Lagunas Costeras, un Simposio. Mem. Simp. Intern. Lagunas Costeras. UNAM-UNESCO, Nov. 28-30, 1967. México, D. F.: 515-536, 5 figs. (1969)

THE MANGROVE COMMUNITY, ASPECTS OF ITS STRUCTURE, FAUNISTICS AND ECOLOGY

K. Rützler *

ABSTRACT

In a brief survey of the literature dealing with mangroves in the sense of a littoral habitat, the points of focus and results of earlier works are summarized. The various biotopes within the community are classified in accordance with their dominant floristic and faunistic components. It is felt that not enough consideration has been given to the sedentary fauna which is reaching dominant importance on mangrove roots in certain regions. The limited abundance and peculiarity of the substrate raises interesting problems concerning interspecific relations and dynamics of associations.
A large number of habitats in mangrove swamps are influenced by the sea. These have been greatly neglected by systematists and ecologists in the past. With coordinated international and interdisciplinary cooperation it should be possible, with reasonable effort, to determine the community structure, i. e. the correlation and self-determination of the bioconotic units.

Introduction

Back to the days of Alexander the Great we can follow the amazement of travellers first confronted with the ghostly evergreen forest raising from the sea. After Nearchus, commander of Alexander's fleet reported on the mangroves he had observed bordering the Arabian Sea, Theophrastus (305 B.C.), student of Aristotle, gave the first recognizable description of *Rhizophora mangle* and its habitat. With Linnaeus a period of morphologic and systematic botanical studies began in the second half of the eighteenth century.

Because of the peculiar embryology of *Rhizophora* and the adaptation of mangrove trees to growth in salt water the interest of biologists soon focused on the ecology of mangrove plant communities and associated vegetation. Studies ant their successions and physiology were carried out by Walter and Steiner (1937) for East Africa, by Davis (1940) for Florida, by Chapman (1943) for Jamaica and by Golley *et al* (1962) for Puerto Rico.

Besides the osmotic properties of *Rhizophora, Avicennia, Laguncularia* and *Sonneratia* the function of the stilt roots and pneumatophores has also engaged many physiologists until Scholander *et al* (1955) proved the hypothesis that they served for ventilation of the rest of the root system which is buried in the anaerobic mud.

An important part of the literature on mangroves has been devoted to practical human interests, from mosquito control (Gilroy and Chwatt, 1945) to economic exploitation for building timber, fire wood, and tannic acid; not to mention the fact that the roots of the living trees serve as hiding places for fish and as substrate for much desired oysters (Holdridge 1939, Mattox 1949). Mangroves were even planted artificially to avoid erosion of railway embankments (Bowman, 1917).

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This leads to the interesting aspects of their role in geology and sedimentology. The function of the mangroves in this respect has sometimes been denied, but more frequently overemphasized. However, it is a fact that during the changes of tides debris accumulates among the roots. This creates, with the aid of massive growing epiphytes, stagnant bodies of water favorable for deposition. In addition, dead leaves and other plant remains pile up and become imbedded. There is no way for the roots themselves to hold the sediments as has been frequently stated; on the contrary, they might aid destruction by breaking through limestone rock [as in the example of the pneumatophores of *Avicennia* (Howard, 1950)]. Thus, in coordination with favorable geomorphological and hydrographical conditions, mangroves are definitely able to help build up land for a protruding terrestrial forest.

Prior to the turn of this century no zoological research had been done in the mangrove community if one neglects the reports of voyagers complaining about mosquito attacks and praising the palatable oysters and crayfish. Later, the mangrove forest was recognized as a littoral habitat where truly terrestrial and typical marine organisms lived in close relationship and periodically overlaped with the change of tides. Also, attention was drawn to the fact that the mangrove is a physiographic unit, the principal components of which are organnisms; therefore, the problems, are predominantly of a biological nature.

Topography and Classification

There are different types of mangroves depending on the various geomorphic features of the coast. Plant ecologists have demonstrated that there are distinct topographical successions which are similar in old world and new world mangroves. Pioneer red mangroves (*Rhizophora*) protrude farthest into the sea or border channels and lagoons. Typically, they are followed by black mangrove (*Avicennia*) — salt marsh associes which are not regularly flooded. Then comes a seldomly flooded transition zone (e. g. *Conocarpus, Hibiscus*) which connects to dry land, frequently rain forest. According to the substrate the mangrove types are classified as reef, sand, mud, and peat mangroves. This classification also expresses different hydrographical conditions, which are of interest to the marine biologist. Reef and sand mangroves are the most exposed towards the open sea with sufficient water exchange to provide a typical marine environment. One of these has been studied closely by the Great Barrier Reef Expedition at Low Isles (Stephenson *et al* 1931), and it was found that all the sedentary fauna from mangrove roots, i. e. corals, sponges, hydroids, anemones and ascidians and also the holothurians clearly belonged to the reef fauna proper.

