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Soft-bottom fauna with emphasis on nematode assemblage structure in a tropical intertidal lagoon in Zanzibar, eastern Africa: I. spatial variability

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Abstract

Twenty stations were sampled in a reef-protected lagoon on the east coast of Zanzibar from a variety of habitats: seagrass beds, fine sand, bare medium sand and coarse sand. Total meiofauna densities ranged from 219 to 3422 ind./10 cm^2. Stations in the upper lagoon (< 400 m from shore) had relatively higher densities of meiofauna than those of other habitats, apart from seagrass beds. Of the 12 major taxa recorded, Nematoda normally was the most abundant taxon, contributing between 13% and 97% of total fauna, followed by Harpacticoida, Polychaeta and Turbellaria. Nematodes were dominated by epistrate feeders in all habitat-types and altogether 100 nematode genera were found within the lagoon. Clear nematode assemblage structures were depicted by non-metric multidimensional scaling ordination in seagrass bed, fine sand and coarse sand habitats. On a larger scale, sediment characteristics seem to determine the gross assemblage structure. Samples from the same station were more similar in terms of generic occurrence and population structure than samples from different stations in similar habitats. This indicates that there are localised factors influencing the nematode populations on a small scale in each habitat-type.

Introduction

Populations of living organisms in nature are generally heterogeneously distributed. Aggregations may occur at scales from a few millimetres to many kilometres, but the causes of such patchy distribution are not always clear. Differences in physico-chemical properties such as temperature, depth, mean grain size, water currents, salinity, food and oxygen tension are known to be associated with differences in density of marine benthic populations between localities (see reviews by Hicks & Coull, 1983; Heip et al., 1985; Decho et al., 1985; Giere, 1993). Physical attributes are also known to exhibit small-scale variations. Hogue & Miller (1981) found, for example, that sediment microtopography accounted for the difference in nematode populations in an intertidal sand-flat. However, many of these factors operate in different ways and the intensity of the effect they exert on the benthic animal populations largely depend on local circumstances. In intertidal regions, meiofauna numbers are known to vary greatly as they are influenced by many biotic and abiotic factors. Salinity and moisture or pore water content in these regions can vary much between seasons and on a diel basis as a result of dilutions during rainfall and day-time evaporation, which is accompanied by high temperature variations during ebb and in windy conditions (Jansson, 1967). Sediment granulometry is mainly influenced by physical factors but macrofaunal bioturbation and disturbance due to feeding and locomotion can modify sediment structure giving rise to a patchy distribution of meiobenthos. For instance, enhancement of meiofauna may occur in microhabitats, e.g. near tube or burrows (Reise & Ax, 1979), in faecal casts (Warwick et al.,1986), and a reduction in feeding or disturbance areas (Warwick et al., 1986; Palmer, 1988; Ólafsson et al., 1990). Hodda (1990) compared the variation of estuarine littoral nematode populations over three spatial scales i.e. cm, tens of m and hundreds of km, and found

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that the variations in the nematode population arose from several sources and estimated that about a third of the variance originated from small-scale variation in conditions. Similarly, Li et al. (1997) found that over 40% of the nematode diversity variance could be explained at cm scales, when comparing meiobenthic variations in North Sea estuaries.

Although the intertidal meiofauna of marine beaches and lagoons has been studied at many latitudes and localities (e.g. see Heip et al., 1985; Coull, 1988 for review), the coverage of some geographic regions has not been extensive. This is particularly true for the tropics. Alongi (1986) studied different functional zones in the Great Barrier Reef, Australia, and found that nematode community structure from the reef crest to the shallow lagoon appeared to be determined by sediment granulometry. Several authors have found significant differences in meiofaunal densities between sediment-types in tropical habitats and have recorded highest numbers of meiofauna in fine sands (see Alongi, 1989b for review; Grelet et al., 1987; Gourbault et al., 1995; Boucher,1997; Gómez Noguera & Hendrickx, 1997). The western Indian Ocean region which includes the coast of eastern Africa has received little coverage in meiobenthic research. The east African coast supports extensive intertidal lagoon flats composed mainly of carbonate sand and in Zanzibar these account for approximately 90% of the total coastal area. In tropical Africa, only two studies conducted in lagoons away from mangroves have so far been published, one on the effects of extensive seaweed farming on meiobenthos (Ólafsson et al., 1995) and the second on selection of meiobenthic prey by *Gerres oyena* (Ndaro & Ólafsson, 1995). The purpose of this study was to quantify the meiofauna in the intertidal lagoon, and to find out which factors influence their distribution, with special emphasis on nematode assemblages. In this paper, we report on the spatial distribution of meiobenthos of a shallow lagoon on the east coast of Zanzibar while a later contribution describes their seasonal variation over a period of two years.

Materials and methods

Study area

The study site, Paje (06° 16′ S, 30° 32′ E) is illustrated in Figure 1. The intertidal lagoon is shallow (< 5 m deep at spring high tide), characterised mostly by medium and fine, poorly sorted coral sands (with occasional pockets of coarse sands, especially close to the reef) and is protected from severe surf and waves by a fringing reef roughly 2 km from shore. Tides are semi-diurnal with the tidal range reaching over 4 m. The hydrodynamic conditions during the investigation period were as follows: water temperature ranged from 30°C to 37°C and salinity ranged from 14 psu to 32 psu.

Field studies

Four transects of 5 stations each were located approximately 500 m apart, and sampled during spring low tide in January 1994. Stations were chosen to represent the main habitats across the lagoon i.e. fine sands, seagrass beds, bare sands and coarse sands (see Figure 1). At each station, a quadrat of 1 m^2 was randomly (person blindfolded and the quadrat thrown into the area) located within an area of ca 50 m^2 and samples retrieved as follows: one 5 cm deep core (9.6 cm^2 area)was pushed into the sediment at a fixed position within a quadrat frame for meiofauna sample and left in position. Adjacent to the meiofauna core, two smaller cores (4 cm^2) were taken for chlorophyll *a* extraction. These were immediately combined and mixed with an equal volume of 90% acetone in a vial and wrapped with aluminium foil. Within the same quadrat position cores (9.6 cm^2) for organic content and mean grain size determination were taken and finally the core for meiofauna was retrieved and fixed with 8% formalin. Within the frame, a hole was dug to the ground water level (when water was absent on the surface) and salinity measured with a refractometer and temperature with a thermometer. At each station, the whole procedure was repeated five times.

