishes are typically cyprinodontiform species, marsh killifish (*Fundulus confluentus*), sheepshead minnows (*Cyprinodon variegatus*), mosquitofish (*Gambusia holbrooki*), and sailfin mollies (*Poecilia latipinna*) (Harrington and Harrington 1961, Tabb et al. 1974, Gilmore 1987). The eggs of the marsh killifish may survive desiccation and aerial exposure of the basin until the next seasonal inundation (Harrington 1959). The poeciliid livebearers, the mosquitofish, and sailfin molly must invade the basin upon inundation from the adjacent estuary or tidal creek. These fishes consume algae and detrital materials in addition to a wide variety of insects and crustaceans and reproduce across the open prairies and salterns while the basin forest is flooded. When the water recedes during the late fall and early winter, the killifishes migrate into the adjacent tidal creeks and ponds, where large numbers are consumed by predaceous crustaceans, fish, reptiles, and birds. This organism migration from the mangrove basin to tidal creek represents a major movement of energy from the basin forest to the adjacent estuary through biological means (Gilmore et al. 1985, 1986, 1987, Gilmore 1987). Additional biological transport occurs as large numbers of a variety of wading birds feed on fish and crustaceans across open salterns and ponds of the basin (Gilmore 1987).

Upland Arboreal Community: Spatial Guild VI This community is associated with a tropical/subtropical hardwood forest typified by mahogany (*Swietenia mahagoni*), cabbage palm (*Sabal palmetto*), Jamaica dogwood (*Piscidia piscipula*), live oak (*Quercus virginiana*), red bay (*Persea borbonia*), gumbo-limbo (*Bursera simaruba*), mastic (*Mastichodendron foetidissimum*), figs (*Ficus* spp.), and various stoppers (*Eugenia* spp.) (Craighead 1971). These trees also support a variety of epiphytes, bromeliads, orchids, and ferns that harbor a microcosmal animal community.

The arboreal animal communities that migrate from the tropical hardwood forest to the adjacent mangrove forest communities are principally birds and insects capable of flight. The principal habitat for these species is the hardwood forest; however, the ecotone at the mangrove/hardwood forest boundary offers a foraging zone for woodpeckers, jays, wrens, gnatcatchers, and a variety of warblers (Odum et al. 1982). Rarely, more sedentary arboreal animals will be seen in the adjacent mangrove canopy, for example, the tree snails (*Liguus fasciatus* and *Oxostylus* spp.) (Craighead 1971), corn snake (*Elaphe guttata guttata*), southeastern five-lined skink (*Eumeces inexpectatus*), and *Anolis* spp. (Ashton and Ashton 1981).

Upland Terrestrial Community: Spatial Guild VII Members of this community are found in association with the understory of the tropical/subtropical hardwood forest. The organisms that interact most readily with the adjacent mangrove community are certain reptiles, for example, yellow rat snake (*Elaphe obsoleta*) and mammals, hispid cotton rats (*Sigmodon hispidus*), raccoons (*Procyon lotor*), white-tailed deer (*Odocoileusus virginianus*), bobcats (*Felis rufus*) and gray fox (*Urocyon cinereoargenteus*) (Layne 1974, Hamilton and Whittaker 1979). Raccoons forage daily in adjacent mangrove swamps while bobcats may feed on wading birds (R. G. Gilmore, personal observation). Most of these animals enter the mangrove swamp to feed and return to the hardwood forest, thus representing an energy export from the mangrove swamp to the adjacent upland, while there is little documented biotic transfer of energy in the opposite direction.

