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MEIOFAUNA OF A MANGROVE SHORE ON THE WEST COAST OF PENINSULAR MALAYSIA

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ABSTRACT. - The meiofauna (size range 53 to 1000 μm) of the mangrove shore sediments in Malaysia consist predominantly of free-living nematodes, harpacticoid copepods, oligochaetes and kinorhynchs, increasing in abundance with decreasing tidal height where water stress is minimal. The highest density of 1109±27 individuals per 10 cm^{-2} occurred in the *Avicennia* station of the lower shore, while a density of 583±186 individuals per 10 cm^{-2} was obtained at the mid-tide level *Rhizophora* station, and the high shore *Bruguiera* station had the lowest density of 407±188 individuals per 10 cm^{-2}. The meiofaunal biomass was 6.16 mg, 7.54 mg and 0.96 mg w.w. per 10 cm^{-2} in the *Avicennia, Rhizophora* and *Bruguiera* stations respectively. The reduction in meiofauna numbers and biomass on the high shore is attributed to habitat instability arising from intense salinity fluctuations, infrequent tidal cover and water stress. The fauna was unevenly constituted with the nematodes forming 80 to 93% of the meiofauna community, and the harpacticoids being the next abundant group. Most meiofauna live in the upper 2 cm layer of the sediment. It may be concluded that the greatest abundance of meiofauna occurred in the lower shore *Avicennia* forest and the lowest abundance in the high shore *Bruguiera* forest.

INTRODUCTION

Few investigations have been attempted on meiofauna of tropical shores (Alongi, 1987c). These include the study of McIntyre (1968) on sandy beaches and an estuarine shore in South India and of Renaud-Mornant & Serene (1967) on beaches of quartz and coral sand in the east coast of peninsular Malaysia. Mangrove swamps or forests are typical of sheltered shores in the tropics. Investigations of faunal communities in mangrove swamps have been confined to the macrofauna (Macnae, 1968; Berry, 1972; Sasekumar, 1974; Frith *et al.*, 1976; Wells, 1983; Kurian, 1984). Meiofaunal studies in mangrove shores have been conducted recently in India (Kondalarao, 1983), tropical Australia (Alongi, 1987a; 1987b) and South Africa (Dye, 1983a; 1983b).

This study is primarily aimed at a description of the meiofauna community on a Malaysian mangrove shore. Data is presented in terms of annual density in relation to physical parameters of the substrate and of possible differences in forest types.

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STUDY AREA

Three stations were studied. Each station was characterised by a dominant stand of mangrove vegetation averaging 15 metres tall. Station 1 was the lower shore of the estuary of the Selangor River and forested by *Avicennia alba* and *Sonneratia alba* (Fig. 1). Station 2 was the *Rhizophora* forest situated about mid-tide level on the Puloh River. The station is 30 km south of Kuala Selangor (Fig. 1). Station 3 was on the high mangrove shore interior to station 1 (Fig. 2). Vegetation consisted of *Bruguiera parviflora* and *B. cylindrica*. In each of these stations samples were taken from permanent sample plots of 5 x 5 meters.