Mud mangroves usually occur near river mouths, thus showing a steep salinity gradient from marine to fresh water. This effect was the subject of an exemplary study by Walsh (1967) in Hawaii.

Peat mangroves grow along sheltered shores and in lagoons without fresh water influences other than subsoil water and rain. This latter type is of great interest for the marine biologist because the environment is such that a typical marine flora and fauna can exist but the factors are so variable and sometimes extreme that the organisms must be strongly selected.

This type of mangrove is rather common in the Western Atlantic and has stimulated the interest of various systematists and ecologists as can be learned from comprehensive studies by Mattox (1949) in Puerto Rico and by Gerlach (1959) in Brazil.

Vertical Zonations

As in all coastal marine habitats the vertical distribution of communities is deter-

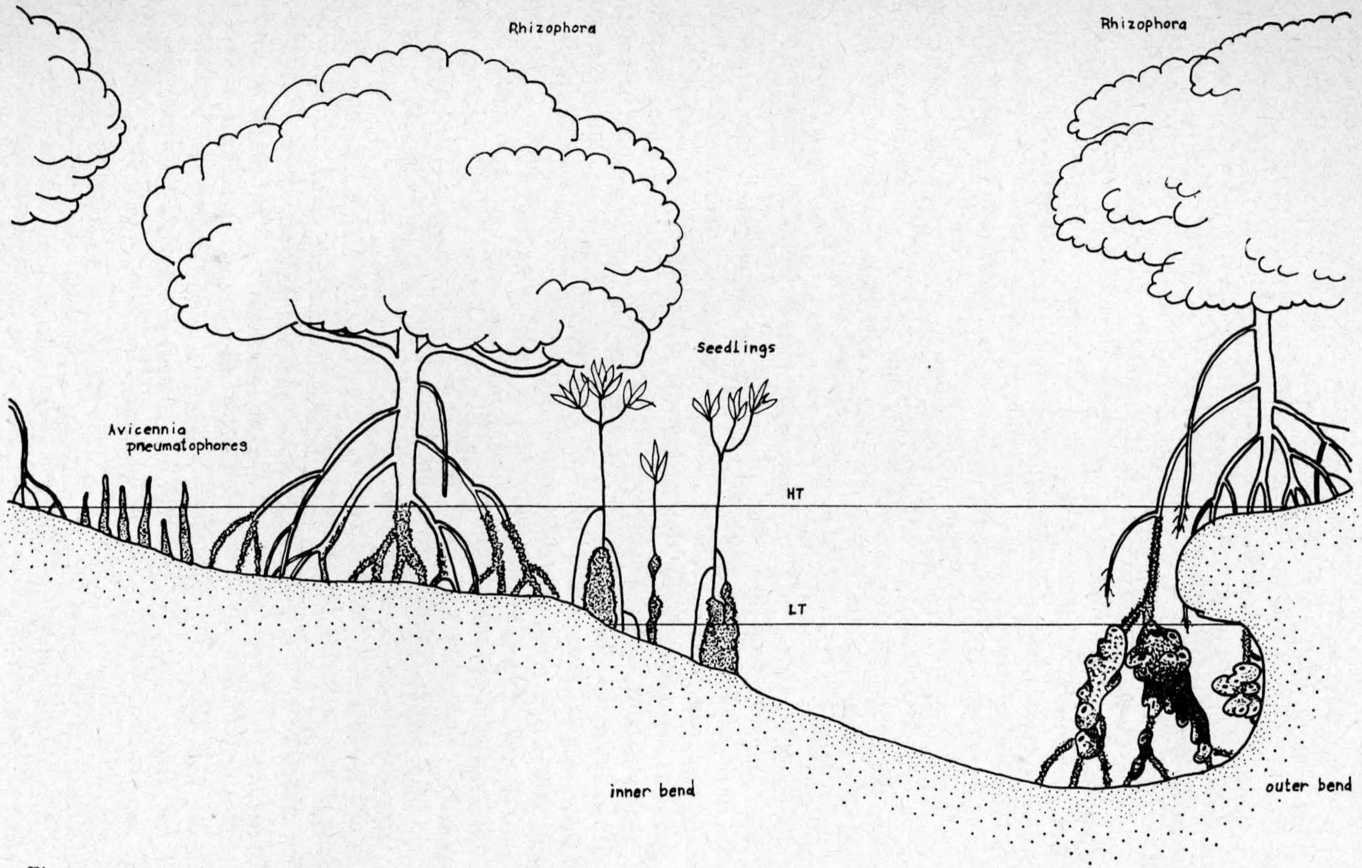

Figure 1. Typical mangrove channels as represented by Bone Fish Creek, East Bimini. On the permanently submerged parts of *Rhizophora* roots limitation of substrate causes spacial competition between sedentary organisms. HT=High tide level. LT= Low tide level.

mined by the exposure to air. The supra-littoral is only a narrow zone because there is no wave action causing spray. However, it is extensive since it is mainly formed by the mangrove trees. Some crabs (*Aratus*, *Sesarma*) and gastropods (*Littorina*, *Neritina*) are dominant here closely following the changing sea level.

