Hydrobiologia **312:** 47–57, 1995.

Meiobenthos in mangrove areas in eastern Africa with emphasis on assemblage structure of free-living marine nematodes

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Received 16 December 1993; in revised form 7 July 1994; accepted 30 August 1994

Abstract

A survey was conducted to examine spatial variations in the population density of major meiofaunal taxa and the assemblage structure of free-living marine nematodes within 5 mangrove areas on the west and east coast of Zanzibar. Meiofauna densities in surface sediments (0–5 cm) ranged from 205 to 5263 ind. 10 cm^2, being on average 1493 ind. 10 cm^2. Of the 17 major taxa recorded, nematodes dominated (64–99%) in all samples while harpacticoid copepods were usually second most abundant. Within all areas the numbers of meiofauna were very variable and significant differences among areas were only detected for oligochaetes and turbellarians. Densities of nematodes, harpacticoids, polychaetes and turbellarians were, however, significantly ($P<0.001$) higher at low water stations compared with mid and high water stations. Harpacticoids were negatively correlated with the numbers of fiddler crab (*Uca* spp.) burrows. Other correlations between environmental factors (grain size, temperature, salinity, oxygen tension, prop root density, fiddler crab burrows) and major meiofaunal taxa were non-significant. A total of 94 nematode genera were recorded from four mangrove areas. The most abundant and frequent genera were *Microlaimus* and *Spirinia*, followed by *Desmodora* and *Metachromadora*. Representatives of the genera most common in current study are found all over the globe. There was a high variation in nematode assemblage structure within and between sampling areas indicating the absence of a well defined nematode assemblage confined to mangrove areas. In a hypersaline area diversity was much reduced and where salinity was over 100‰ the fauna was restricted to 3 nematode genera, *Microlaimus*, *Theristus* and *Bathylaimus*. Multidimensional scaling ordination (MDS) of the nematode genera separated samples taken from low water stations from other stations, the assemblage structure being significantly different at the low water stations. Numbers of selective deposit feeders were negatively correlated with average grain size and positively correlated with silt content.

Introduction

Tidal mangrove forests cover a vast area of the world's tropical coastlines. These forests are believed to play an important role in the support of estuarine and coastal food webs (e.g. Alongi, 1989, 1990a). Within the mangrove forests a great variety of benthic assemblages is found. The importance of the mangroves as both nursery ground and habitat for important fish species is becoming well established (e.g. Little *et al.*, 1988; Robertson & Duke, 1987, 1990). Numerically the most important infaunal (metazoan) group is the meiofauna (e.g. Hodda & Nicholas, 1985) which is known to be preyed upon by the juveniles of a large number of fish species (see Gee 1989 for review) and benthic macrofauna including shrimps, crabs, polychaetes and gastropods (see Ólafsson & Moore (1990) for references).

Ecologists working in mangrove areas have increasingly focused on the role of the meiobenthos in these systems. Descriptive studies on the temporal and spatial distribution of the meiobenthos have been performed (Dye, 1983; Alongi, 1987a, 1990; Hodda & Nicholas, 1985, 1986; Nicholas *et al.*, 1991; Vanhove *et al.*, 1992) along with studies on trophic relations (Krishnamurthy *et al.*, 1984; Dye & Lasiak, 1986), nutrient re-cycling (Hopper *et al.*, 1973) and the effects of physical/chemical disturbances (Alongi, 1987b; Alongi & Christoffersen, 1992). In east Africa one study on the meiobenthos of mangrove sediments has been published (Vanhove *et al.*, 1992).

The fringing zones of the mangrove forests in Zanzibar offer a variety of habitats. These areas occur at all intertidal levels and may therefore exhibit a large variation in temperature and salinity. Several mangrove species extend their aerial prop roots (pneumatophores) in these zones and their cover is variable. In many areas the sediment is completely worked over by fiddler crabs, both at the sediment surface, during feeding and deeper, when digging burrows for shelter. Apart from a semi-qualitative description of the fauna associated with mangrove forests (Ngoile & Shunula, 1992) no investigation has been published on the ecology of benthic animals inhabiting the intertidal areas of Zanzibar. The main aim with this survey was to give an account of the meiobenthos in mangrove swamps in Zanzibar and to try to identify those factors responsible for differences in density and assemblage structure.