In the laboratory, animal samples were washed through 500 and 40 μm sieves and the meiofauna extracted from the 40 μm sediment fraction using Ludox colloidal silica at a specific gravity 1.15 (Platt & Warwick, 1983). Macrofauna animals retained on the 500 μm sieve were sorted out, counted and identified to major taxa. Meiofaunal higher taxa were identified and counted under a dissecting microscope. From each meiofauna sample approximately 100 nematodes were transferred to glycerine and mounted on slides for genus identification under a high power stereo-microscope using the pictorial keys of Platt & Warwick (1983). We were unable to correctly assign to genus level all animals within the genera *Chromaspirinia* and *Spirinia*, so these were taken together in one group. Nematodes were assigned to trophic groups according to the scheme of Wieser (1953).

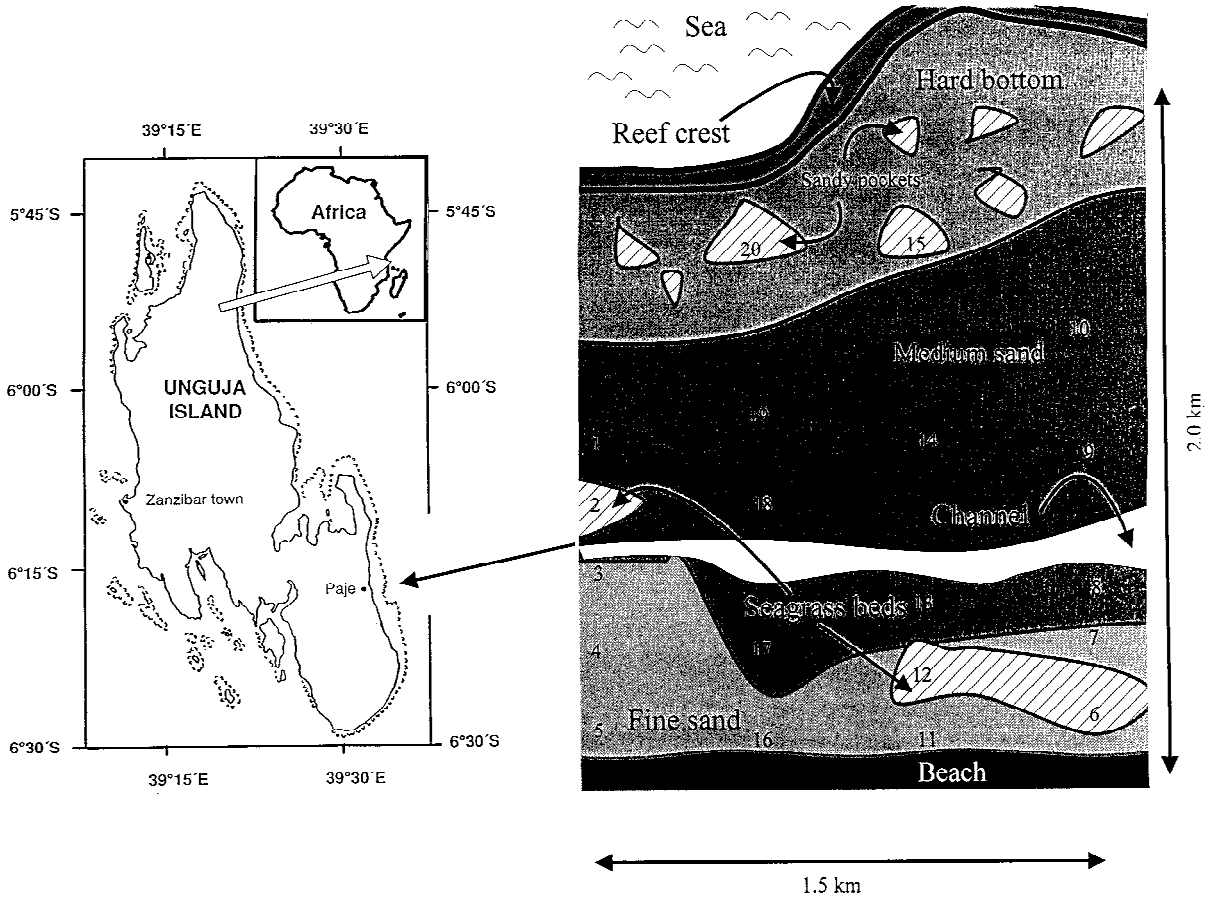


Figure 1. The study site at Paje on the east coast of Zanzibar. Major habitats occurring in the area are shown with numbers indicating stations sampled.

Mean grain size was determined according to Morgans (1956) and sediment classified on basis of Wentworth scale as described in Giere (1993). Chlorophyll *a* was estimated spectrophotometrically using the formula of Parsons et al. (1984). For assessment of organic content, sediment samples were dried at 60 °C for 24 h to constant weight and then ashed in a muffle furnace at approximately 550 °C for 5 h and weighed again. Organic content was expressed as the proportion of the initial dry weight.

Statistical analyses

Differences in faunal density and environmental variables among habitats were investigated by means of 1-way analysis of variance (ANOVA). Paired *a posteriori* comparisons of density estimates were carried out with a Tukey test, using 95% confidence limits. Prior to the analysis of variance all data were $\log_{10}$ transformed and Cochran's *C*-test used to check the assumption of homoscedasticity. When conditions for the use of a parametric test were not fulfilled, Kruskal Wallis or Mann-Whitney *U* tests were employed. Species diversity was assessed using the Shannon-Wiener information function (H'), Pielou evenness (J') (both using $\log_2$), Simpson's index (D) and the number of species at the 50 individual level using Hurlbert's (1971) rarefaction method (S). Multiple regression analysis (Sokal & Rohlf, 1995) was used to investigate the relationship between meiofaunal densities and several environmental variables simultaneously.

Major meiofaunal taxa and nematode genera abundance data were double square root transformed and subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure and group average clustering. The ANOSIM randomisation test (Warwick et al., 1990) was used to test for significant differences in nematode assemblage structure between habitats and the dissimilarity percentage program (SIMPER,

Warwick et al., 1990) used to identify the genera making the greatest contribution to differences between stations observed in the MDS plots.

