FWS/OBS-81/24
January 1982
Reprinted September 1985

THE ECOLOGY OF THE MANGROVES OF SOUTH FLORIDA: A COMMUNITY PROFILE

by

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Washington, D.C. 20240

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CHAPTER 6. COMMUNITY COMPONENTS - INVERTEBRATES

6.1 ECOLOGICAL RELATIONSHIPS

The mangrove ecosystem, with its tree canopies, masses of aerial roots, muddy substrates, and associated creeks and small embayments, offers many habitat opportunities for a wide variety of invertebrates. While there are few comparisons of species richness with other types of coastal ecosystems, mangrove swamps appear to be characterized by moderately high invertebrate species diversity. Abele (1974) compared H' (Shannon Weaver) diversity of decapod crustaceans between various littoral marine communities and found mangrove swamps in an intermediate position with more decapod species than Spartina marshes but considerably less than were associated with rocky substrate communities.

There is little doubt that the maze of prop roots and muddy substrates under intertidal mangrove trees provides habitat for a wide range of invertebrates and fishes (Figure 10) (see section 7 for the latter). The nursery value of the prop root complex for juvenile spiny lobsters, Panulirus argus, is well established (Olsen et al. 1975; Olsen and Koblic 1975; Little 1977; Witham et al. 1968). According to these researchers, the phyllosome larvae of spiny lobsters often settle among the prop roots and remain there for much of their juvenile lives. The prop roots provide protection from predators and a possible source of food in the associated populations of small invertebrates. To provide the best habitat, a section of the prop roots should extend below mean low tide. If conditions are suitable, the juveniles may remain in close association with the prop root community for as much as 2 years until they reach a carapace length of 60 to 70 mm.

In addition to its value as spiny lobster habitat, mangrove ecosystems also harbor the following invertebrates: barnacles, sponges, polychaete worms, gastropod mollusks, pelecypod mollusks, isopods, amphipods, mysids, crabs, caridean shrimp, penaeid shrimp, harpacticoid copepods, snapping shrimp, ostracods, coelenterates, nematodes, a wide variety of insects, bryozoans, and tunicates. The most obvious and dominant organisms are usually barnacles, crabs, oysters, mussels, isopods, polychaetes, gastropods and, tunicates.

A striking characteristic of most mangrove swamps is the pattern of horizontal and vertical zonation of invertebrates (Figure 9). Characteristic vertical zonation patterns are found on the prop roots (Rutzler 1969) and not so obvious horizontal distributions occur as you move back into the center of the swamp (Warner 1969). Invertebrate biomass in the red mangrove zone on the edge of the swamp may be very high, often in excess of 100 dry g/m^2 of organic matter in many locations (personal observation). In the center of the swamp, particularly where there is little flooding, biomass is usually an order of magnitude less; Golley et al. (1962) found an average of 6.4 g/m^2 of invertebrates in the center of a Puerto Rican mangrove swamp.

Mangrove-associated invertebrates can be placed in four major categories based on trophic position:

(1) direct grazers - limited to

(a) insects and the mangrove tree crab, Aratus pisonii, all of which feed on leaves in the mangrove canopy and

(b) a group of small invertebrates which graze the prop root and mud algae directly;

(2) filter feeders - largely sessile prop root invertebrates which filter phytoplankton and detritus from the water;

(3) deposit feeders - mobile invertebrates which skim detritus, algae and occasional small animals from the surface of the mud and forest floor;

(4) carnivores - highly mobile invertebrates which feed upon the three preceding groups in all locations from the tree canopy (largely insects) to the mud surface. Food sources in mangrove swamps and energy flow are discussed in section 3.6.