In the medio-littoral, the substrate and the living habits and morphological and physiological properties of organisms influence the community structure. In order to avoid coverage by mud sedentary organisms must be confined to vertical stable substrates like stems, air-roots, and seedlings of the mangrove trees. Because they are exposed, however, the danger of desiccation during low tide is greatest. A characteristic intertidal algal community the "*Bostrychietum*" has a high osmotic resistance and withstands desiccation. As field and laboratory experiments have proven (Biebl, 1962), it is not very resistant to light. Solar radiation, however, is comparatively low because of the protecting canopy of the mangrove leaves. Animals with closeable shells like oysters (*Crassostrea*) and barnacles (*Balanus*, *Chthamalus*) or with tubes within which they can retract, such as serpulids, remain inactive but protected during the dry period.

On the extended mud flats (the most investigated habitat to date) representatives of the vagrant macrofauna alternate in their activity periods. Fish, such as gobiids and blenniids remain buried in mud or in clumps of algae during low tide. Crabs such as *Uca* remain in their humid, but air-containing burrows during high tide; others, like *Aratus*, avoid the rising water by climbing trees. The famous mud-skipper (*Periophthalmus*) is probably one of the very few truly amphibious mangrove animals.

Small, or true micro-organisms are, from the viewpoint of their micro-environment, inhabitants of the infra-littoral. During low tide they have to withstand high or, in case of rainfall, low salinities but not desiccation. They either remain protected in crevices, bore holes in their substrate (mangrove roots, oyster shells), live endophyticly in clumps of algae, live endozoicly in oysters or sponges, or live interstitially in mud or sand. In these cases the chemical and physical conditions provided by the substrate determine the community structure.

It is difficult to obtain all references on systematics and distribution of mangrove dwelling organisms since they are frequently hidden in some specialized taxonomic work. However, I have tried to summarize from a literature study all organisms characteristic for the different environments in both Eastern and Western mangroves. The results are presented in table 1.

INFRA-LITTORAL TIDE CHANNELS

The proper infra-littoral, since the occurrence of mangrove trees is limited by water depth, is almost exclusively restricted to a number of channels through which the water of the changing tides flows and to lagoons or ponds devoid of trees. Here the only solid substrate uncovered by mud are the roots of bordering *Rhizophora*. The stilt roots of these trees extend to deeper water than the stems. At the current-exposed outer sides of the channel bends ("Prallhang") the soil is washed out, thus exposing a wickerwork of mud-roots under a mud-cornice. This overhang is left in the upper medio-littoral because the water current is very slow near the peak of the tide. Examples of this formation can be found in narrow parts of mangrove channels where the current is accelerated such as in Bone Fish—or other creeks in the mangroves of East Bimini, Bahamas (figure 1).[1]

[1] Observations from Bimini mentioned here were made during work under Office of Naval Research Contract NONR 552(07). I am indebted to Mr. Robert Mathewson, director of the Lerner Marine Laboratory.

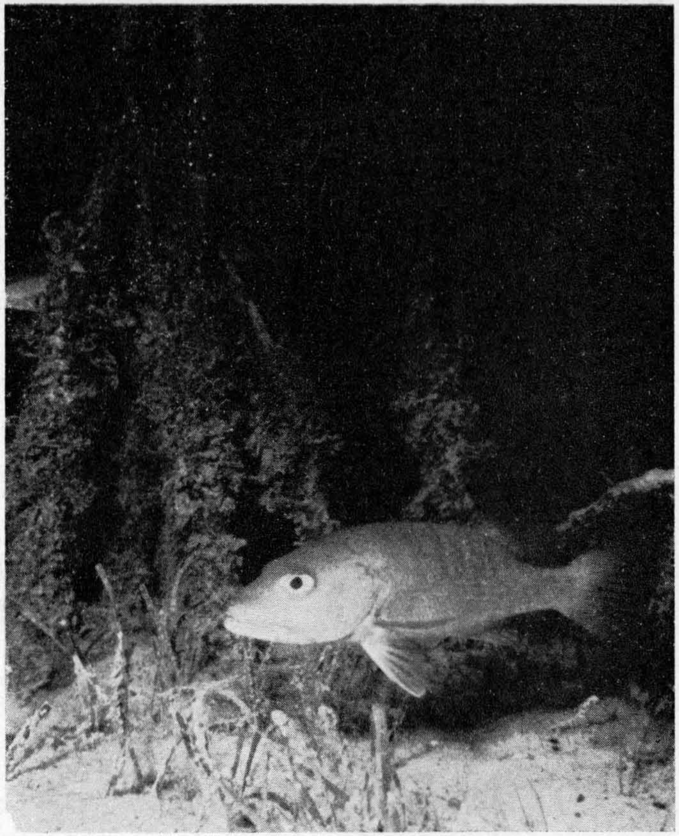

Figure 2. *Bostrychietum* grows on the intertidal parts of the red mangrove roots. At high tide numerous fishes find here hiding space.