RESOURCE USE AND MANAGEMENT EFFECTS

Historical and Current Land Uses of the Mangrove Forest and Associated Vegetative Communities

As mangrove forests are limited to low hydric coastal areas of Florida they had little value, until recently, for human habitation or utilization. In fact, these forests and swamps were considered by many (even respected scientists) as having no biological value to humans or containing other resources important to humans (see letter from Dr. Howard Humm in Odum 1970). Until the completion of William Odum's dissertation in 1970 and its publication (Odum and Heald 1972), mangrove forest communities were considered only a nuisance and primarily a source of insect pests such as mosquitos (*Aedes* spp.) and sandflies (*Culicoides* spp.). The wood of the red and white mangroves was used infrequently as sources of tannin and firewood (Harrar and Harrar 1962). The hard resilient wood of the black mangrove had greater though limited value as lumber (flooring or boat keels, personal communications with local fisherman, Indian River County, Florida). Subsequently, when humans developed the means to destroy these communities either to control mosquitos or to produce waterfront habitation sites, considerable acreage around urban centers in the southern half of the Florida Peninsula were impounded, drowned, or filled. Approximately 92% (13,083 ha) of the red and black mangrove forest habitat on the Indian River lagoon was impounded between 1955 and 1974 (R. G. Gilmore, unpublished data from mosquito control districts of the Indian River lagoon). Similar destruction of mangrove forests occurred along the Gulf Coast of Florida, particularly in the Tampa Bay area as industrial and urban access to the shores of Tampa Bay required the filling or removal of 44% of the tidal vegetation in this estuary (Lewis et al. 1979). In fact, the greatest direct impact on mangrove communities in Florida has been by direct destruction for mosquito control or human habitation. There is a yet-to-be defined impact of freshwater displacement and management, which has reduced overland sheetflow in the Everglades and subsequently impacts the largest mangrove forest in Florida along the southwest coast (see Chapter 6 in this volume).

The population growth rate of Florida is among the highest in the United States, with coastal regions growing most rapidly. This rapid coastal growth and urbanization are the principal causes of deleterious impacts on indigenous plant and animal communities. The future of most mangrove forest communities in the state of Florida remains dubious as the increase in the size of urban centers will require more land, more fresh water, and more mosquito control. Although laws have been passed to protect the red mangrove, these laws are poorly enforced and do not protect the other woody and herbaceous plant species that also play an important role in the estuarine wetland ecology of Florida.

Urbanization

The direct and indirect effects of urbanization and human population growth form a major threat to mangrove communities of the southeastern United States. The greatest population increase has occurred in south Florida (Fernald 1981) within the range of the mangrove forest. Urbanization requires space; and thus a direct impact is made by the removal of mangroves, particularly for waterfront property. Unprecedented bulkheading, fill, and removal of mangrove forests occurred along both coasts of Florida during the 1950s and 1960s. State laws were passed during the early and mid-1970s to protect the red mangrove. These laws have been variously enforced with considerable mangrove community loss still occurring through ignorance, blatant removal with little threat of retribution, variances, and major changes in jurisdiction by state agencies. A property owner selling waterfront acreage for several hundred thousand dollars has little to lose by paying minor fines for mangrove removal. In addition to the threat of direct removal for profit, those mangroves left in place must survive the periodic assault of the property owner, who is legally allowed to "trim" the tree. The authors have observed individual trees and entire stands that have been trimmed to within a meter of the sediment, often with fatal consequences. Trees that survive the permitted trimming have considerably reduced canopies and in no way represent the complex productive structure that stood before the uncontrolled pruning.

The greatest urban assault on the mangrove forest community today is not on the red mangrove fringe but on the landward basin forests, which often do not have major stands of the protected red mangrove. These forests are complex communities typically with intermixed meadows of herbaceous species such as black needlerush, saltwort or glasswort, and algal salterns. The principal mangrove species are typically the black or white. These communities are often not protected legally and their destruction is frequently condoned at the expense of preservation of the red mangrove fringe community. Recent research indicates that the basin forests may have as great or greater ecological value than the fringe forest. Invasion of fishes during high-water periods allows considerable energy produced in the basin to be consumed and subsequently transported to the adjacent estuary with the emigration or consumption of these organisms (Harrington and Harrington 1961, 1982). Until all wetland plant communities (including algal species) in association with all species of mangrove are protected, there is little prospect that viable coastal mangrove ecosystems of Florida will survive except on protected public lands.