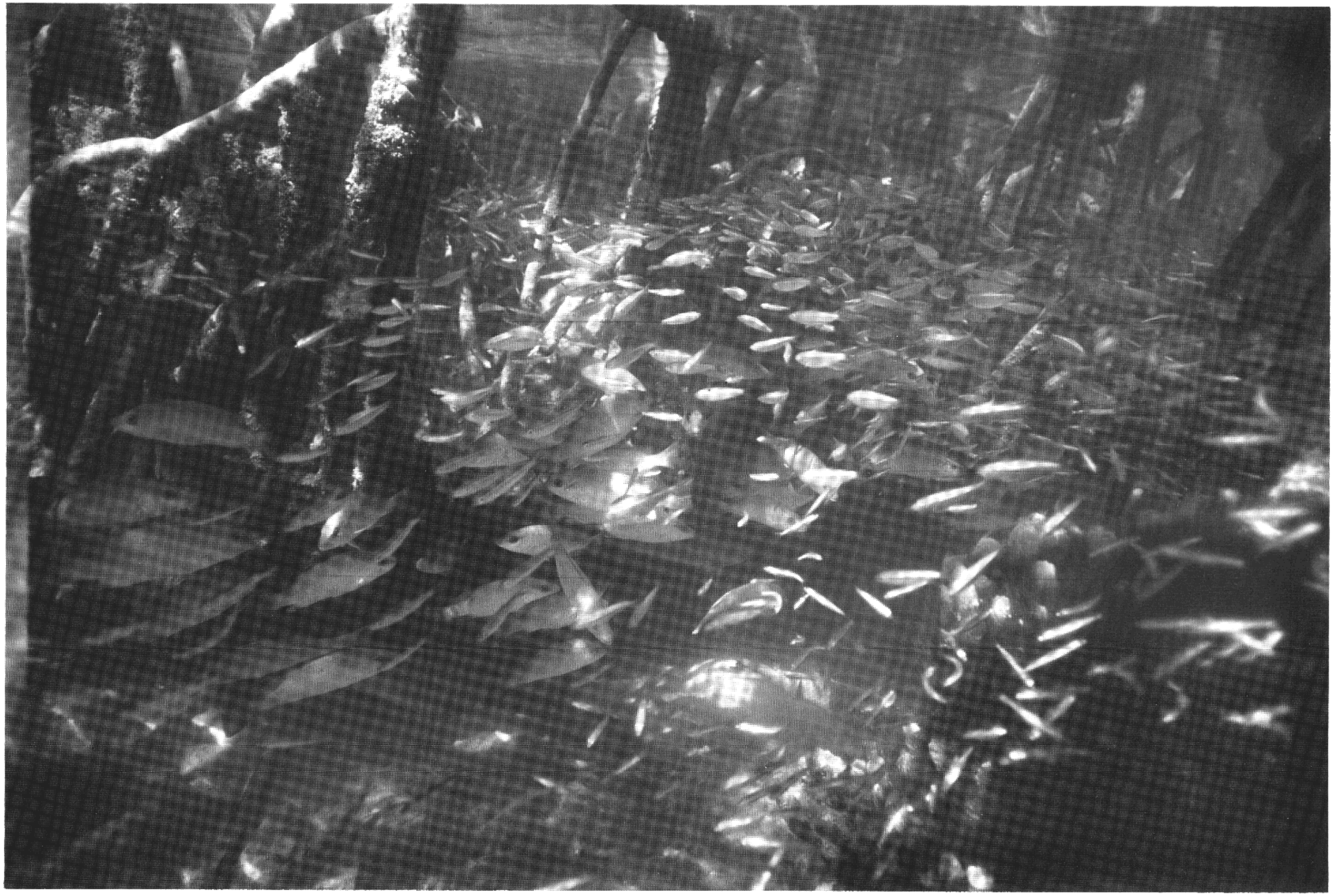

Figure 10. Photograph of red mangrove prop root habitat in clear shallow water with associated animal and plant populations. Photograph is by Bianca Lavies (copyright, National Geographic Society).

6.2. ARBOREAL ARTHROPOD COMMUNITY

A surprising variety of arthropods inhabit the mangrove canopy. Because they are frequently secretive or possess camouflage coloration, their numerical importance often has been overlooked. Beever et al. (1979) pointed out that arboreal arthropods have a variety of ecological roles: (1) direct herbivory on mangrove leaves, (2) predator-prey interactions, and (3) biomass export through frass production and leaf defoliation. Direct grazing is typically patchy in distribution. It is not unusual to find extensive stretches of mangroves that have scarcely been grazed. In nearby areas, as much as 80% of the leaves may have some damage (Beever et al. 1979). As a general rule, it is probably safe to state that healthy, unstressed mangrove stands normally have less than 10% of their total leaf area grazed (Heald 1969). In many locations, percent leaf area damaged is on the order of 1% to 2% (Beever et al. 1979). There are exceptions. Onuf et al. (1977) reported biomass loss to arthropod grazers as high as 26% in a mangrove stand where growth and nitrogen content of the leaves had been enhanced by input of nutrients from a bird rookery.

In terms of numbers of species, the dominant group of arboreal arthropods is insects. The most thorough inventory of mangrove-associated insects was conducted by Simberloff and Wilson to obtain the raw data for their papers on island biogeography (Simberloff and Wilson 1969; Simberloff 1976). These papers list over 200 species of insects associated with overwash mangrove islands in the Florida Keys. There is no reason to expect lesser numbers in other types of mangrove communities, except for the mangrove scrub forests. The most thorough study of insect grazing on mangrove leaves is that of Onuf et al. (1977) (see section 2.6).