Results

Environmental characteristics

Table 1 shows measurements of abiotic factors in the lagoon. Most of the factors in the lagoon were quite variable among stations. Sediment organic content ranged between 3.9% (station 7) and 9% (station 3). Sorting of grain size ranged between 0.80 phi (station 1) and 1.34 phi (station 2) implying that sediment was generally poorly sorted. Mean grain size ranged between 120 μm (very fine sand, station 12) and 860 μm (coarse sand, station 20), although the majority of the stations were either medium or fine sands. Chlorophyll *a* values ranged between 0.7 g carbon ml^{-1} (station 13) and 3.7 g carbon ml^{-1} (station 4). The water temperature varied between 30 °C (station 13) and 37 °C (station 6) and no trends were evident between transects with increasing depth. Salinity ranged between 14 psu and 32 psu. Station 11 received freshwater intrusion from seepage and springs opening up in the area and had salinity ranging between 14 psu and 23 psu. Stations stood at different shore-levels, the closest 55 m from shore and the farthest was 1500 m from shore (see Table 1).

Major Taxa

Twelve major meiofaunal taxa were identified i.e. Nematoda, Harpacticoida, Cyclopoida, Polychaeta, Amphipoda, Ostracoda, Oligochaeta, Turbellaria, Insecta, Hydroida, Gastropoda and Cumacea. Meiofauna density was variable among stations (Table 2). Total meiofauna numbers ranged between 219 ind. 10 cm^{-2} and 3422 ind. 10 cm^{-2}. Apart from the seagrass stations, all stations in the upper shore (< 400 m from shore) had relatively higher densities of meiofauna than those at other shore levels. Nematodes dominated at most stations (except at stations 19 and 20 which had medium and coarse sands, respectively) contributing between 13% and 97% of the total population. Macrofauna (including larger copepods, amphipods, polychaetes, ostracods and turbellarians) numbers were low compared to meiofauna, ranging between 3 and 84 ind. 10 cm^{-2}. Mean value of macrofauna in bare sand stations was 23 ind. 10 cm^{-2}, whereas in seagrass stations it was 60 ind. 10 cm^{-2}. Table 3 shows the average and standard deviation of organic content, chlorophyll *a*, nematode trophic groups, meiofauna and total macrofauna in the four main habitats of the lagoon. Nematoda, most nematode feeding groups, Polychaeta, Ostracoda, total meiofauna and total macrofauna numbers were relatively higher in both fine and seagrass habitats than in coarse sand and medium sand habitats. There was a significant difference in the densities of all meio- and macrofauna groups among habitats ($P < 0.05$, 1-way ANOVA and Kruskal Wallis test, Table 4). The results of multiple regression analysis are shown in Table 5. Nematodes and total meiofauna were highly correlated with sediment characteristics (mean grain size, sorting coefficient, skewness and kurtosis simultaneously) ($P < 0.001$, $r^2 = 0.5$ and $P < 0.001$, $r^2 = 0.3$ for nematodes and total meiofauna, respectively). Both showed significant correlation with organic content of sediment and chlorophyll *a* simultaneously, but the r^2 value was quite low in both cases (Table 5). Copepoda (adult harpacticoid copepods plus copepodites) was neither correlated to sediment characteristics nor organic content and chlorophyll *a*. Polychaeta was not correlated with sediment characteristics but was slightly correlated with organic content and chlorophyll *a* (Table 5).

Nematode assemblage structure

A total of 100 nematode genera belonging to 25 families were recorded in the lagoon (Table 6). Three families made up almost half of all individuals identified, i.e. Desmodoridae (19.8% of total genera), Linhomoeidae (16.3%) and Chromadoridae (11.3%). Most families contributed less than 1% of the total abundance (Table 6). Seventeen genera occurred only once while 7 genera had a frequency of 50% or more. The most frequent genera were *Chromaspirina/Spirinia* (79%), *Daptonema* (74%), *Leptolaimus* (70%), *Microlaimus* (66%), *Marylynnia* (59%), *Chromadorina* (57%) and *Linhomoues* (50%). Most genera (83 genera) were poorly represented (< 1% total abundance), while 11 genera were moderately abundant (1–5% of total). Five genera occurred with high abundance (5–10% of total) and only one genus, *Chromaspirina/Spirinia* had very high abundance (> 10% of total).

At major taxa-level, neither multi-dimensional scaling ordination nor Bray-Curtis cluster analysis (not shown here) revealed distinct clusters of stations with respect to their taxonomic composition.

Table 1. Average values (N = 5) of abiotic factors measured at various stations in Paje during January 1994. Stations are arranged according sediment type and to distance from shore, seagrass stations have been grouped together. Habitat type: b.s = bare sand; s.g. = seagrass; v.s.s. = very sparse sea grass or seaweed

Station	Chl *a* ($gCml^{-1}$)	Mean grain (μm)	Sorting (phi)	Skewness	Kurtosis	Org. cont. %	Distance (m)	Sed.type	Habitat	Salinity (psu)	Temp. (°C)
16	1.44	134	1.06	−0.44	1.77	3.98	55	Fine	b.s	30	31
5	1.32	172	1.00	−0.29	1.46	6.30	60	Fine	b.s.	30	37
11	1.47	184	1.38	−0.55	3.98	4.53	79	Fine	b.s.	23	32
17	1.03	160	0.98	−0.11	1.30	5.04	350	Fine	b.s.	31	31
4	3.72	148	0.95	−0.35	1.32	5.56	400	Fine	b.s.	30	33
8	2.37	172	1.17	−0.29	2.24	4.69	600	Fine	b.s.	30	31
13	0.65	196	1.10	−0.24	1.75	4.23	600	Fine	v.s.s.	31	31
7	1.65	290	0.98	−0.33	1.87	3.86	300	Medium	b.s.	29	31
3	1.44	282	1.15	−0.37	2.74	8.95	650	Medium	v.s.s.	30	33
18	1.26	304	1.13	−0.26	2.74	4.24	800	Medium	b.s.	31	31
1	1.37	254	0.80	−0.27	1.04	4.73	1000	Medium	v.s.s.	31	32
9	1.39	442	1.19	−0.08	3.65	7.32	1000	Medium	v.s.s.	32	32
14	1.15	318	1.18	−0.38	3.12	4.54	1000	Medium	b.s.	32	30
19	1.97	290	0.91	−0.21	1.70	5.50	1000	Medium	b.s.	31	31
10	1.35	354	0.95	−0.15	1.84	7.07	1300	Medium	b.s.	31	32
15	2.13	262	0.80	−0.40	1.06	4.61	1500	Medium	b.s.	31	32
20	1.58	864	0.90	−0.29	2.50	6.81	1500	Coarse	v.s.s.	31	32
6	2.57	152	1.21	−0.55	2.71	7.54	200	Fine	s.g	30	31
2	1.65	270	1.34	−0.38	4.34	6.81	800	Medium	s.g	31	33
12	1.97	116	0.94	−0.40	1.17	5.31	250	Very Fine	s.g.	31	32