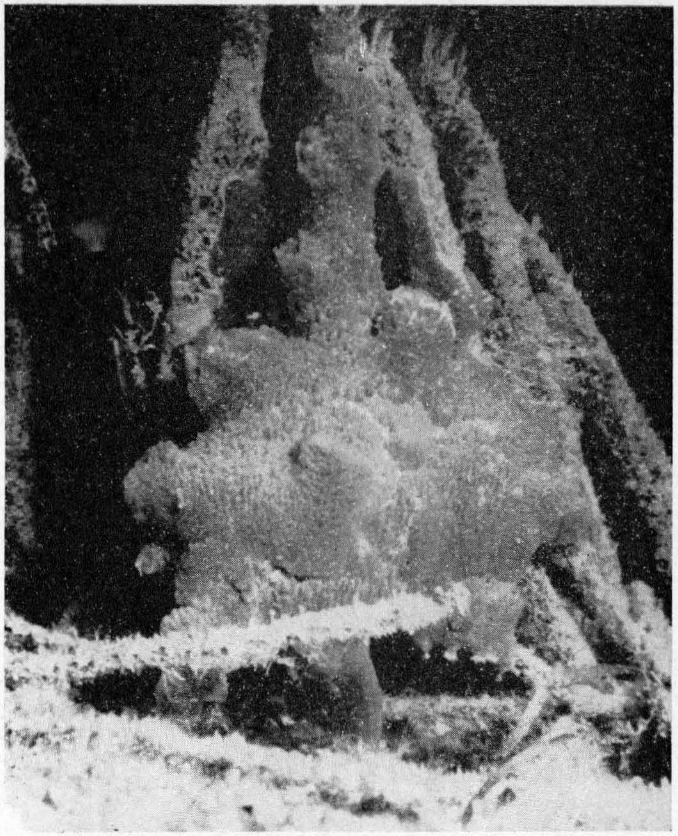

Figure 3. *Tedania ignis* is one of the most common mangrove sponges. Because of its toxic properties, which even effect the human skin on touch and because of its flame-red color it is commonly called the fire-sponge.

TABLE 1

MARINE ORGANISMS CHARACTERIZING DIFFERENT TYPES OF MANGROVE SWAMP HABITATS

LITTORAL TYPE	TYPE OF SUBSTRATE	NATURE OF SUBSTRATE	DOMINANT FLORA AND FAUNA	NUMBER OF MANGROVE SPECIES PER TAXON. GROUP	LIVING HABIT BV=*benthic vagrant* BS=*benthic sessile* I=*interstitial* B=*burrowing, boring*	ACTIVITY PERIOD HT=*high tide* LT=*low tide* C=*continuous*	GEOGRAPHY E=*Eastern mangrove* W=*Western mangrove*	AUTHOR f=*fide*
SUPRA-LITTORAL	SOLID	MANGROVETREE (lower branches and stem)	ARTHROPODA (DECAPODA)	10+				
			Aratus pisonii		BV	C	W	Glynn, 1964
			Uca murificenta		BV	C	W	Rodriguez, 1963
			Sesarma bidens		BV	C	E	Stephenson *et al*, 1931
			MOLLUSCA (GASTROPODA)	15+				
			Littorina angulifera		BV	C	W	Gerlach, 1958
			Neritina lepricurii		BV	C	W	Rodríguez 1963
			Nerita lineata		BV	C	E	Stephenson *et al*, 1931
			Melampus coffeus		BV	C	W	Glynn, 1964
			Cerithidae		BV	C	E	Macnae, 1963
	MOBILE	SOIL (terrest.)	ARTHROPODA (DECAPODA)	3+				
			Cardisoma guanhumi		BV, B	C	W	Glynn, 1964
MEDIO-LITTORAL	SOLID	MANGROVETREE (stem, pneumatophores and stiltroots)	DIATOMS	++	BS	—	E, W	Var. authors
			CYANOPHYTA	++	BS	—	E, W	Var. authors
			CHLOROPHYTA	5+				
			Acetabularia		BS	—	W	Rützler, unpubl.
			Caulerpa		BS	—	E	Stephenson *et al*, 1931
			Valonia		BS	—	E, W	Margalef, 1962