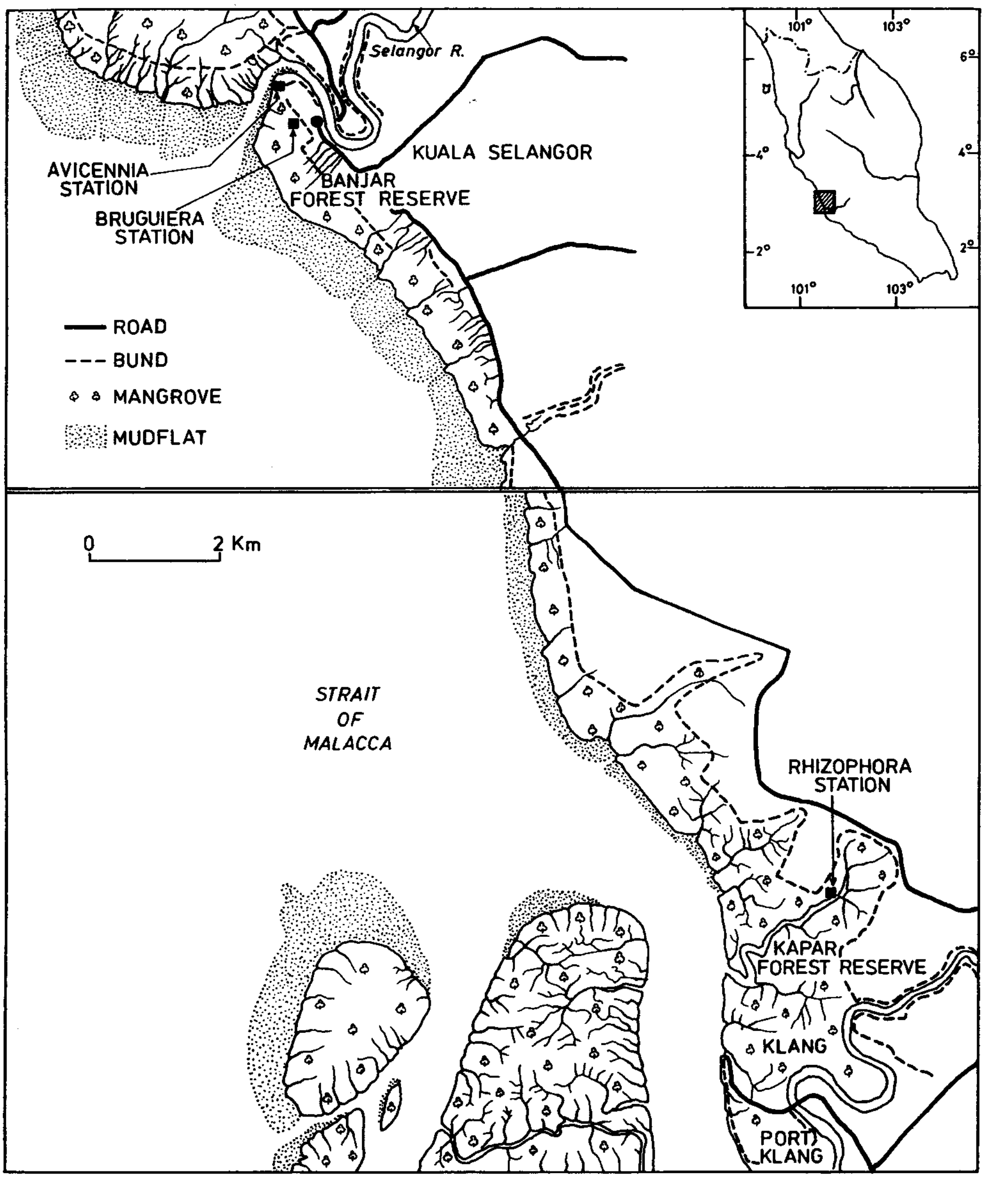

Fig. 1. Map of Selangor coast showing location of study sites.

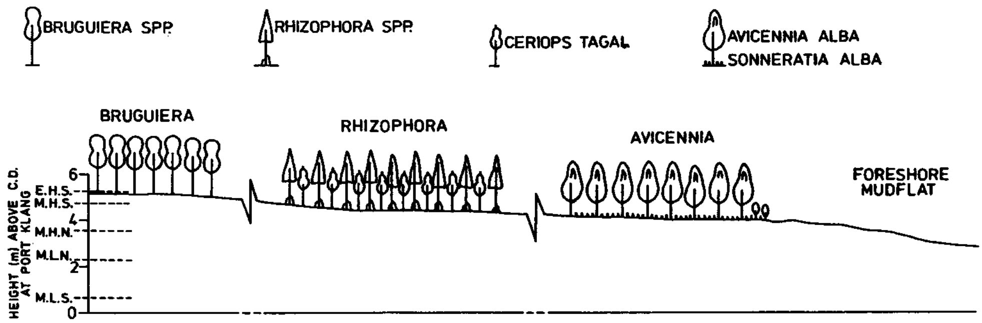

Fig. 2. The combined profile of the stations on shore showing the distribution of mangroves.

METHODS

A brass tube of 2 cm diameter, sharpened at one end to form a cutting edge was used to take samples. A cork piston was introduced into the lower end of the tube and the core extruded. Cores were sliced immediately at lengths 2 cm, 5 cm and 7 cm, placed separately in small polythene bags and deposited in a large thermos flask containing ice cubes. Four random core samples were taken at each station per visit. Samples were taken at monthly intervals for 12 months from August 1971 to July 1972. Additional cores were taken for interstitial water content, sediment granulometric analysis and organic carbon content. In sampling, tree roots, crab holes or mounds were deliberately avoided so as to sample an area as homogeneous as possible in the sample plot.

In the laboratory, Rose Bengal solution (1 gm in 1 litre of filtered sea water) was poured into each polythene bag and thoroughly mixed. The samples were stored in a deep freeze and sorted subsequently. Such storage may have contributed to loss of soft-bodied animals like turbellarians. For separation, samples were poured through a 1000 μm sieve and organisms that were retained by the 105μm and 53μm sieves were considered meiofauna. The material remaining on the sieves was diluted onto several petri dishes and the meiofauna picked up with a pair of fine forceps under a binocular microscope. The petri dish was placed on a checkered black movable base for greater searching efficiency. Extraction efficiency was 85% for nematodes and 95-100% for harpacticoids.

Variance ratios of faunal counts of the first four random samples taken at the first sampling were not significant at the 5% level (F test). Hence the samples were homogeneous and all samples in each station then and subsequently were drawn from the same parent population.

pH was determined using a glass calomel electrode, while Eh was determined using a Beckman 39273 platinum electrode. Hydrogen sulphide was detected using Model HS-6 Test Kit (Hach Chemical Co.). Interstitial water content was determined for 0-2, 2-5, 5-7 and 7-10 cm segments of two core samples. Samples were dried in an oven at 105°C to constant weight. Wet weight minus dry weight was interpreted as an estimate of the interstitial water. Mechanical analysis of the top 5 cm soil and an estimate of organic carbon was obtained on ignition at 600°C of oven dried soil (Buchanan & Kain, 1971).

Wet weights of meiofauna (excluding nematodes) were assessed by weighing 100 representative specimens of each group on a microbalance after the excess moisture was blotted. Wet weights of nematodes were calculated following Weiser (1960).