Material and methods

Study area

Unguja island is the largest island of Zanzibar and supports seven distinct mangrove stands occupying an area of approximately 6000 hectares (Ngoile & Shunula, 1992). The largest forest is situated inside Chwaka Bay on the east coast with the remainder of the stands located on the west coast (Fig. 1). This survey was confined to the following mangrove areas.

1. Maruhubi 06 °09'S 39 °12'E (sampling 25.10.92). A small mangrove forest situated about 1 km north of Zanzibar town.

2. Chukwani 06 °12'S 39 °12'E (sampling 26.10.92). Another small mangrove stand about 5 km south of Zanzibar town.

3. Chwaka Bay 06 °11'S 39 °25'E (sampling 30.10.92). The largest mangrove forest, covering an area of more than 3000 ha., on the east coast of Unguja island.

4. Muwanda 05 °55'S 39 °13'E (sampling 09.11.92). A large mangrove stand on the north coast of Unguja island. The high water stations were all situated on a plateau which is only submerged during spring tides. This part is hypersaline, and used by local people to extract salt.

5. Kitogani 06 °17'S 39 °26'E (sampling 12.11.92). A part of the mangrove complex on the south west coast of Unguja island (Fig. 1).

Samples

In each mangrove area, apart from Kitogani, 5 stations where chosen to represent a typical bottom type of the fringing zone. At Kitogani fringing areas were not accessible so the sampling took place in the midst of the forest. Sampling was carried out at spring low tides and the approximate tidal level (high, mid and low water) of each station estimated from the low water mark. At each station a quadrate of 1 m^2 was haphazardly located and the number of crab holes and prop roots within the frame counted. Two 5 cm deep cores (9.6 cm^2 area) were then retrieved from a fixed position within the frame. One of the samples was immediately fixed with 8% formalin and the other was taken untreated to the laboratory. Within the frame a hole was dug to the ground water level and salinity measured with a refractometer and oxygen saturation and temperature with a portable oxygen electrode probe.

In the laboratory, grain size samples were dried in an oven at *c.* 100 °C and subsequently sieved through a series of sieves (2, 1, 0.5, 0.250, 0.125 and 0.063 mm) and grain size determined on the basis of the weight of each size fraction (Morgans, 1956). 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 of 1.15 (Platt & Warwick, 1983). Major meiofaunal taxa were identified and counted under a dissecting microscope. From each sample approximately 100 nematodes were transferred to glycerine and mounted on slides for genus identification under a high-power microscope, using the pictorial keys of Platt & Warwick (1983). Nematodes were assigned to trophic groups according to the scheme of Wieser (1953). Nematodes were not identified from the Kitogani samples.

Statistics

Differences in density were investigated by means of one-way analysis of variance. Paired *a posteriori* comparisons of density estimates were carried out with the 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 parametric tests were not fulfilled, Kruskal-Wallis test was employed. Generic diversity was assessed by using the Shannon-Wiener information function (H'), Pielou evenness (R') (both using $\log_2$), Simpson's index (D) and the expected number of genera at the 50 indi-