However, when applied to nematode genera abundance data a multi-dimensional scaling ordination gave clearer pattern with some stations close together or overlapping and others widely separated from each other (Figure 2a). There was generally more similarity within stations than among stations even if some stations formed clusters. All replicates from station 20 including one replicate from station 9 had coarse sand. Station 20 separated from the rest of the stations (Figures 2b and 3). The samples from fine sand stations and seagrass bed stations overlapped and were not significantly different in pair-wise comparisons (ANOSIM, $P>0.05$, Figures 2b and 3), while all other pair-wise comparisons between habitats resulted in significant difference (ANOSIM, $P<0.05$, Figure 3). Some grouping occurs according to grain size and distance from shore (Figure 2b–c), while no pattern was discernible with chlorophyll *a* (Figure 2d).

The results of SIMPER for the similarity comparison of nematode genera between habitats are shown in Table 7. The greatest dissimilarity was found between coarse sand habitat and fine sand habitat (dissimilarity = 81%).

Fine sand nematode assemblage

The density of nematodes was highest in fine sand habitats. The five most abundant genera in fine sand habitat were *Chromaspirina/Spirinia* (14% of total abundance), *Leptolaimus* (10%), *Metalinhomoeus* (10%), *Marylynnia* (9%) and *Sabatieria* (7%). Three genera were found in higher numbers than in the other habitats i.e. *Chromadorina, Sabatieria* and *Metalinhomoeus* and, therefore, contributed relatively more than other species to the dissimilarity between the habitats (see Table 7). In terms of trophic structure, fine sands were inhabited by higher percentage of none-selective deposit feeders (1B) and predators/omnivores (2A) than the other habitats (Table 8).

Seagrass nematode assemblage

Density of nematodes was relatively high in this habitat. The five most dominant genera in seagrass bed were *Chromaspirina/Spirinia* (22%), *Terschellingia* (17%), *Daptonema* (9%) and *Leptolaimus* and *Spilophorella* each contributing 8% of the total abundance. *Terschellingia* was found in highest numbers

Table 2. Average numbers per 10 cm^2 (Avg) N = 5, standard deviation (sd) and percentage (%) of major meio - and macrofauna taxa found in 20 stations at Paje during January 1994, arranged according to sediment size class and distance from shore. The last 3 stations are seagrass beds

		MEIOFAUNA										MACROFAUNA									
		Nema-toda	Harpact-icoida	Naup-lii	Poly-chaeta	Amphi-poda	Ostra-coda	Oligo chaeta	Turbell-aria	Others	total	Cope-poda	Amphi-poda	Poly-chaeta	Oligo-coda	Ostra-worms	Arrow aria	Turbell-ceans	Cuma-	Others	total
Fine, 55m	Avg.	1918	225	28	59	0	0	1	15	0	2246	0	0	5	0	0	0	8	0	0	13
(st. 16)	SD	557	109	22	22	0	0	2	9	0		0	0	2	0	0	0	6	0	0	
	%	85	10	1	3	0	0	0	1	0		0	0	36	2	0	0	61	2	0	
Fine, 60m	Avg.	1192	27	5	10	0	0	0	4	0	1238	0	0	2	0	0	0	7	0	0	9
(st. 5)	SD	440	16	3	9	0	0	1	1	0		0	1	3	1	0	0	6	0	0	
	%	96	2	0	1	0	0	0	0	0		0	4	23	4	0	0	68	0	0	
Fine, 79m	Avg.	672	218	66	46	0	0	0	27	0	1029	0	0	8	0	0	0	9	0	0	17
(st. 11)	SD	168	57	58	21	0	0	0	22	0		0	0	5	0	0	0	10	0	0	
	%	65	21	6	4	0	0	0	3	0		0	0	48	0	0	0	51	0	1	
Fine, 350m	Avg.	1170	22	0	9	0	0	0	2	0	1203	0	0	3	0	0	0	0	0	0	3
(st. 17)	SD	395	11	0	3	0	0	0	2	0		0	0	3	0	0	0	1	0	0	
	%	97	2	0	1	0	0	0	0	0		0	0	89	0	0	0	11	0	0	
Fine, 400m	Avg.	3039	114	6	223	14	11	0	14	1	3422	3	16	33	2	6	0	0	0	1	61
(st. 4)	SD	1272	42	2	48	12	9	1	5	1		6	2	5	3	8	0	0	0	1	
	%	89	3	0	7	0	0	0	0	0		5	27	55	3	10	0	0	0	1	
Fine, 600m	Avg.	515	236	10	93	57	14	0	8	2	935	5	49	24	0	6	0	0	0	0	84
(st. 8)	SD	244	124	4	35	10	4	0	6	3		9	13	13	1	7	0	0	0	0	
	%	55	25	1	10	6	2	0	1	0		6	58	28	0	7	0	0	0	0	
Fine, 600m	Avg.	198	82	9	11	2	1	0	5	1	309	9	1	4	0	0	0	0	0	0	14
(st. 13)	SD	120	81	17	9	3	1	0	3	1		5	1	2	0	0	0	0	0	0	
	%	64	27	3	4	1	0	0	2	0		59	9	29	0	0	1	0	1	0	
Medium, 300m	Avg.	818	117	1	115	0	1	0	14	1	1067	0	0	16	1	0	0	0	0	0	17
(st. 7)	SD	138	150	1	27	1	1	0	4	1		0	0	4	1	0	0	0	0	0	
	%	77	11	0	11	0	0	0	1	0		0	0	93	5	1	0	0	0	1	
Medium, 650m	Avg.	244	160	17	97	7	10	0	10	2	547	5	15	0	2	0	0	0	0		22
(st. 3)	SD	98	53	12	30	6	14	0	8	2		8	2	8	1	3	1	0	1	0	
	%	45	29	3	18	1	2	0	2	0		18	18	52	1	7	1	0	1	0	
Medium, 800m	Avg.	280	267	16	8	4	1	0	14	2	592	6	2	4	0	0	1	0	1	0	14
(st. 18)	SD	179	344	31	14	7	1	1	13	3		7	3	2	0	0	0	0	1	0	
	%	47	45	3	1	1	0	0	2	0		47	15	27	0	0	6	0	5	0	