RESULTS

Environmental data

Calculated tidal data indicates that the lower shore *Avicennia* station was exposed to the air for 84% and the landward edge *Bruguiera* station for 99% of the time. The pH of the soil water in the stations varied only within a narrow range of 6.4±0.2 to 6.7±0.4 (Table 1). The redox potential of the water puddles on the soil surface showed negative values and varied from -104±60 to -144±115 mv. The few measurements of these surface water puddles indicated the presence of hydrogen sulphide, but in very small amounts (Table 1).

Salinity measurements were confined to stagnant pools since in most cases water did not collect in core holes because of high clay content. Surface water salinity in the *Avicennia* station showed marked fluctuations ranging from 13.9 o/oo to 36.4 ‰ while in the *Rhizophora* and *Bruguiera* stations they ranged 24 to 36 ‰ and 11.2 to 40.7 ‰ respectively (Table 1).

Table 1. Summary of environmental data in the three stations of the mangrove shore in Selangor. Each value is the mean of 4 or more replicate measurements taken through Aug. 1971 to July 1972. Ranges given in parentheses.

Stations Variable	*Avicennia*	*Rhizophora*	*Bruguiera*
1. Air temp. °C	29.6 (29-31)	29.5 (29-30)	30.1 (28-31)
2. Water in stagnant pools			
a. Temp. °C	27.8 (27-30)	26.7 (26-27.5)	27.2 (26-28.5)
b. pH	6.7 (6.4-7.4)	6.4 (6.1-6.7)	6.7 (6.4-7.0)
c. Eh (mv)	-144 (-50 to -300)	-104 (-20 to -160)	-109 (-45 to -160)
d. H2S (ppm)	0.18 (0.02-0.4)	0.006 (0.0-0.02)	0.06 (0.0-0.12)
e. Salinity (ppt)	28.0 (13.9-36.4)	30.5 (24-36.3)	29.5 (11.2-40.7)
3. Core hole water salinity (ppt)	-	34.6 (31.6-37.4)	28.4 (13.8-38.5)

The substrate in the *Bruguiera* and *Avicennia* stations in Kuala Selangor consisted exclusively of silt and clay (Fig. 3). The substrate in the *Rhizophora* station is coarse and included fine sand fractions (105-210 μm). The surface sediments in the *Avicennia* and *Bruguiera* stations retained greater amounts of water than the *Rhizophora* station. There was significant decrease in the interstitial water content with depth in the *Avicennia* and *Bruguiera* stations, while in the *Rhizophora* station there was no significant difference with depth. The sediment in the former two stations contained more than 85% silt and clay, and was stiff and compact below 2 cm depth indicative of poor porosity.

The surface soil in the *Avicennia* station had a mean organic carbon content of 12%, while the *Rhizophora* and *Bruguiera* stations had values of 21.8% and 18.3% respectively. The lower value of the *Avicennia* station is not surprising since much of the leaf litter is washed away by daily tidal inundation. Infrequent tidal wettings aid the retention of litter in the other two stations since several days or weeks are available for its decomposition and incorporation in the sediment.