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			PHAEOPHYTA	6+				
			Ectocarpus		BS	—	E, W	Stephenson *et al*, 1931
			Padina		BS	—	W	Margalef, 1962
			RHODOPHYTA ("BOSTRYCHIETUM")	30+				
			Bostrychia		BS	—	E, W	f. Gerlach, 1958
			Caloglossa		BS	—	E, W	f. Gerlach, 1958
			CNIDARIA	3				
			Bougainvillia		BS	HT	W	Mattox, 1949
			Pennaria		BS	HT	W	Mattox, 1949
			ANNELIDA (POLYCHAETA)	2+				
			Serpulidae		BS	HT	W	Rützler, unpubl.
			ARTHROPODA (CIRRIPEDIA)	5+				
			Balanus amphritite		BS	HT	W	Gerlach, 1958
			Chtamalus rhizophorae		BS	HT	W	Gerlach, 1958
			ARTHROPODA (DECAPODA)	10				
			Stenopsus hispidus		BV	HT	W	Mattox, 1949
			Portunus		BV	HT	W	Rützler, unpubl.

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			ARTHROPODA					
			(ISOPODA)	3+				
			Sphaeroma tenebrans		BV, B	HT	W	Davis, 1940
			MOLLUSCA					
			(BIVALVIA)	15+				
			Crassostrea rhizophorae		BS	HT	W	Mattox, 1949
			Ostrea mordax		BS	HT	E	Stephenson *et al*, 1931
			Modiolus guyanensis		BS	HT	W	f. Gerlach, 1958
			Mytilus haematus		BS	HT	W	Mattox, 1949
			Teredo manni		BS	HT	W	f. Gerlach, 1958
			Chama macerophyllia		BS	HT	W	Glynn, 1964
			Isognomon alatus		BS	HT	W	Glynn, 1964
			Arca zebra		BS	HT	W	Glynn, 1964
			TENTACULATA					
			(BRYOZOA)	1				
			Bugula nerita		BS	HT	W	Mattox, 1949
			ASCHELMINTHES					
			(NEMATODA)	17				
			Paracyatholaimus vitraeus		BV	C	W	Gerlach, 1958

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			ANNELIDA (OLIGOCHAETA)	5+				
			Michaelsena		BV	C	W	Gerlach, 1958
		(EPIPHYTIC) ALGAE	ANNELIDA (POLYCHAETA)	2				
			Opisthosyllis arboricola		BV	C	W	Hartmann-Schöder, 1959
			ARTHROPODA (COPEPODA)	4				
			Nitocra dubia		BV	C	W	Gerlach, 1958
			ARTHROPODA (AMPHIPODA)	3				
			Orchestia darwinii		BV	C	W	Gerlach, 1958
		SESSILE MACRO-BENTHOS	PORIFERA	3				
			Haliclona tubifera		I	HT	W	Mattox, 1949
			Pleraplysilla		I	HT	W	Mattox, 1949
			PLATHELMINTHES (TURBELLARIA)	1				
			Pseudoceras superbus		I	C	W	Mattox, 1949
			ANNELIDA (POLYCHAETA)	1+				
			Polydora		I	C	W	Mattox, 1949

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			ARTHROPODA (CIRRIPEDIA)	1				
			Balanus eberneus		BS	HT	W	Mattox, 1949
			MOLLUSCA (GASTROPODA)	1				
			Murex brevifrons		BV	HT	W	Mattox, 1949
	MOBILE	MUD, SAND	PLATHELMINTHES (TURBELLARIA)	7				
			Nygulgus evelinae		I	C	W	Gerlach, 1958
			ASCHELMINTHES (NEMATODA)	43				
			Anoplostoma subulatum		I	C	W	Gerlach, 1958
			Sabatieria quadripapillata		I	C	W	Gerlach, 1958
			ANNELIDA (OLIGOCHAETA)	12+				
			Protodrilus bermudensis		I	C	E	Stephenson *et al*, 1931
			ANNELIDA (POLYCHAETA)	21				
			Polydora redeki		I	C	W	Gerlach, 1958
			Scoloplos armiger		I	C	W	Hartmann-Schröder, 1959

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			ARTHROPODA (COPEPODA)	6				
			Nannopus palustris		I	C	W	Gerlach, 1958
			ARTHROPODA (OSTRACODA)	3				
			Cyprideis multidentata		I	C	W	Gerlach, 1958
			ARTHROPODA (DECAPODA)	30+				
			Uca thayeri		BV, B	LT	E, W	f. Gerlach, 1958
			Uca pugnax rapax		BV, B	LT	W	Gerlach, 1958
			Alpheus heterochaelis		BV, B	C	W	Gerlach, 1958
			Ubogebia brasiliensis		BV, B	HT	W	Gerlach, 1958
			Scylla serrata		BV, B	HT	E	Stephenson *et al*, 1931
			Thalamita crenata		BV, B	HT	E	Stephenson *et al*, 1931
			Sesarma bidens		BV, B	LT	E	Stephenson *et al*, 1931
			Thalassina anomala		BV, B	HT	E	Stephenson *et al*, 1931
			Clibanarius striolatus		BV	LT	E	Stephenson *et al*, 1931
			ARTHROPODA (ISOPODA)	1				
			Ligia australiensis		BV, B	HT	E	Stephenson *et al*, 1931