Table 2. Continued

		MEIOFAUNA										MACROFAUNA									
		Nema-toda	Harpact-icoida	Naup-lii	Poly-chaeta	Amphi-poda	Ostra-coda	Oligo chaeta	Turbell-aria	Others	total	Cope-poda	Amphi-poda	Poly-chaeta	Oligo-coda	Ostra-worms	Arrow aria	Turbell-ceans	Cuma-	Others	total
Medium, 1000m	Avg.	447	173	2	37	0	1	0	58	1	719	7	0	8	0	2	0	0	0	0	17
(st. 1)	SD	120	140	2	13	0	1	0	19	1		2	0	5	0	2	0	0	0	1	
	%	62	24	0	5	0	0	0	8	0		40	0	45	1	12	0	0	0	2	
Medium, 1000m	Avg.	477	274	8	49	1	2	0	14	0	825	1	2	12	0	1	1	0	0	0	17
(st. 9)	SD	141	126	11	16	2	2	0	8	1		2	1	5	0	1	1	0	0	0	
	%	58	33	1	6	0	0	0	2	0		7	12	70	0	4	6	0	1	0	
Medium, 1000m	Avg.	287	71	0	49	3	0	1	17	2	430	8	1	7	1	0	0	0	1	0	18
(st. 14)	SD	43	47	1	29	2	1	1	9	3		4	2	3	2	0	0	0	1	0	
	%	67	17	0	11	1	0	0	4	0		43	6	38	7	1	1	0	3	1	
Medium, 1000m	Avg.	160	167	1	10	2	1	0	5	2	348	11	1	4	0	1	0	0	2	0	19
(st. 19)	SD	54	145	1	21	2	2	0	6	3		9	1	3	0	1	1	0	4	0	
	%	46	48	0	3	1	0	0	2	1		58	4	19	1	4	2	0	10	0	
Medium, 1300m	Avg.	312	168	7	51	2	2	0	19	1	562	4	6	17	0	2	0	0	3	0	32
(st. 10)	SD	135	77	7	33	5	2	0	6	1		4	3	7	0	3	0	1	4	0	
	%	55	30	1	9	0	0	0	3	0		13	18	52	0	7	0	1	9	0	
Medium, 1500m	Avg.	460	56	0	5	3	0	0	14	4	542	10	6	3	0	1	0	0	0	0	20
(st. 15)	SD	188	56	0	5	6	1	0	12	2		5	7	3	0	3	0	0	0	0	
	%	85	10	0	1	1	0	0	3	1		49	30	13	0	6	0	0	1	0	
Coarse, 1500m	Avg.	29	168	1	14	0	1	0	6	0	219	0	0	5	0	0	0	1	0	0	6
(st. 20)	SD	16	42	1	10	1	1	0	4	0		0	1	3	0	0	0	1	0	0	
	%	13	77	0	7	0	0	0	3	0		0	6	79	0	3	0	9	3	0	
Fine, 200m	Avg.	489	248	2	69	21	11	1	4	1	846	0	30	27	0	4	0	0	0	0	61
(st. 6)	SD	91	219	4	58	11	1	2	3	2		0	13	15	1	3	0	0	0	0	
	%	58	29	0	8	2	1	0	0	0		0	49	44	1	6	0	0	0	0	
Medium, 800m	Avg.	431	273	23	50	23	20	2	14	0	836	3	24	13	1	11	0	0	0	1	53
(st. 2)	SD	230	158	12	40	8	10	3	10	1		2	7	4	1	9	0	0	0	1	
	%	52	33	3	6	3	2	0	2	0		6	46	24	1	22	0	0	0	1	
Very fine, 250m	Avg.	1371	191	2	65	13	8	4	4	0	1658	1	28	32	1	3	0	0	0	1	66
(st. 12)	SD	142	42	2	31	11	9	4	2	0		1	16	12	1	3	0	0	0	1	
	%	83	11	0	4	1	0	0	0	0		1	42	49	2	5	0	0	0	1	