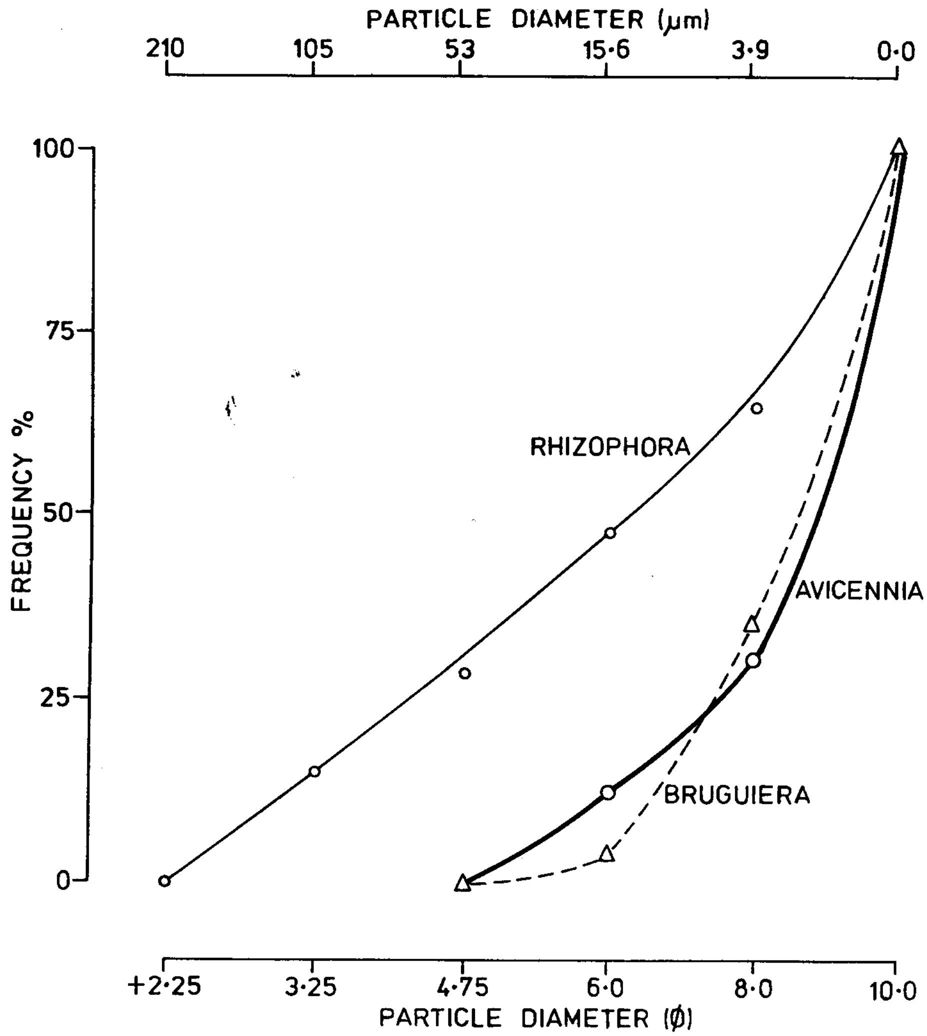

Fig. 3. Cumulative curves for the sediment granulometric analysis data of the three stations.

Metazoan meiofauna

The metazoan meiofauna consisted mainly of nematodes, harpacticoid copepods, oligochaetes and kinorhynchs (Table 2). The nematodes constituted more than 80% of the meiofauna in all stations. Harpacticoids were second in overall abundance. A kinorhynch, *Echinoderes* sp. made up 5% of the meiofauna in the *Avicennia* station and occurred in small numbers in the *Rhizophora* station but was absent in the *Bruguiera* station. Other meiofauna encountered in small numbers included halarcarid mites, turbellarians, small polychaetes, juvenile sipunculids and juvenile bivalves. These constituted less than 1% of the meiofauna.

Nematodes

There were significant ($P < 0.001$) differences in the density of nematodes between the stations (Table 2). The *Avicennia* station contained the largest number of species (51),

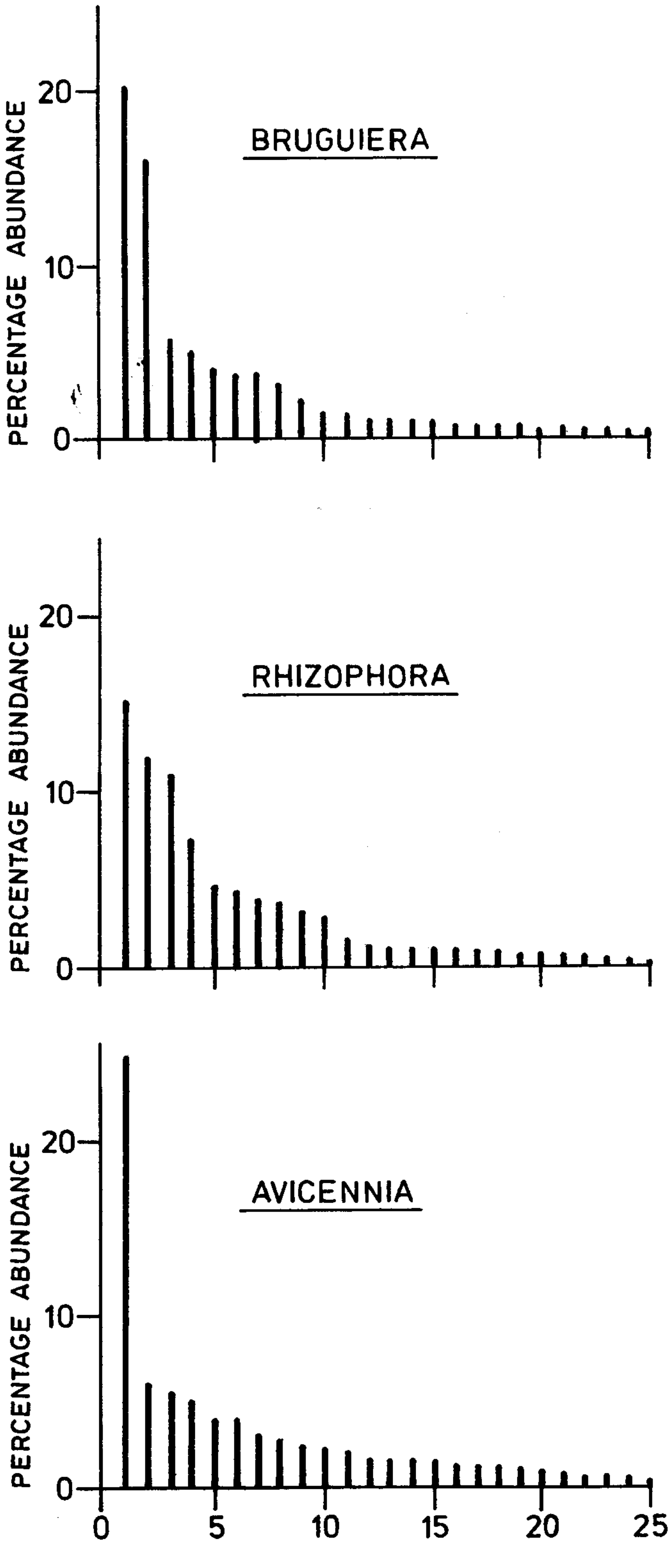

Fig. 4. Average composition of the 25 most abundant nematode species in the three stations. Each line indicates percentage abundance of one species in the total nematode population.

Table 2. Composition of the metazoan meiofauna in stations.