Water Management: Impoundment and Flood Control

Water management within the lower Florida Peninsula has been a major human activity since the turn of the century. Typically, there were three principal objectives for managing water: (1) drain water off land to expose earth for the purposes of housing or agriculture, and to prevent storm damage and flooding; (2) manipulate water for storage and consumption either by agriculture or urban communities; and (3) flood coastal wetland impoundments to control salt marsh mosquito populations (*Aedes* spp.). All these objectives for managing water increase in importance as the human population increases.

Reduction in surface water has occurred principally as freshwater sheetflow control through canaling. A complex system of canals and floodgates controls water movement to the coastal regions of the state. This includes the flow of water south and west through the Taylor Slough in the Everglades National Park (see Chapter 6 in this volume). Notable changes in estuarine salinities have taken place in association with the manipulation of Everglades overland sheetflow and reveal changes that may have a major impact on downstream ecosystems, such as the mangrove forest (Odum and Johannes 1975). Reduced freshwater sheetflow represents a reduced energy subsidy in a low tidal energy system. Export of dissolved and particulate materials from the extensive mangrove basin forests of southwest Florida to the adjacent estuaries and Gulf of Mexico could be reduced. This could also affect the production of a wide variety of aquatic organisms and their predators, which depend on mangrove swamp submergence either to complete their life cycle or to ensure population maintenance above mortality levels.

Mangrove forest impoundment is principally limited to the Indian River lagoon estuary of east-central Florida. Impoundments were constructed strictly for controlled flooding of the mangrove swamp for mosquito control. Mangrove mortality often resulted from drowning pneumatophores and prop roots. In addition to the destruction of the indigenous flora, impoundment also deprived transient aquatic organisms access to the wetland. Basin forests were the type usually eradicated with impoundment as the fringing red mangroves were typically left undisturbed outside the impoundment dike. Approximately 92% of the mangrove swamp and salt marsh habitat in Brevard, Indian River, and St. Lucie Counties along the Indian River lagoon were impounded between 1955 and 1974.

Recent progress in impoundment management has allowed revegetation of many impoundments through periodic restoration of tidal access and careful control of impoundment water levels. Tidal access is allowed from September to April or May. After April the impoundment is closed for the summer mosquito breeding season. This management process is called Rotational Impoundment Management or RIM and allows aquatic organism migration between the estuary and impounded wetland for at least 6 months, including tidal exchange of dissolved and particulate materials.

Conservation

The majority of the mangrove habitat in south Florida lies in either national or state preserves. The greatest acreage is found in Everglades National Park, while considerable additional acreage is owned by the state of Florida in Charlotte Harbor and smaller parcels in the Indian River lagoon. The Merritt Island National Wildlife Refuge contains some stands of extralimital mangrove growth, mostly black and white. However, these latter stands are impounded. Upstream overland sheetflow manipulations of water are impacting much of the most pristine mangrove forest in the Everglades National Park.

The dependence of fishery species on mangrove forest habitats should also add considerable impetus to the renewal of natural hydroperiod patterns. The conservation of fishery resources is now known to be directly dependent on the availability of viable habitat. If mangrove swamp habitats are not available to the immigration of indigenous larvae/juvenile invertebrates and fishes due to dry or impounded conditions, their survival may be jeopardized.

Additional watershed purchase and preservation should be encouraged along with a logical water management scenario that may benefit both urban population centers and the adjacent natural preserves, along with their associated flora and fauna.

ECOLOGICAL RESEARCH AND MANAGEMENT OPPORTUNITIES

Microbial Community Studies

Bacterial and fungal mats are common components of basin forest saltern habitats, stagnant depressions, and certain creek and riverine microhabitats in addition to mangrove leaf litter deposits. They are consumed by a wide variety of organisms and thus play an important trophic role in addition to the cycling of inorganic and organic materials. These complex autotrophic and heterotrophic systems need considerable study as they profoundly influence the hydrochemistry and dynamics of the entire ecosystem. Studies of bacterial/fungal communities under a variety of experimental photic, sedimentary, and hydrological conditions with and without higher organism influence would considerably enhance our understanding of mangrove forest ecosystem function and dynamics.