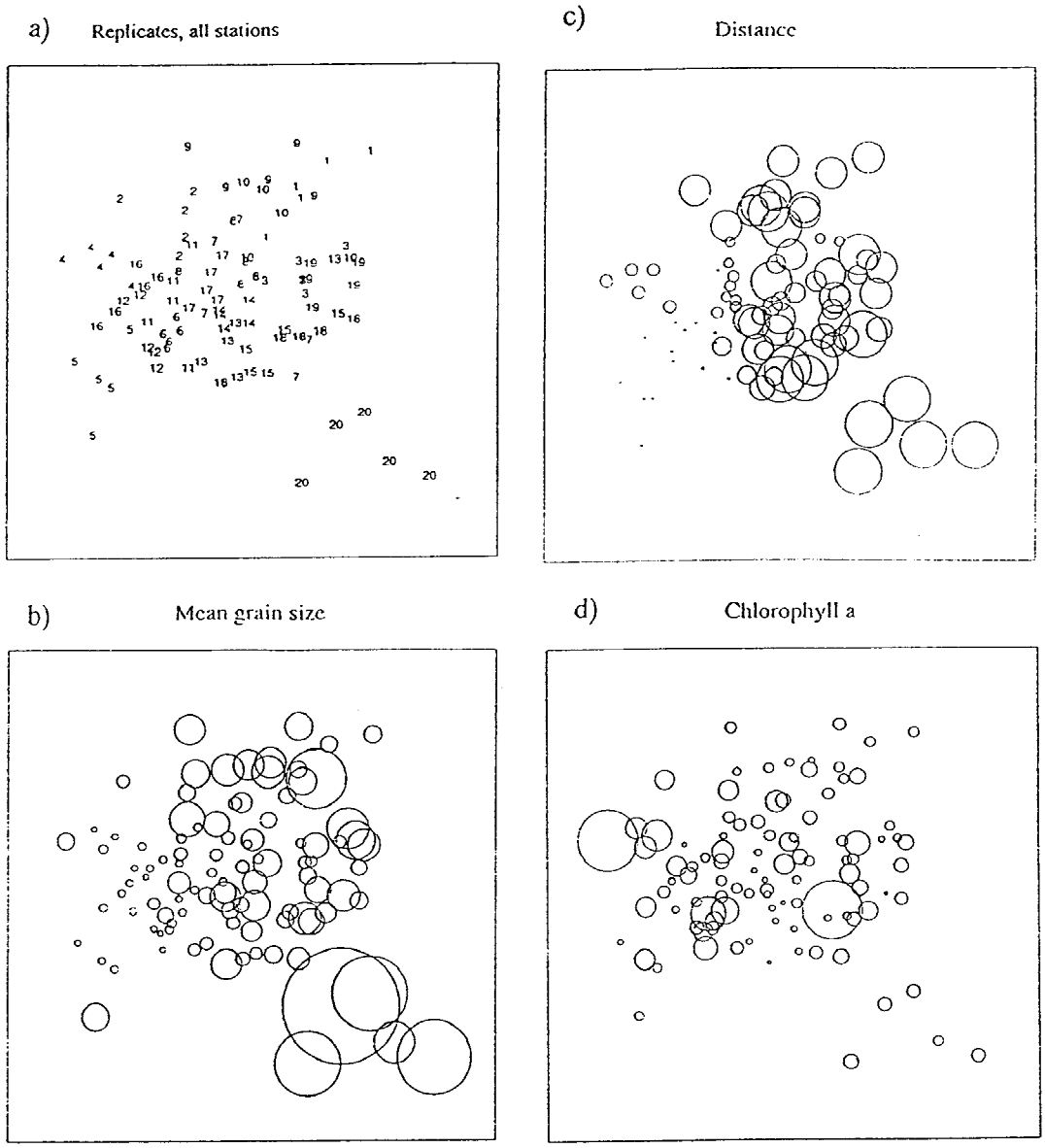


Figure 2. Multi-dimensional scaling ordination of nematode genera abundance data from all samples. (a) all replicates within stations shown, number indicates station (see Figure 1), circles proportional to mean grain size (b), distance from shore (c) and chlorophyll *a* concentrations (d).

in the seagrass habitat resulting in highest percentage (27%) of selective deposit feeders among the habitats (Table 8).

Medium sand nematode assemblage

The medium sand habitat had in general lower nematode densities when compared to both fine sand and seagrass habitats. The five most dominant genera were *Chromaspirina/Spirinia* (38%), *Daptonema* (15%), *Leptolaimus* and *Richtersia* (each contributing 8% of the total abundance) and *Gammanema* (3%). Several genera found in high numbers in both fine sand and seagrass habitat were relatively rare in the medium sand assemblage i.e. *Chromadorina, Metlinhomoeus, Terschellengia* and *Sabatieria*. The trophic structure resembled mostly the fine sand assemblage (Table 8).

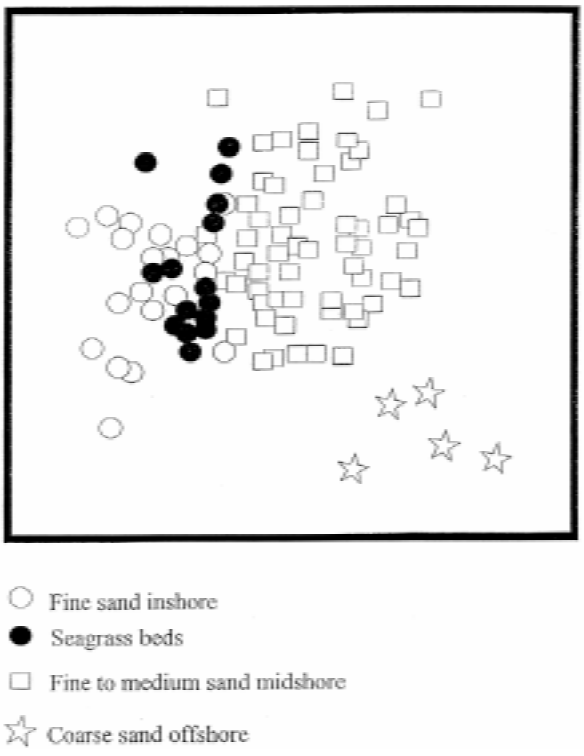


Figure 3. Multi-dimensional scaling ordination of nematode genera abundance data from the four main habitats (shown in symbols).

Coarse sand nematode assemblage

Densities of nematodes were low. The five most dominant genera were *Chromaspirina/Spirinia* (46%), *Leptolaimus* (15%), *Promonhystera* (13%), *Chromadorina* (4%) and *Epsilonema* (3%). Highest percentage of epistrate feeders was found in this environment (63%). Many nematode genera occurring in other habitats were absent in the coarse sand habitat (probably due small sample size, only 6 replicates in total) but two genera, *Rhips* and *Trochamus* were only encountered at this coarse sand station.

Discussion

The total abundance of meiofauna, and the variability of densities observed in this study, fall within ranges found in similar habitats (e.g. Alongi, 1986,1989a,b; Vargas, 1988; Suresh et al., 1992; Dittman, 1995; Ólafsson et al., 1995; Boucher, 1997; Gómez Noguera & Hendrickx, 1997). Dominance of nematodes in tropical intertidal systems have also been documented for Australia (70%, Dittman, 1995), in Costa Rica (82%, Vargas, 1988) and in Mombasa Kenya (53–95%, Vanhove et al., 1992).

In the current study, the family Chromadoridae was found dominating in terms of number of nematode genera, but the family Desmodoridae lead in abundance. Epistrate feeders dominated in all habitat-

Table 3. Average (Avg) and standard deviation (sd) of organic content (%), chlorophyll *a* ($gCml^{-1}$), abundance of nematode trophic groups, meiofauna and total macrofauna in the the different habitats of the lagoon. Faunal abundances are expressed per 10 cm^2

		Coarse sand (n = 6)	Medium and (n = 42)	Fine sand (n = 52)	Seagrass beds (n = 15)
Organic content	Avg	7	5	5	7
	sd	1	2	3	2
Chlorophyll *a*	Avg	2	1	2	2
	sd	0	0	1	1
Trophic groups:					
1A	Avg	12	43	155	191
	sd	8	46	197	196
1B	Avg	9	112	310	120
	sd	21	117	413	67
2A	Avg	42	228	482	373
	sd	74	170	437	240
2B	Avg	4	20	102	30
	sd	5	72	166	34
Meiofauna:					
Nematoda	Avg	70	424	1094	759
	sd	103	230	1044	468
Harpacticoida	Avg	154	172	127	237
	sd	51	164	106	151
Polychaeta	Avg	17	48	62	61
	sd	10	41	74	42
Amphipoda	Avg	0	2	10	19
	sd	1	4	19	10
Ostracoda	Avg	1	1	4	13
	sd	1	3	8	9
Oligochaeta	Avg				3
	sd				3
Nauplii	Avg	1	8	15	9
	sd	1	15	29	12
Turbellaria	Avg	5	20	10	7
	sd	4	17	12	8
Total meiofauna	Avg	247	676	1323	1109
	sd	85	271	1103	467
Total macrofauna	Avg	7	19	28	57
	sd	3	9	28	19