Stations	Avicennia A	Avicennia B	Rhizophora A	Rhizophora B	Bruguiera A	Bruguiera B
Fauna						
Nematodes	885.1±226.5	79.9%	543.6±175.5	93.1%	347.2±151.2	85.3%
Harpacticoids	147.2±45.7	13.3	27.4±12.3	4.7	43.3±38.3	10.6
Oligochaetes	11.6±7.0	1.0	8.0±4.8	1.4	15.4±11.0	3.8
Kinorhynch	56.6±26.1	5.1	2.4±2.2	0.4	-	-
Others	8.8±5.8	0.8	1.9±1.3	0.3	1.1±0.5	0.3
Total	1109.3±27		583.3±186		407.0±188	

Column A = Mean annual density (numbers 10 cm-2).
Column B = Percentage abundance

Bruguiera had more than 40 species, with *Rhizophora* containing the lowest number (29) (Tables 3, 4 and 5). Unidentified nematodes constituted 9.9%, 19.1% and 17.8% of the total nematodes sampled in the *Avicennia*, *Rhizophora* and *Bruguiera* stations respectively. Seven nematode species occurred in all three stations. These were *Terschellingia longicaudata*, *Ptycholaimellus* sp., *Spirinia* sp., *Sabateria* sp., Desmoscolecidae sp. 1, *Dolicholaimus* sp. and *Sphaerolaimus* sp. 4. An analysis of the species composition of the 25 most abundant species in each station is shown in Fig. 4. The *Avicennia* station was dominated by *Ptycholaimellus* with an abundance of 25.1%. The *Rhizophora* station was dominated by three, namely Siphonolaimidae sp. 1 (15.2%), Siphonolaimidae sp. 2 (12%) and *Terschellingia longicaudata*. The *Bruguiera* station had two species with high dominance namely, *Terschellingia longicaudata* (20.4%) and *Ptycholaimellus* sp. (16.2%).

Harpacticoid copepods

Twenty five species of harpacticoids were collected from the three stations. They occurred in high densities in the *Avicennia* station with a mean annual density of 147.2 individuals per 10 cm^{-2} and low densities in the *Rhizophora* station with a mean annual density of 28.0 individuals per 10 cm^{-2}. The densities of harpacticoids in the landward *Bruguiera* station were higher than at the *Rhizophora* station with a mean annual density of 43.3 individuals per 10 cm^{-2} (Table 2).

Kinorhynch

There is a distinct zonation of the *Echinoderes* sp. in the mangrove shore. It is most abundant in the *Avicennia* station while its occurrence declines towards the high shore. The mean annual density of the species in the *Avicennia* station was 56.7 individuals per 10 cm^{-2}, while the maximum density recorded was 104 per 10 cm^{-2}.

Oligochaetes

Their importance as components of the meiofauna increased towards the high shore (Table 4).

Table 3. Total numbers, percentage abundance, frequency and feeding type of nematode species at *Avicennia* station. Frequency refers to the number of samples in which a species was found based on 48 samples. Feeding types based on scheme of Wieser (1959).

	Species	Numbers	% abundance	Frequency in 48 samples	Feeding type
1.	*Ptycholaimellus* sp.	3428	25.1	48	2A
2.	*Sabateria* sp.	874	6.4	48	1B
3.	Chromadoridae sp. 1	785	5.7	48	2A
4.	*Spilophorella longicaudata*	693	5.1	46	2A
5.	*Spirinia* sp.	555	4.0	46	2A
6.	*Theristus* sp. 1	552	4.0	42	1B
7.	Sp. A 1	430	3.1	47	2A
8.	Sp. A 2	369	2.7	45	1A
9.	*Theristus* spp.	328	2.4	-	1B
10.	*Theristus* sp. 2	313	2.3	38	1B
11.	*Oncholaimus* sp. 1	293	2.1	38	2B
12.	Desmoscolecidae sp. 1	235	1.7	43	1A
13.	*Terschellingia longicaudata*	234	1.7	37	1A
14.	Chromadoridae sp. 2	234	1.7	34	2A
15.	Eurystominidae sp. 1	221	1.6	40	2B
16.	Chromadoridae sp. 3	207	1.5	37	2A
17.	*Sphaerolaimus* sp. 1	174	1.3	42	2B
18.	Chromadoridae spp.	172	1.3	-	2A
19.	Sp. A 3	163	1.2	31	2A
20.	Sp. A 4	160	1.2	38	2A
21.	Sp. A 5	142	1.0	38	1A
22.	*Sphaerolaimus* sp. 3	130	0.9	32	2B
23.	*Dolicholaimus* sp.	118	0.8	38	2B
24.	Sp. A 6	110	0.8	33	2B
25.	*Sphaerolaimus* sp. 4	108	0.8	36	2B
26.	Sp. A 7	99	0.7	28	2B
27.	*Sphaerolaimus* sp. 5	97	0.7	32	2B
28.	Chromadoridae sp. 4	96	0.7	36	2A
29.	*Oncholaimus* spp.	92	0.7	-	2B
30.	Sp. A 8	88	0.6	19	1A
31.	*Sphaerolaimus* sp. 2	86	0.6	32	2B
32.	*Sphaerolaimus* spp.	80	0.6	-	2B
33.	Sp. A 9	75	0.5	25	1A
34.	Chromadoridae sp. 5	73	0.5	17	2A
35.	*Oncholaimus* sp. 2	57	0.4	10	2B
36.	*Sphaerolaimus* sp. 6	54	0.4	22	2B
37.	*Oncholaimus* sp. 3	53	0.4	17	2B
38.	Eurystominidae sp. 2	51	0.4	14	2B
39.	Sp. A 10	39	0.3	15	1A
40.	Sp. A 11	34	0.2	18	1B
41.	Sp. A 12	33	0.2	15	1A
42.	Sp. A 13	27	0.2	17	1B
43.	*Theristus* sp. 5	23	0.2	12	1B
44.	*Sphaerolaimus* sp. 7	22	0.2	12	2B
45.	Sp. A 14	19	0.1	8	1B
46.	Dorylaimidae sp. 1	17	0.1	11	2A
47.	Sp. A 15	14	0.1	12	1A
48.	Sp. A 16	11	0.1	7	2B
49.	*Halichoanolaimus* sp.	11	0.1	8	2B
50.	*Cinctonema* sp. 1	10	0.1	2	2A
51.	Sp. A 17	6	0.04	3	1A
	Unidentified nematodes	1356	9.9	-	
TOTAL NUMBER OF SPECIMENS		13651			