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			MOLLUSCA (GASTROPODA)	15				
			Alderia uda		BV	HT	W	Gerlach, 1958
			Pyrazus palustris		BV	HT	E	Stephenson *et al*, 1931
			Telescopium telescopium		BV	HT	E	Stephenson *et al*, 1931
			MOLLUSCA (BIVALVIA)	5+				
			Arca tuberculosa		BS	HT	W	f. Gerlach, 1958
			Pellina palatam		BV, B	HT	E	Stephenson *et al*, 1931
			PISCES	5+				
			Gobinellus smaragdus		BV, B	HT	W	Gerlach, 1958
			Periophthalmus koelreuteri		BV, B	HT	E	Stephenson *et al*, 1931
			REPTILIA	2				
			Crocodylus porosus		BV	C	E	f. Gerlach, 1958
INFRA-LITTORAL	SOLID	MANGROVETREE (stem, stilt and mud roots washed out by current)	DIATOMS	++	BS	—	E, W	Stephenson *et al*, 1931
			CYANOPHYTA	++	BS	—	E, W	Stephenson *et al*, 1931
			CHLOROPHYTA	5				
			Caulerpa		BS	—	E, W	Stephenson *et al*, 1931
			Acetabularia		BS	—	W	Margalef, 1962
			Valonia		BS	—	W	Margalef, 1962
			Penicillus		BS	—	W	Rützler, unpubl.

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			PHAEOPHYTA	8+				
			Ectocarpus		BS	—	E, W	Stephenson *et al*, 1931
			Padina		BS	—	W	Margalef, 1962
			Dictyota divaricata		BS	—	W	Biebl, 1962
			RHODOPHYTA	6+				
			Laurencia obtusa		BS	—	W	Biebl, 1962
			PORIFERA	28+				
			Tedania ignis		BS	C	W	Hechtel, 1965
			Ircinia fasciculata		BS	C	W	Rützler, unpubl.
			Chondrilla nucula		BS	C	W	Rützler, unpubl.
			Dysidea fragilis		BS	C	W	Hechtel, 1965
			Sigmadocia caerulea		BS	C	W	Hechtel, 1965
			Anthosigmella varians		BS	C	W	Rützler, unpubl.
			Myriastra		BS	C	W	Rützler, unpubl.
			Biemna microstyla		BS	C	W	Laubenfels, 1950
			Desmacella jania		BS	C	W	Laubenfels, 1950
			Spongia officinalis		BS	C	E	Stephenson *et al*, 1931
			Spirastrella purpurea		BS	C	E	Stephenson *et al*, 1931
			CNIDARIA (ANTHOZOA)	2				
			Bartholomea annulata		BS	C	W	Glynn, 1964
			Condylactis		BS	C	W	Rützler, unpubl,

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			CNIDARIA (HYDROZOA)	14+				
			Myrionema amboinense		BS	C	E, W	Stephenson *et al*, 1931
			Eudendrium		BS	C	W	Rützler, unpubl.
			ANNELIDA (POLYCHAETA)	4				
			Sabellastarte magnifica		BS	C	W	Glynn, 1964
			Spirorbis		BS	C	W	Margalef, 1962
			MOLLUSCA (BIVALVIA)	1				
			Brachydontes recurvus		BS	C	W	Glynn, 1964
			ECHINODERMATA (OPHIURIDEA)	3				
			Ophiotrix angulata		BS	C	W	Glynn, 1964
			ECHINODERMATA (HOLOTHURIOID.)	2				
			Stichopus badionotus		BS	C	W	Glynn, 1964
			Holothuria palva		BS	C	W	Glynn, 1964

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			TENTACULATA (BRYOZOA)	5+				
			Aetea anguina		BS	C	W	Osburn, 1940
			Bugula neritina		BS	C	W	Osburn, 1940
			Caulibugula armata		BS	C	W	Osburn, 1940
			TUNICATA (ASCIDIACEA)	10+				
			Policitor olivaceus		BS	C	E	f. Gerlach, 1958
			Ecteinascidia turbinata		BS	C	W	Mattox, 1949
			Ascidia nigra		BS	C	W	Mattox, 1949
			Clavelina oblongata		BS	C	W	Glynn, 1964
			Microcosmus exasperatus		BS	C	W	Glynn, 1964
			Botrylus		BS	C	W	Mattox, 1949
			Didemnum		BS	C	W	Rützler, unpubl.
		ROCKS AND GRAVEL (in channels, cleaned from sediments by currents)	PORIFERA	10+				
			Adocia toxia		BS	C	E	Stephenson *et al*, 1931
			Spirastrella purpurea		BS	C	E	Stephenson *et al*, 1931
			Dysidea fragilis		BS	C	E	Stephenson *et al*, 1931
		SESSILE MACRO-BENTHOS	ARTHROPODA (DECAPODA)	3				
			Synalpheus brevicarpus		BV, I	C	W	Glynn, 1964