Table 4. Results of 1-way ANOVA and Kruskal-Wallis tests for meiofauna densities, nematode diversity indices, and trophic groups, some environmental variables and macrofauna between the different habitats (seagrass beds=S, fine=F, medium=M and coarse=C sands) of the lagoon

	1 - way ANOVA			Kruskal-Wallis
	F-ratio	sig.lev	Post hoc.	sig. lev.
Meiofauna				
Nematoda				***
Harpacticoida				*
Copepoda				**
Polycheata				*
nematode div. index				
richness	4.6	**	S > F.M	
Shannon				***
eveness				***
Environ. variables				
organic content	4.7	**	S > F	
chlorophyll *a*				*
sorting	1.9	NS		
skewness	4.7			M > S
Trophic groups				
1A	11.1	***	S F > C M	
1B				*
2A				**
2B	7.34	***	F > C M	
Macrofauna				
Copepoda				**
Amphipoda				***
Polychaeta	6.2	***	S > C F M	
Ostracoda				**
Turbellaria				*

***=$P<0.001$, **=$P<0.01$, *=$P<0.05$, NS=not significant.

Table 5. Results of multiple regression analysis (R squared, F -ratio, P -value and significance level) for major meiofauna taxa abundance (logx+1) transformed data simultaneously on mean grain size, sorting coefficient, skewness kurtosis and simultaneously on organic content and chlorophyll*a* values from a tropical intertidal lagoon

	Mean grain size, sorting coefficient, skewness			Chlorophyll *a*, organic content		
	R2	F-ration	signi. lev.	R2	F- ratio	signi. lev.
Nematoda	0.5	23.8	***	0.08	4	*
Copepoda	0.06	1.6	NS	0.5	2.7	NS
Polychaeta	0.08	2.2	NS	0.08	4.3	*
Total meiof.	0.3	11.8	***	0.08	4.5	*

***=$P<0.001$, *=$P<0.05$, NS=not significant.

types of the lagoon in Zanzibar. Similarly in Australia, Alongi (1986) observed the family Chromadoridae dominating other nematode families in terms of number of genera, but the family Desmodoridae recorded the highest abundance and epistrate feeders were found dominant. He found that at the reef crest and at the shallow lagoon area experiencing intense wave nematode mean densities were significantly lower than in sands within other zones. Faunal groups were distinct among different reef zones: coarse to medium sands were inhabited primarily by omnivorous and epistrate-feeding nematodes while fine sands of the lagoon were inhabited by non-selective or selective deposit feeders. Boucher (1997) worked on three different soft-bottom types in a lagoon in New Caledonia and showed that coarse sand close to the reef had fewer nematode genera compared to medium and fine sands in other bottoms. He also found epistrate feeders dominating in sandier bottoms and noted different familial dominance in different bottom-types. The family Desmodoridae was found to be the most abundant followed by the family Chromadoridae. In an earlier study, in the same lagoon in Zanzibar, Ólafsson et al. (1995) showed that epistrate feeders dominated in sandier sediments.

Most of the genera observed in this study commonly occur elsewhere in the world. The dominance of epistrate feeders and the paucity of selective deposit feeders and other feeding guilds in coarse sands indicates that sediment granulometry influences nematode distribution in the lagoon on the east coast of Zanzibar. There appears to be different and distinctive nematode assemblage structures differing in density, generic and trophic composition within fine sand, medium sand and seagrass habitats which is in agreement with Alongi (1986) and in partial agreement with the findings of Boucher (1997). It has been demonstrated by several other studies that sediment granulometry very much influence the distribution of nematodes indirectly through its control on interstitial space (i.e. pore-size) and directly through individual grain surface areas that relate to biofilms and bacterial colonisation (e.g. Heip et al., 1985). In general, there is a tendency for the proportion of epistrate feeders to be higher in larger grain sediments and for the deposit feeders to dominate in fine sediments (Wieser, 1959; Tietjen, 1969; Hodda & Nicholas, 1986; Alongi, 1986; Giere, 1993; Boucher, 1997).

The low number of nematodes recorded in the coarse sand may have several explanations, one being sampling design. We decided to take core samples down to 5 cm after doing a preliminary survey in the fine and medium sand, where we found that over 95% of all nematodes were found in upper 5 cm of 10 cm deep cores (n=6). In coarse sand, however, nematodes are likely to be distributed much deeper (e.g. Ólafsson, 1991) and, therefore, we may have only sampled a small part of the nematode population in these coarse sandy pockets.

It was clear that samples within stations were more similar than samples among stations although in some instances a limited overlap or clustering of stations could be observed (see Figure 2a). This must be expected since samples within stations (i.e. replicates) were physically much closer and were likely to experience more or less similar abiotic and biotic conditions. Samples among stations not only stood much further apart but also occurred at different shore-levels where they were likely to be affected by large-scale variations.

Table 6. Nematode family percentage (%) abundance and number of genera (N) in each family identified from Paje

Family	%	N
Desmodoridae	19.8	8
Linhomoeidae	16.3	6
Chromadoridae	11.3	14
Cyatholaimidae	9.8	12
Leptolaimidae	9.7	3
Xyalidae	9.1	8
Comesomatidae	8.4	6
Microlaimidae	4.2	1
Ethmolaimidae	3.3	4
Selachinenematidae	2.4	5
Oncholaimidae	0.6	4
Epislonematidae	0.6	3
Axonolaimidae	0.3	3
Trefusiidae	0.3	1
Enoplidae	0.3	2
Oxystominidae	0.2	3
Ceramonematidae	0.2	3
Ironidae	0.2	2
Enchelidiidae	0.1	4
Anticomidae	<0.1	3
Anoplostomatidae	<0.1	1
Monhysteridae	<0.1	1
Paramicrolaimidae	<0.1	1
Diplopeltidae	<0.1	1
Desmoscolecidae	<0.1	1

Table 7. Abundance 10 cm^{-2} of nematode genera averaged across replicates in fine sand inshore (n = 52), seagrass (n = 15), medium sand midshore (n = 42) and coarse sand offshore (n = 6) stations. Genera are ranked according to average Bray-Curtis dissimilarity between samples from different habitats. Mean values representing the contribution of each genus to dissimilarity are shown as percentage and cumulative percentage; a cut-off to the genera list was applied at cumulative percentage dissimilarity, 50%