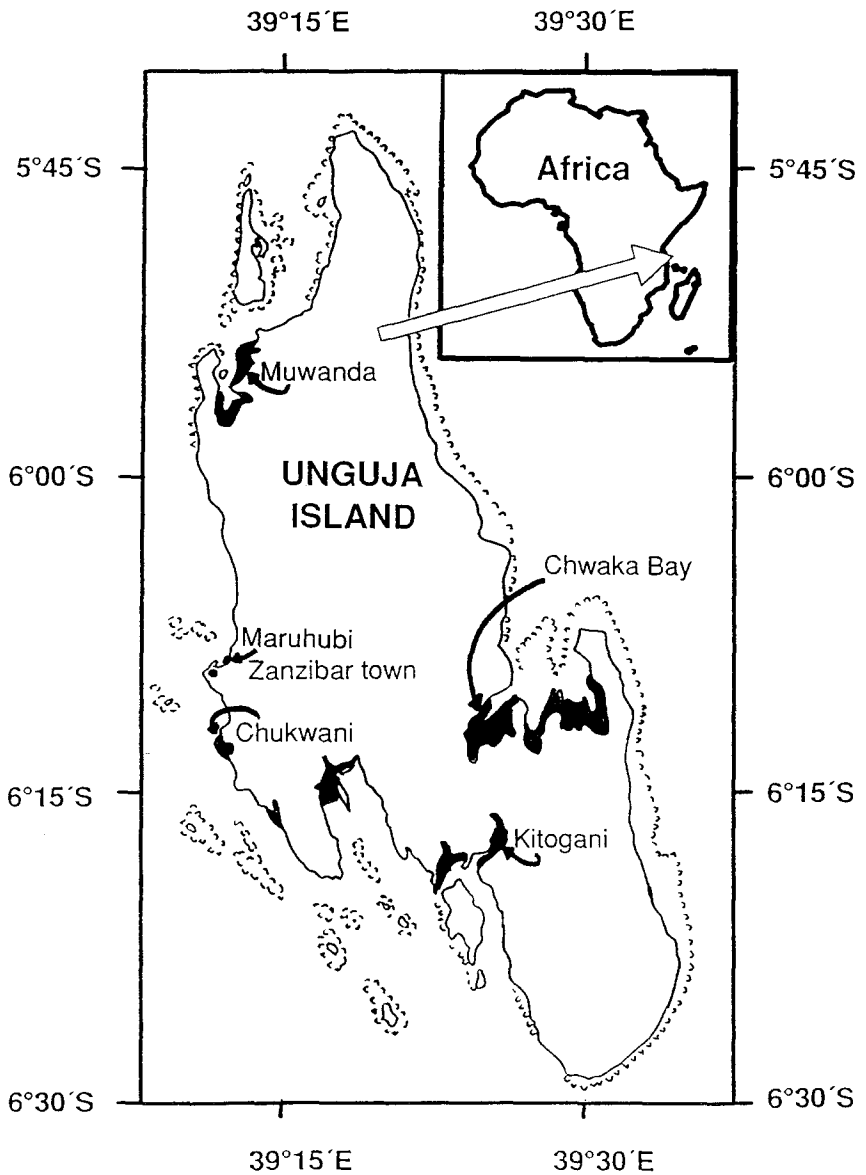

Fig. 1. A map of Unguja island showing the mangrove areas (shaded) and the sampling sites.

vidual level (*S*) using Hurlbert's (1971) rarefaction method.

Nematode genus abundance data were double square root transformed and subjected to multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure. The ANOSIM randomisation test was used to test for differences in nematode assemblage structure and the SIMPER computer program was used to identify those genera contributing to differences observed in the MDS analysis (Warwick *et al.*, 1990a, b).

Results

Physical variables

1. Maruhubi 06 °09'S 39 °12'E. All stations sampled were in close vicinity of *Avicennia marina* which extended from high water to low water level. Apart from station 2, fiddler crabs (*Uca* spp.) were abundant (Table 1). The sediment was rather coarse with mean grain size ranging from 553 to 874 μm (Table 1). Oxygen tension in the ground water was variable with

Table 1. Abiotic and biotic factors estimated at each station. Prop roots belong to species written in bold (A.mar = *Avicennia marina*, S.alb = *Sonneratia alba*, C.tag = *Ceriops tagal*, R.muc = *Rhizophora mucronata*, B.gym = *Bruguiera gymnorrhiza*) * crabs were *Scylla serrata*.