Although not as numerically impressive as the insects, the mangrove tree crab, Aratus pisonii, appears to be potentially as important in terms of grazing impact (Beever et al. 1979). The life history of this secretive little crab has been described by Warner (1967). In Jamaica its numbers range from 11 to 16/m^2 at the edge of fringing swamps to 6/m^2 in the center of large swamps. Beever et al. (1979) reported typical densities for a variety of sites in south Florida of 1 to 4 crabs/m^2. These same authors reported some interesting details about the crab: (1) the diet is omnivorous ranging from fresh mangrove leaves to caterpillars, beetles, and various insects; (2) the crab suffers highest predation pressure while in the planktonic larval stage; (3) predation on the crabs while in the arboreal community is low and comes from birds such as the white ibis, raccoons, other mangrove tree crabs and, if the crabs fall in the water, fishes such as the mangrove snapper; and (4) in one location in south Florida (Pine Island Sound) they found in accordance with normal biogeographical theory, the highest densities of crabs associated with fringing forests and the lowest densities on distant islands, but at Sugar Loaf Key the unexplainable reverse distribution was found.

Other invertebrates may visit the canopy from below either for purposes of feeding or for protection from high tides. Included in this group are the pulmonate gastropods, Littorina angulifera, Cerithidea scalariformis, and Melampus coffeus, the isopod, Ligea exotica, and a host of small crabs.

In summary, with the exception of a half dozen key papers, the arboreal mangrove community has been generally ignored. Both insects and the mangrove tree crab play significant ecological roles and may affect mangrove productivity to a greater extent than has been recognized.

6.3 PROP ROOT AND ASSOCIATED MUD SURFACE COMMUNITY

These two somewhat distinct communities have been lumped together because of the large number of mobile organisms which move back and forth between tidal cycles. The aerial roots are used as protective habitat and to some extent for feeding while the nearby mud substrates are used principally for feeding.

The prop roots support an abundance of sessile organisms. The vertical zonation of both mobile and sessile invertebrates has been studied extensively in other parts of the world (Goodbody 1961; Macnae 1968; Rutzler 1969; Coomans 1969; Bacon 1970; Kolehmainen 1973; Sasekumar 1974; Yoshioka 1975). Vertical zonation certainly exists on Florida red mangrove roots. The generalized scheme shown in Figure 9 essentially contains two zones: an upper zone dominanted by barnacles and a lower zone dominated by mussels, oysters and ascidians. Between mean high tide and mean tide, the wood boring isopod, Sphaeroma terebrans (discussed at length in section 2.7) is important, both numerically and through the provision of numerous holes for use by other organisms (Estevez 1978).

The most complete study of the Florida mangrove prop root community is Courtney's (1975) comparison of seawall and mangrove associations. He reported an extensive list of invertebrates from mangrove prop roots at Marco Island, Florida, including: Crassostrea virginica, Littorina angulifera, Crepidula plana, Diodora cayenensis, Urosalpinx perrugata, Pisania tincta, Brachidontes exustus, nine species of polychaetes, Sphaeroma terebrans, Palaemon floridanus, Periclimenes longicaudatus, Synalpheus fritzmuelleri, Thor floridanus, Petrolisthes armatus, and at least eight species of crabs. The following species were found only on mangrove roots and not on seawalls: Turitella sp., Melongena corona, Anachis semiplicata, Bulla striata, Hypselodoris sp., Arca imbricata, Carditamera floridana, Pseudoirus typica, and Martesia striata.

Tabb et al. (1962) and Odum and Heald (1972) reported a variety of invertebrates associated with prop roots in the Whitewater Bay region. Although many species coincide with Courtney's (1975) list, there are also significant differences due to the lower salinities in this region. It is probably safe to conclude that prop root communities vary somewhat from site to site in response to a number of factors including latitude, salinity, and proximity to other communities such as sea grass beds and coral reefs.

Sutherland (1980), working on red mangrove prop root communities in Venezuela, found little change in the invertebrate species composition on individual prop roots during an 18-month period. The species composition varied greatly, however, between adjacent prop roots, presumably in response to stochastic (chance) processes.