	Avg. abundance 10 cm^{-2}		Percentage	cum%
	fine sand	seagrass		
	55% Dissimilarity			
Genus				
Sabatieria	180	19	4	4
Metalinhomoeus	240	12	4	9
Terschellingia	64	120	4	13
Marylynnia	149	29	4	17
Gomphionema	99	2	4	20
Chromadorina	122	27	4	24
Linhomoeus	54	13	3	27
Spilophorella	43	55	3	31
Microlaimus	45	18	3	34
Dichromadora	38	8	3	37
Daptonema	43	61	3	39
Halichoanolaimus	33	9	3	42
Chromaspirina/Spirinia	138	155	3	45
Chromadora	10	11	3	48
	fine sand	medium sand		
	67% Dissimilarity			
Chromadorina	122	7	5	5
Metalinhomoeus	240	2	5	10
Marylynnia	149	26	4	15
Spilophorella	43	2	4	19
Sabatieria	180	1	4	23
Linhomoeus	54	9	4	27
Halichoanolaimus	33	0	4	31
Terschellingia	64	1	4	34
Gomphionema	99	4	4	38
Microlaimus	45	28	3	41
Daptonema	43	55	3	45
Chromaspirina/Spirinia	138	135	3	47
	medium sand	seagrass		
	62% Dissimilarity			
Terschellingia	1	120	6	6
Spilophorella	2	55	4	10
Chromadorina	7	27	4	14
Sabatieria	1	19	3	17
Marylynnia	26	29	3	21
Richtersia	33	0	3	24
Microlaimus	28	18	3	27
Metalinhomoeus	2	12	3	30
Halichoanolaimus	0	9	3	32
Linhomoeus	9	13	3	35

Table 7. Continued

	Avg. abundance 10 cm^{-2}		Percentage	cum%
Euchromadora	1	8	3	38
Chromadora	4	11	3	41
Promonhystera	8	6	3	43
Comesoma	14	1	2	46
Leptonemella	4	14	2	48
	coarse sand	fine sand		
	81% Dissimilarity			
Chromadorina	1	122	6	6
Metalinhomoeus	0	240	6	11
Marylynnia	0	149	6	17
Linhomoeus	0	54	5	22
Chrospirina/Spirinia	2	138	4	26
Sabatieria	0	180	4	30
Spilophorella	1	43	4	34
Gomphionema	2	99	4	38
Halichoanolaimus	0	33	4	42
Terschellingia	0	64	4	46
Daptonema	0	43	4	50
	coarse sand	seagrass		
	78% Dissimilarity			
Terschellingia	0	120	6	6
Daptonema	0	61	6	12
Chromaspirina/Spirinia	2	155	5	17
Spilophorella	1	55	4	21
Chromadorina	1	27	4	25
Sabatieria	0	19	4	29
Maylynnia	0	29	3	32
Metalinhomoeus	0	12	3	35
Microlaimus	1	18	3	38
Linhomoeus	0	13	3	41
Halichoanolaimus	0	9	3	44
Epsilonema	2	0	3	47
Chromadora	0	11	3	49
coarse sand	medium sand			
	75% Dissimilarity			
Daptonema	0	55	7	7
Chromaspirina/Spirinia	2	135	7	14
Richtersia	0	33	4	18
Epsilonema	2	1	4	22
Microlaimus	1	28	4	26
Marylynnia	0	26	4	30
Paracyatholaimus	2	1	4	33
Comesoma	0	14	4	37
Promonhystera	0	8	3	40
Leptolaimus	10	49	3	44
Chromadorina	1	7	3	47
Lnhomoeus	0	9	3	50

Habitats such as seagrass beds provide generally unique micro-habitats (see Decho et al., 1985) enhancing meiofauna colonisation and provide refuges for small predators of meiofauna. The lack of significant difference between assemblages derived from seagrass beds and inshore fine sands in the current study was unexpected, and we can only infer that the results suggest the overwhelming dominance of sediment grain size as a factor influencing meiofaunal density. Seagrass reduces water movement and redirect currents resulting in deposition of fine grains (see Decho et al., 1985). Ecologically such an action would tend to provide a habitat with fine sands which favour colonisation by nematodes. This may have led to the occurrence of defined nematode assemblage structures which showed different trophic group proportions and to some extent different species composition compared with the sandy habitats.

In this study, macrofauna numbers seem to be quite high when densities are considered per m^2 (see Decho et al., 1985), even though we have used sampling device designed for meiofauna, i.e. small cores. Most of the stations in this study were either in barren sands or in very sparse seagrass. Only three stations were truly seagrass patches (stations 2, 6 & 12). A number of studies associated with macrofauna have noted higher densities and greater number of species present in seagrass areas compared to adjacent areas lacking seagrass (e.g. Orth & Heck, 1980; Summerson & Peterson, 1984; Decho et al., 1985).

On the whole, the seagrass habitat has more macrofauna species than adjacent unvegetated sand areas. The reasons often given for such observations are: 1. large predators control the abundance of small predators which would prey on meiofauna in barren areas (e.g. Evans, 1983), 2. seagrass provide refuge for macrofauna (e.g. Hooks et al., 1976), which are potential predators of meiofauna residing in seagrass. The relatively high number of macrofauna observed in stations within seagrass in this study lends support to this idea. However, our results on organic matter content of sediment show high values (4–9%) and contrast those reported elsewhere (e.g. Alongi, 1986; Schrijvers et al., 1995). We suspect that the method used was not appropriate as it is known that carbonate sands if overheated tend to decompose giving free carbon dioxide and water which contribute to the loss in weight, thus leading to higher apparent organic matter percentage.

To understand differences in nematode assemblage structure among habitats it may be necessary to give careful considerations regarding distributions and refrain from generalisations based on correlative analysis alone. The use of experimental manipulations in finding community control mechanisms or in trying to establish causes of observed populations densities seem indispensable, if meaningful results are to be expected.

Table 8. Percentage abundance of each nematode feeding group in the 4 habitats (1A=Selective deposit feeders, 1B= non-selective deposit feeders, 2A=Epistrate feeders, 2B=Predators/Omnivores)

	Fine sand	Medium sand	Coarse sand	Seagrass bed
1A	15	11	18	27
1B	30	28	13	17
2A	46	57	63	52
2B	10	5	6	4

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