Location	Station. Height	Temp. °C	Sal. ‰	Oxy. %	Grain size mean (μm)	sand (%)	silt (%)	*Uca* spp. burrow no/m²	Prop root no/m²	Tree species in the vicinity of sampling station
	1, HW	31.3	30	< 8	634	41	9	116	0	A.mar,
Maruhubi	2, MW	31.7	40	60	874	79	2	0	130	**A.mar,**
	3, MW	33.0	40	55	822	75	1	54	101	**A.mar,**
06°09′S 39°12′E	4, MW	31.5	35	22	683	62	1	71	176	**A.mar,**
	5, LW	34.0	40	7	553	36	2	108	67	**A.mar,**
	1, LW	29.8	35	20	695	47	5	0	82	**S.alb,**
Chukwani	2, LW	28.4	39	17	660	39	1	0	160	**S.alb,**
	3, LW	27.7	35	20	181	32	1	0	81	**S.alb,**
06°12′S 39°12′E	4, LW	28.5	36	100	673	42	2	0	72	**S.alb,**
	5, HW	—	—	—	358	12	7	30	170	**A.mar,** S.alb
	1, HW	29.6	38	18	571	59	7	48	0	C.tag, B.gym, A.mar
Chwaka	2, HW	—	—	—	217	3	23	56	5% cover	**R.muc,** B.gym
	3, MW	34.9	10	48	262	2	15	60	22	**A.mar,** R.muc
06°11′S 39°25′E	4, LW	42.0	35	7	387	22	9	86	35	**S.alb,** A.mar
	5, LW	31	32	9	429	27	12	122	0	S.alb, A.mar
	1, HW	29.6	85	25	450	25	3	73	39	**A.mar,**
Muwanda	2, LW	30.3	35	19	434	26	8	25*	105	**S.alb,**
	3, LW	28.9	35	18	450	26	1	0	113	**S.alb,**
05°55′S 39°14′E	4, HW	31.2	>100	78	533	40	3	25	0	A.mar
	5, HW	—	—	—	373	14	0	19	154	**A.mar,**
	1, MW	27.4	30	7	448	35	22	10	50% cover	**B.gym,** C.tag
Kitogani	2, MW	27.3	30	9	744	56	17	70	50% cover	**B.gym,** C.tag
	3, MW	27.5	29	7	467	40	25	25	0	B.gym, R.muc, C.tag
06°17′S 39°25′E	1, HW	29.0	40	10	131	1	60	12	0	R.muc
	5, HW	28.4	40	9	158	2	55	51	0	B.gym

low values at both the high and low water stations (Table 1).

2. Chukwani 06 °12′S 39 °12′E. The low water stations were situated in an approximately 10 m wide and 1 km long *Sonneratia alba* forest. In the fringing area seagrass was present together with drift seaweeds. No crabs were present at the low water stations but polychaete mounds were quite common. Mean grain size ranged from 480 to 695 μm at the low water stations but was lower (358 μm) at the high water station (Table 1). The high water station was situated among prop roots of *A. marina*, with some fiddler crabs present. It was surrounded by rocky sills and was too dry to yield ground water.

3. Chwaka Bay 06 °11′S 39 °25′E. The high water Stations were surrounded by several species of mangrove, i.e. *Ceriops tagal, Bruguiera gymnorrhiza, Rhizophora mucronata* and *A. marina*. Fiddler crabs were common on all stations (Table 1). Sediment type varied from sandy (station 1) to mud and clay sediments (stations 2 and 3).

4. Muwanda 05 °55′S 39 °13′E. The high water stations were hypersaline (Table 1). The *Avicennia marina* were smaller than at other locations and the fiddler crabs slower in movements, presumably due to salinity stress. At the first low water station there were numerous *Scylla serrata* crabs. Grain size was similar at all stations, mean grain size ranging from 373 to 533 μm.

5. Kitogani 06 °17′S 39 °26′E. This stand is mainly composed of *Bruguiera gymnorrhiza* and *Rhizophora mucronata* trees without accessible fringing areas. Here the sediment was clearly more silty than in other areas examined (Table 1).