Meiofauna biomass

The *Rhizophora* station had the greatest biomass with a value of 7.54 mg per 10 cm^{-2} (Table 6). The *Avicennia* station which had the largest number of meiofauna had a smaller biomass. The greater biomass of the *Rhizophora* station is due to the presence of larger species of nematodes such as Siphonolaimidae sp. 1.

Between 72 to 92% of the meiofauna biomass in the mangrove shore is contributed by nematodes. The harpacticoids contributed 17% of the biomass in the *Avicennia* station while their biomass in the high shore was much less.

Table 4. Total numbers, percentage abundance, frequency and feeding types of nematodes at *Rhizophora* station. Frequency refers to the number of samples in which a species was found based on 48 samples. Feeding types based on scheme of Wieser (1959).

	Species	Numbers	% abundance	Frequency in 48 samples	Feeding type
1.	Siphonolaimidae sp. 1	1247	15.2	46	1A
2.	Siphonolaimidae sp. 2	981	12.0	43	1A
3.	*Terschellingia longicaudata*	923	11.2	48	1A
4.	Eurystominidae sp. 1	619	7.5	48	2B
5.	*Ptycholaimellus* sp.	406	4.9	48	2A
6.	Sp. R 3	337	4.1	43	1A
7.	*Spirinia* sp.	299	3.6	28	2A
8.	Sp. R 4	269	3.3	46	1B
9.	*Dolicholaimus* sp.	262	3.2	45	2B
10.	*Sabateria* sp.	167	2.0	40	1B
11.	Sp. R 5	126	1.5	34	1A
12.	Chromadoridae spp.	177	1.4	-	2A
13.	*Sphaerolaimus* sp. 10	100	1.2	32	2B
14.	*Oncholaimus* spp.	94	1.1	28	2B
15.	*Theristus* spp.	83	1.0	-	1B
16.	Sp. R 6	78	0.9	27	1A
17.	*Sphaerolaimus* sp. 4	72	0.9	30	2B
18.	*Sphaerolaimus* spp.	70	0.8	-	2B
19.	Eurystominidae sp. 2	61	0.7	22	2B
20.	Sp. R 7	61	0.7	30	2B
21.	*Sphaerolaimus* sp. 11	60	0.7	14	2B
22.	Desmoscolecidae sp. 1	58	0.7	24	1A
23.	Sp. R 8	49	0.6	27	1A
24.	Sp. R 9	43	0.5	20	1A
25.	Sp. R 10	16	0.2	7	1A
26.	Sp. R 11	14	0.2	10	2A
27.	*Sphaerolaimus* sp. 5	11	0.1	5	2B
28.	Sp. R 12	7	0.1	5	1B
29.	*Sphaerolaimus* sp. 1	4	0.1	4	2B
30.	Unidentified nematodes	1568	19.1	-	-
TOTAL NUMBER OF SPECIMENS		8202			

Table 5. Total numbers, percentage abundance, frequency and feeding types of nematodes at *Bruguiera* station. Frequency refers to the number of samples in which a species was found based on 48 samples. Feeding types based on scheme of Wieser (1959).