The mud flats adjacent to mangroves provide feeding areas for a range of invertebrates that scuttle, crawl, and swim out from the cover of the mangrove roots. Some emerge at low tide and feed on algae, detritus, and small invertebrates on the mud flats while they are high and dry. Others emerge while the tide is in, particularly at night, and forage across the flooded flats in search of the same foods plus other invertebrates which have emerged from the mud. In many ways the mangrove-mud flat relationship is analogous to the coral reef (refuge) sea grass (feeding area) relationship reviewed by Zieman (in prep.). The net effect is that the impact of the mangrove community may extend some distance beyond the boundaries of the mangrove forest.

In addition to the organisms which move from the mangroves to the mud flats, there is a small group which uses the substrate adjacent to mangroves for both habitat and feeding. In the Whitewater Bay region, four crabs exploit the intertidal muds from the safety of burrows: Uca pugilator, U. speciosa, U. thayeri, and Eurytium limosum (Tabb et al. 1962). In low salinity mangrove forests of south Florida, the crayfish, Procambarus alleni, is a dominant member of the burrowing, benthic community (Hobbs 1942) as is the crab, Rhithropanopeus harrisii (Odum and Heald 1972). Both organisms are found in a remarkable number of fish stomachs.

The benthic fauna and infauna of creek and bay bottoms near mangrove forests are highly variable from one location to the next. Many of these organisms, particularly the deposit and filter feeders, benefit from particulate organic matter originating from mangrove litter fall (Odum and Heald 1972, 1975b). Tabb and Manning (1961) and Tabb et al. (1962) present lists and discussions of many of the benthic invertebrates adjacent to mangrove areas of Whitewater Bay. Weinstein et al. (1977) compared the benthic fauna of a mangrove-lined creek and a nearby man-made canal on Marco Island. They found (1) the mangrove fauna to be more diverse than the canal fauna and (2) a higher diversity of organisms at the mouths of mangrove creeks than in the "heads" or upstream ends. Courtney (1975) found the same pattern of upstream decreases in diversity, presumably in response to decreasing oxygen concentrations and increasingly finer sediments.

Finally, the irregularly flooded substrates in the center of mangrove forests contain a small but interesting assemblage of invertebrates. The litter layer, composed largely of mangrove leaves, evidently includes a variety of nematodes. Due to the usual taxonomic difficulties in identifying nematodes, complete species lists do not exist for mangrove forests; however, many species and individuals are associated with the decaying leaves (Hopper et al. 1973). In addition to nematodes, the wetter sections of the swamp floor can contain mosquito and other insect larvae, polychaetes, harpacticoid copepods, isopods, and amphipods. Simberloff (1976) lists 16 species of insects associated with the muddy floor of mangrove forests. Roaming across the forest floor during low tide are several crustaceans including the mangrove tree crab, _Aratus pisonii_, crabs of the genus _Sesarma_, and the pulmonate gastropods, _Melampus coeffeus_ and _Cerithidea scalariformis_. Both snails clearly have the ability to graze and consume recently fallen leaves (personal observation). With favorable conditions (relatively frequent tidal inundation plus the presence of red mangroves) _Melampus_ populations can exceed $500/m^2$ and average 100 to $200/m^2$ (Heald, unpublished data). _Cerithidea_ is found largely in association with black mangroves and can reach densities of at least $400/m^2$.

6.4 WATER COLUMN COMMUNITY

This section is embarrassingly short; the reasons for this brevity are (1) the paucity of research on zooplankton in Florida mangrove-dominated areas and (2) our inability to discover some of the work which undoubtedly has been done. Davis and Williams (1950) are usually quoted as the primary reference on Florida mangrove-associated zooplankton, but their paper only lists zooplankters collected in two areas. Zooplankton near mangroves are probably no different from those found in other shallow, inshore areas in south Florida. Based on Davis and Williams (1950) and Reeve (1964), we can hypothesize that the community is dominated by copepod species of genus _Acartia_, particularly _Acartia tonsa_. In addition, we could expect a few other calanoid copepods, arrow worms (_Sagitta_ spp.), many fish, polychaete and crustacean larvae and eggs. Another component of the "plankton," particularly at night, are benthic amphipods, mysids, and isopods which leave the bottom to feed (personal observation).

Plankton are not the only invertebrates in the water column. Swimming crabs, such as the blue crab, _Callinectes sapidus_, are plentiful in most estuarine mangrove regions of south Florida. Other swimming crustaceans include the caridean shrimp (_Palaemonetes_ spp. and _Periclimenes_ spp.), the snapping shrimp (_Alpheus_ spp.), and the penaeid shrimp (_Penaeus_ spp). All of these swimming crustaceans spend considerable time on or in the benthos and around mangrove prop roots. From the economic point of view, the pink shrimp, _Penaeus duorarum_, is probably the most important species associated with mangrove areas (see discussion in section 11).