TABLE 1 (CONTINUATION)

MARINE ORGANISMS CHARACTERIZING DIFFERENT TYPES OF MANGROVE SWAMP HABITATS

LITTORAL TYPE	TYPE OF SUBSTRATE	NATURE OF SUBSTRATE	DOMINANT FLORA AND FAUNA	NUMBER OF MANGROVE SPECIES PER TAXON. GROUP	LIVING HABIT *BV=benthic vagrant* *BS=benthic sessile* *I=interstitial* *B=burrowing, boring*	ACTIVITY PERIOD *HT=high tide* *LT=low tide* *C=continuous*	GEOGRAPHY *E=Eastern mangrove* *W=Western mangrove*	AUTHOR *f=fide*
		(EPIPHYTIC) ALGAE	TENTACULATA (BRYOZOA)	5+				
			Bugula neritina		BS	C	W	Osburn, 1940
			ARTHROPODA (DECAPODA)	2+				
			Ubogebia		BV, B	C	E	Macnae, 1963
	MOBILE	SAND, MUD	BACTERIA	++	I	C	W	Margalef, 1962
			PROTISTA	++	I	C	W	Margalef, 1962
			CNIDARIA (HYDROZOA)	1+				
			Cassiopea		BV	C	W	Rützler, unpubl.
			ASCHELMINTHES (NEMATODA)	26				
			Sabatieria clavicauda		I	C	W	Gerlach, 1958
			ARTHROPODA (COPEPODA)	5				
			Nitocra hyperitis		I	C	W	Gerlach, 1958
			ARTHROPODA (OSTRACODA)	2				
			Mesocythere elongata		I	C	W	Gerlach, 1958
			ARTHROPODA					

TABLE 1 (CONTINUATION)

MARINE ORGANISMS CHARACTERIZING DIFFERENT TYPES OF MANGROVE SWAMP HABITATS

LITTORAL TYPE	TYPE OF SUBSTRATE	NATURE OF SUBSTRATE	DOMINANT FLORA AND FAUNA	NUMBER OF MANGROVE SPECIES PER TAXON. GROUP	LIVING HABIT *BV=benthic vagrant* *BS=benthic sessile* *I=interstitial* *B=burrowing, boring*	ACTIVITY PERIOD *HT=high tide* *LT=low tide* *C=continuous*	GEOGRAPHY *E=Eastern mangrove* *W=Western mangrove*	AUTHOR *f=fide*
			(DECAPODA)	4+				
			Calinectes sapidus		BV	C	W	Rodríguez, 1963
			Panulirus		BV	C	W	Rützler, unpubl.
			MOLLUSCA					
			(GASTROPODA)	4+				
			Polymesoda arctata		BV	C	W	Rodríguez, 1963
			Tridachia crispata		BV	C	W	Rützler, unpubl.
	PELAGIC		COPEPODE					
			NAUPLII, ETC.	50+			W	Davis and Williams, 1950
			DIATOMS, ETC.	30+			W	Mattox, 1949
			CILIATES	++			W	Margalef, 1962
			ARTHROPODA					
			(ANOSTRACA)	1			W	Glynn, 1964
			PISCES, VAR.	10+			E, W	Var. authors
			Artemia salina					

Figure 4. Mass development of *Chondrilla nucula* on mangrove root prohibiting any other sedentary organisms to settle.