	Species	Numbers	% abundance	Frequency in 48 samples	Feeding type
1.	*Terschellingia longicaudata*	1068	20.4	45	1A
2.	*Ptycholaimellus* sp.	847	16.2	48	2A
3.	Chromadoridae sp. 6	314	6.0	38	2A
4.	*Sabateria* sp.	275	5.2	42	1B
5.	*Dolicholaimus* sp.	218	4.2	47	2B
6.	*Theristus* spp.	201	3.8	-	1B
7.	Sp. B 1	200	3.8	27	1B
8.	Sp. B 2	167	3.2	31	2A
9.	Sp. B 3	126	2.4	30	1A
10.	Sp. B 4	82	1.6	34	2A
11.	Sp. B 5	77	1.5	23	1A
12.	Sp. B 6	75	1.4	35	1B
13.	Sp. B 7	73	1.4	21	2A
14.	Sp. B 8	51	1.0	8	2A
15.	*Sphaerolaimus* sp. 9	49	0.9	20	2B
16.	Sp. B 9	47	0.9	13	1A
17.	Sp. B 10	45	0.9	20	1A
18.	Sp. B 11	40	0.8	3	1A
19.	Spirinia sp.	40	0.8	14	2A
20.	Sp. B 12	31	0.6	14	1A
21.	Sp. B 13	30	0.6	4	1A
22.	*Sphaerolaimus* sp. 12	24	0.5	11	2B
23.	*Sphaerolaimus* spp.	24	0.5	-	2B
24.	Dorylaimidae spp.	22	0.4	-	2B
25.	*Cinctonema* sp. 1	22	0.4	7	2A
26.	*Sphaerolaimus* sp. 4	21	0.4	14	2B
27.	*Oncholaimus* spp.	20	0.4	-	2B
28.	Ironidae sp. 1	16	0.2	12	2B
29.	*Sphaerolaimus* sp. 8	15	0.2	12	2B
30.	Sp. B 14	13	0.2	13	2A
31.	*Sphaerolaimus* sp. 2	12	0.2	8	2B
32.	Sp. B 15	11	0.2	4	1A
33.	Desmoscolecidae sp. 1	11	0.2	7	1A
34.	Sp. B 16	9	0.2	5	2A
35.	Chromadoridae sp. 7	7	0.1	-	2A
36.	*Paracanthonchus* sp.	6	0.1	2	2A
37.	Sp. B 17	5	0.1	1	2B
38.	Sp.B 18	4	0.1	3	2A
39.	Sp. B 19	4	0.1	1	1B
40.	*Halichoanolaimus* sp.	3	0.1	3	2B
41.	Unidentified nematodes	936	17.8	-	-
TOTAL NUMBER OF SPECIMENS		5241			

Table 6. Biomass of mangrove meiofauna. Units are mg (wet weight) per 10 cm-2 based on meiofauna weights in eight cores (2 cm diameter) in each station.

	Nematodes	Copepods	Oligochaetes	Others	Total
Avicennia (above M.H.W. Neaps)	4.44	1.06	0.24	0.41	6.16
Rhizophora (below M.H.W. Springs)	7.22	0.17	0.13	0.02	7.54
Bruguiera (extreme H.W. Springs)	0.79	0.08	0.09	-	0.96

DISCUSSION

There was a general decline in the densities of meiofauna with increase in tidal height on the mangrove shore (Table 2). Highest densities of 1109±27 were found in the *Avicennia* station and their densities declined to 583.3±186 in the *Rhizophora* station. Lowest densities of 407±188 occurred in the high shore *Bruguiera* station. Densities of meiofauna recorded in this study were similar to those recorded in the mangrove estuaries of tropical eastern Australia (Alongi, 1987c). In general it may be concluded that tropical intertidal mud substrates (exemplified in this study) does not support high population densities of meiofauna as found in temperate mud substrates (Rees, 1940; Capstick, 1959; Weiser & Kanwisher, 1961; Teal & Weiser, 1966; Barnett, 1968).

Meiofauna community structure

The few studies on meiofauna communities in tropical sandy shores indicate that they support a rich variety of meiofauna, consisting of several groups (McIntyre, 1968; Renaud-Mornant & Serene, 1967). The former found densities of 968-1960 individuals per 10 cm^{-2} consisting of nematodes, harpacticoids, turbellarians, gastrotriches and ten other groups in well-sorted sand (Md: 220-240 μm). The latter in their brief survey of five stations on the east coast of Peninsular Malaysia recorded the richest samples (10212 meiofauna per 10 cm^{-2}) on estuarine sand (Md: 185 μm) consisting of nematodes, harpacticoids, tardigrades, polychaetes and turbellarians. The most impoverished fauna of 288 individuals per 10 cm^{-2} was found in coral sand (Md: 770 μm), however it supported a greater variety of fauna made up of nine groups (Renaud-Mornant & Serene, 1967).

In contrast, meiofauna communities in these mangrove shores consist exclusively of nematodes, harpacticoids, kinorhynch and oligochaetes (Alongi, 1989). The striking differences in the meiofauna community structure of sandy and muddy shores can be explained in terms of the greater availability of space in the interstices of sand substrates. In mud substrates with a great amount of silt and clay (*Avicennia* and *Bruguiera* stations), the meiofauna is able to colonize only the top two centimeters. The majority of the meiofauna do not penetrate the deeper layers of the mud. In sandy shores, the meiofauna is able to utilize a greater variety of niches, thus achieving considerable diversity in terms of taxa, species and trophic levels. Sandy environments provide a wider scope for specialization in feeding on attached material due to the availability of a range of particle sizes and a variety of recent biogenic material such as fragments of mollusc shells (McIntyre & Murison, 1973; Anderson & Meadows, 1978; Coull & Bell, 1979).

Biomass

Few studies on tropical intertidal meiofauna give biomass data. In the present study, maximum meiofauna biomass was recorded in the *Rhizophora* station though higher meiofaunal numbers were recorded in the *Avicennia* station (Tables 2 and 6). The slightly lower biomass of the *Avicennia* station probably reflects the small size of the common nematode species. The nematode biomass data obtained in the present study for the *Rhizophora* station (about mid-tide level) and *Bruguiera* station (above high tide level) are comparable to those obtained by Teal & Wieser (1966) for a salt marsh, where the values were 7.6 mg per 10 cm^{-2} and 0.2-0.6 mg per 10 cm^{-2} respectively for similar tide levels.