Botanical Research

The most obvious botanical research needs are the determination of the distribution and association of algal, herbaceous, and woody plant populations, principally within basin and higher elevation mangrove forest systems. A great diversity of plant species contribute to these communities but have received little research attention, particularly the herbaceous and the periphyton components (i.e., halophyte prairies and algae).

Phytoplankton communities and epiphytic microalgal components have major impacts on water chemistry and therefore survival of both higher plants and animal populations. An abundant zooplankton community depends on phytoplankton and other microbial components for survival and are in turn consumed by a wide variety of higher organisms. The recruitment of the planktotrophic larvae of a wide variety of organisms to mangrove ecosystems and their distribution relative to preferred food types and abundance is in need of study.

There is considerable need for a study of various anthropogenic impacts on mangrove forest plant communities, principally through hydrological changes, whether by impoundment or by changes in freshwater flows from upland sources. Human impact on growth, metabolism, reproduction, detrital turnover, and a variety of other parameters of mangrove and associated floral communities needs further study.

Zoological Research

Few comprehensive quantitative zoological studies of animal populations of the mangrove forest have been conducted, though several investigators have made recent observations (Robertson and Kushlan 1974, Gilmore 1987, Pinto 1987, Robertson and Duke 1987, Thayer et al. 1987, Little et al. 1988). The dynamics of these animal communities and their relative dependence on basin and fringe mangrove forests have been major objectives of these studies. The relative importance of various microhabitats for food, shelter, and reproduction needs detailed study.

Considerable export of mangrove forest productivity occurs through the ontogenetic development and subsequent emigration of transient organisms and consumption of resident organisms by transients that utilize this ecosystem. The construction and subsequent examination of general models quantifying these relationships will enhance the basic understanding of the dynamics of the mangrove ecosystem.

Life histories of individual species need detailed treatment. Factors dictating reproductive success in mangrove residents will impact the energetics and dynamics of the entire ecosystem. Intra- and interspecific social interactions and predator–prey selection need detailed study, particularly for predator–prey behavior, density, and microhabitat distribution patterns.

The study of the ecological physiology of organisms that commonly use the anoxic, sulfurous mangrove forest ecosystem would greatly enhance our understanding of the abilities of the indigenous biota to utilize this habitat. A variety of organisms that commonly utilize this habitat are air breathers or organisms that hold world records in salinity and temperature tolerance (Gilmore et al. 1982). The mechanisms by which these animals can withstand these environmental rigors need considerable study (Gilmore and Peterson 1989).

An increased understanding of the entire zoological component will also aid fisheries managers and habitat managers in resource conservation.

Ecosystem Research

A comprehensive simultaneous examination of the abiotic and biotic components of a specific accessible mangrove forest system would improve the understanding of the intricacies of hydrological, climatic, sedimentary, and micro- and macrobiotic interactions. An understanding of abiotic/biotic relationships in this ecosystem is necessary to allow determination of all other biological activities and potential effects of anthropogenic impacts. Logical protection, conservation, and management of mangrove forest communities depend on a conceptual understanding of the ecosystem (i.e., the development of a comprehensive basic, though versatile, and complex model), which could be tested through a variety of theoretical and basic research activities and/or through practical use. Present models of mangrove ecosystems are inadequate and simplistic.

ACKNOWLEDGMENTS

We thank Ben McLaughlin, Douglas Scheidt, Mark Peterson, Ron Brockmeyer, Jane Snedaker, and Marilyn Gilmore for comments on the manuscript and Pat Linley for proofreading the final draft. This constitutes contribution No. 540 of the Harbor Branch Oceanographic Institution, Inc., Fort Pierce, Florida.

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