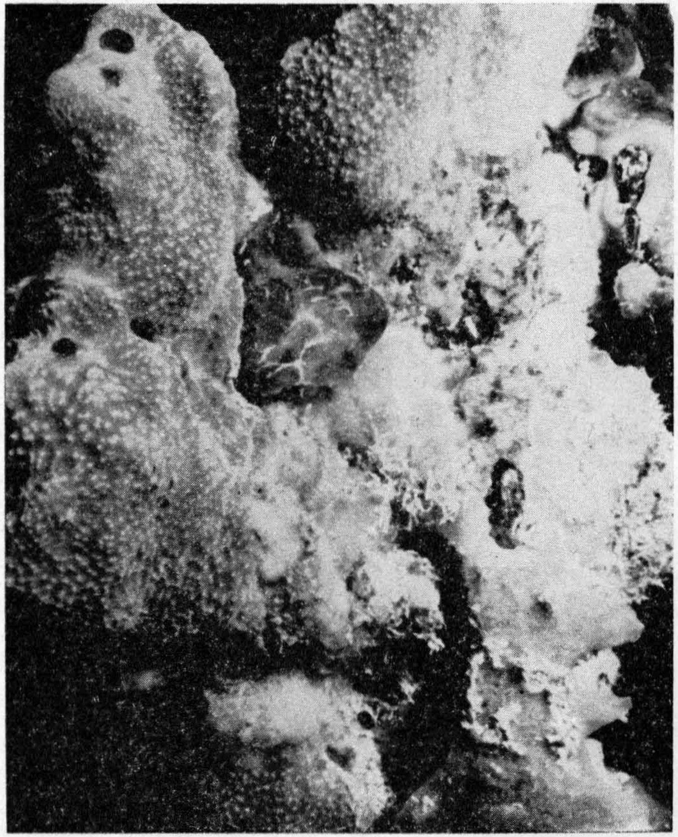

Figure 5. On the shaded backside of dominating *Ircinia fasciculata* four different species of sponges occur epizoicly.

The bottom of these channels is covered with a thin layer of mud containing shell fragments and diatoms, which is inhabited by a rich microfauna. The underlaying peat is rich in H_2S and organic carbon (Kornicker, 1958) and therefore poorly inhabited. In areas more exposed to tidal currents there are occasional stands of seagrass (*Thalassia, Cymodocea*) and green algae (*Penicillus, Caulerpa*).

The intertidal parts of stilt roots and seedings are covered with a thick layer of *bostrychietum* (figure 2). No oysters or barnacles are present in the Bimini mangrove. Just below low tide level, heavy clusters of sponges cover the stilt roots, down to the point where the bottom sediments set a limit. Dominant are the species *Tedania ignis, Ircinia fasciculata* and *Chondrilla nucula* (figures 3, 4). The only space competitors are the tunicate *Ecteinascidia turbinata,* some hydroids, mainly *Eudendrium* sp, and *Myrionema* sp, and the anemone *Condylactis* sp.

Behind a curtain of stilt roots the above mentioned mud-caves are located; there again, on the exposed mud-roots of *Rhizophora,* sponges dwell abundantly. The dominating species are *Anthosigmella varians, Myriastra* sp, and *Haliclona* sp.

Spacial Competition

The very restricted availability of substrate suggests studies on the spacial competition of sponges and other *sedentaria.* Earlier observations on isolated hard-bottom structures have shown (Rützler, 1965) that the lack of substrate can be overcome by certain species which are able to settle and survive on other species through specialized morphological and chemical adaptations. A comparable situation can be found on the mangrove roots where numerous small sponge crusts, hydroids, and some bryozoans grow on the dominant primary settlers. Also a horizontal zonation according to light can be observed, the epizoa preferring the semi-obscure surfaces which are faced toward the mud bank (figure 5).

Nothing is known yet about the effect of tannic acid and other chemical substances precipitated by the mangrove roots on the settlement of larvae. Other limiting factors are undoubtedly food supply and physical action of the tide current. The latter is naturally strongest in the undercuts. Sponges of a certain size originating there are frequently torn loose, leaving space for new successions. A study concentrating on these environmental factors and their biocoenotic consequences is currently under way with the aid of an instrument combination recently assembled (Forstner and Rützler, 1969). Main emphasis is given to long-term in situ measurements of micro-climatic factors (mainly light quality and quantity, water turbulences, temperature, salinity and oxygen), with the aim of identifying and arranging micro-environments according to their ecological significance.

Environmental Affinities

The question arises finally, to which other habitats the mangrove community can be related. In fact, there are four environment complexes superimposed.

The tree tops are strictly terrestrial, usually inhabited by the flora and fauna of a tropical rain forest. Lower branches and parts of the stem are comparable with the supra-littoral and pneumatophores, parts of the stilt roots and bases of tree stems with the medio-littoral of unexposed shaded rocky coasts. The mud flats are true marine medio-littoral soft bottom environments, which have been compared with the shoals of moderate latitudes, such as the North German "Wattenmeer" (Gerlach, 1958).

The channels and lagoons, even in the middle of the swamp, represent a marginal biotope. The muddy bottom with decomposing plant remains underneath and the composition of the sedentary organisms growing on plant structures as sole substrate indicate a close relationship to shallow seagrass meadows in open bays. The main difference is that the outflowing tide carries water masses which, for several hours, were subject to considerable temperature and salinity changes and to all the metabolic processes of the intertidal swamp community.

Conclusions

Plant systematists and sociologists have devoted much work to the mangrove community during the past decades. A great amount of data is also available on topographical, geological and economical aspects. Although the salinity ranges are wide the mangrove forest is restricted to the intertidal marine environment and sets the stage for the transition from marine to terrestrial life.

The large number of organic, inorganic, and behavioristic factors involved would justify an international monographic study in order to get away from the practice of presenting numerous valuable but uncorrelated single studies and to arrive at an ecological synthesis.

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