Spatial distribution of meiofauna on mangrove shore

There was significant quantitative differences between the meiofauna of the three stations (Table 2). This difference in densities of nematodes as well as other groups is attributed to the differences in the physical environment of the three stations. The *Avicennia* station near Mean High Water Neaps is inundated by tides more often than the other two stations higher up the shore. The stations higher up the shore experience varying degrees of terrestrial conditions for long periods in the absence of tidal cover. In the extreme case, *Bruguiera* station was only submerged by tides eleven times in the year with a maximum interval of 133 days between tidal wettings. Thus the station had an impoverished meiofaunal community with a mean annual density of 407 meiofauna per 10 cm^{-2}, and resembles the Supralittoral zone of the Brazilian mangrove shore characterised by *Hibiscus tiliaceus* where the meiofauna was also poor (Gerlach, 1958). This study confirms that meiofauna densities are highest in the low intertidal zone in the mangrove shore (Hodda & Nicholas, 1985; Alongi, 1987c).

Rainfall may have considerable effect on soil water salinities during neap tidal periods. Such a situation occurred during September 1971 when a salinity of 11 ‰ was recorded in the *Bruguiera* station (Table 1). However, depressed salinities do not persist for more than several hours. Diffusion of salts from the subsoil normalises the salinity of the top soil where most of the meiofauna live. Meiofauna could avoid low salinities by burrowing deeper into the anoxic soil where normal saline conditions prevail. Conversely, during short dry spells, soil surface salinities rise due to evaporation. Such a situation was recorded in March 1972. Further, the water content of the sediment surface may be reduced during dry spells as a result of intense evaporation. Thus during May 1972 the water content of the surface was appreciably reduced to a low minimum of 55.2%. This is probably an additional stress factor in high shore mud substrates. The effect of monsoonal rains on intertidal meiobenthos in mangrove estuaries has been reviewed by Alongi (1987c). In general, there was an increase from low to high tide level stations in the degree of instability and severity of the environmental conditions (e.g. salinity and soil water content). Tannins derived from mangrove litter have been found to have negative effect on meiofaunal abundance (Alongi, 1987b). Predation and disturbance by deposit feeders like crabs and gastropods may partly explain lower meiofauna numbers in tropical and substrates (Dye & Lasiak, 1986).

Vertical distribution of meiofauna

In the *Avicennia* and *Bruguiera* stations almost all the meiofauna was found in the 0-2 cm layer of the sediment. About 2.7% to 19% of the meiofauna were recorded in the 2-5 cm layer of the sediment and this comprised mostly of nematodes. A greater number of meiofauna occurred in the 2-5 layer of the sediment in the *Rhizophora* station than in the other two stations. Meiofauna living in this layer accounted for between 12.6 to 28.2% of the total meiofauna and consisted exclusively of nematodes.

Most workers have observed the decline in numbers of meiofauna with increasing depth in both mud and sand substrates. This subject was discussed in considerable detail by Tietjen (1969) and McLachlan (1978). The former discussed the possible causes for this decline and cited the following factors: (i) vertical pH changes, (ii) vertical decreases in oxygen, (iii) vertical decreases in interstitial water content, (iv) vertical differences in organic matter. In the present study, no attempt was made to measure vertical differences in pH or O_2. However, in poorly sorted mangrove sediments (with as much as 50-90% silt and clay) it can be assumed that there is total absence of oxygen less than two centimeters below on the basis of information available from fine sandy substrates (Brafield, 1972). The reducing conditions indicated by low Eh values and the presence of H_2S (Table 1) suggests low availability of free oxygen. The oxidation of organic matter by anaerobic bacteria is the primary cause of reducing conditions (Fenchel, 1969). However, the activity of the many burrowing animals in the mangrove shore may play a role in the oxidation of the sediments. An oxidized microzone is always visible around the burrows of crabs and sipunculids. The effect of this is probably limited to the immediately vicinity of the burrows.

In the study sites of *Avicennia* and *Bruguiera* stations crab burrows were present, but in sampling for meiofauna these were intentionally avoided so as to obtain homogeneous samples. Crab burrows were more common in the *Rhizophora* station. There are indications that less reducing conditions prevail in this sediment than in the other two stations. H_2S was hardly detectable in the sediment (Table 1). This situation is possibly aided by the presence of a large number of crab burrows and the coarse granulometry of the sediment.

There were significant decreases in the interstitial water content of the sediment with depth in the *Avicennia* and *Bruguiera* stations. The effects of decreased water content probably affect the oxygen content and living space of the sediment (Tietjen, 1969). There was no significant difference in the interstitial water content with depth in the *Rhizophora* station. This is brought about by the porous nature of the soil (Md: 12.5 (m) and the presence of crab burrows.

The final factor causing the decline in the numbers of meiofauna with depth is the availability of food. Benthic diatoms and other algae grow on the mud surface (Estrada *et al.*, 1974), and these are consumed by epigrowth and omnivorous nematodes and harpacticoids.

The most important factors restricting the meiofaunal colonization of deeper layers of mangrove sediments (e.g. *Avicennia* and *Bruguiera* stations) is the lack of space caused by the compacted clayey nature of the sediment (result of reduced water content) and the concomitant absence of free oxygen. In the *Rhizophora* station more meiofauna lived in the deeper layers (2-5 cm) of the sediment because of the favourable conditions provided by the high interstitial water content and porous nature of the soil.

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