Table 2. Number of major meiofaunal taxa per 10 cm^2 at each station.

Location	Station, Height	Nematoda	Harpacticoida	Polychaeta	Oligochaeta	Turbellaria	Chironomida	Other	Total
	1, HW	764	6	0	9	6	42	3	831
Maruhubi	2, MW	830	167	166	62	2	5	74	1307
	3, MW	335	20	0	2	20	2	0	378
06°09′S 39°12′E	4, MW	345	82	37	8	14	6	6	499
	5, LW	2135	86	53	210	23	0	1	2508
	1, LW	1651	99	151	14	31	0	19	1964
Chukwani	2, LW	1594	68	23	3	53	18	8	1766
	3, LW	1544	53	64	3	161	11	32	1869
06°12′S 39°12′E	4, LW	1413	309	43	14	233	0	56	2067
	5, HW	1560	274	2	14	43	10	37	1941
	1, HW	674	9	0	0	0	2	6	691
Chwaka	2, HW	1458	3	0	6	0	3	6	1477
	3, MW	952	36	14	8	9	0	12	1032
06°11′S 39°25′E	4, LW	3091	26	588	33	62	0	8	3810
	5, LW	1213	15	88	99	9	0	0	1424
	1, HW	805	6	0	0	33	29	0	873
Muwanda	2, LW	2841	312	85	6	40	0	46	3330
	3, LW	4435	394	206	10	148	21	50	5263
05°55′S 39°14′E	4, HW	345	0	0	0	0	3	0	348
	5, HW	629	3	0	110	22	22	0	786
	1, MW	1204	71	0	0	17	5	22	1318
Kitogani	2, MW	459	33	9	0	6	0	18	526
	3, MW	166	34	2	0	0	0	2	205
06°17′S 39°25′E	4, HW	714	14	5	0	0	0	15	747
	5, HW	419	0	6	0	0	0	0	425

Major taxa

Seventeen major taxa were recorded: nematodes were the dominant group in all samples with harpacticoid copepods usually the second most abundant taxon. Small polychaetes and oligochaetes were also quite abundant in many samples (Table 2). Other common groups were Turbellaria, Chironomida and Kinorhyncha, while Amphipoda, Tanaida, Isopoda, Halacaroidea, Gastrotricha, Tardigrada, Ostracoda and Cumacea were only found in low numbers and infrequently.

The highest density was recorded at Mwanda station 3 (5263 ind. 10 cm^2) and the lowest density at Kitogani station 3 (205 ind. 10 cm^2) (Table 2). Within all areas meiofaunal density was very variable (Table 2) and a significant difference among areas was only detected for oligochaetes and turbellarians (Table 2, $P<0.005$). Apart from the chironomidae, all major taxa were found in highest numbers at the low water stations (Fig. 2). This difference was highly significant for nematodes, harpacticoids, polychaetes and turbellarians ($P<0.001$) but not significant for oligochaetes ($P>0.05$). A significant negative correlation was detected between the number of crab holes and the number of harpacticoid copepods ($R=-0.49$, $P<0.05$, $N=18$). All other correlations between environmental factors and major taxa were non-significant.

Nematode assemblage

A total of 94 genera belonging to at least 30 families were recorded (Table 3). About 40% of these genera were only recorded once while 10 genera had frequency of 50% or more. The family with highest number of genera was Chromadoridae (13), but most individuals (37%) belonged to Desmodoridae. The most

Table 3. Nematode family, genus and feeding group status for all genera found in four mangrove areas in Zanzibar. The relative abundance of each station is presented by L = low abundance (<5% of total), M = medium abundance (5–10% of total) and H = high abundance (>10% of total). Generic frequency is expressed as percentage of occurrence. Family and genus abundances are expressed as percentage of total numbers.

Family	Genus	Feeding group	Maruhubi					Chucwani					Chwaka Bay					Muwanda					frq.	Family	Genus
			1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	%	%	%
Anoplastomatidae	Anoplostoma	1b	L	-	-	-	L	-	-	-	-	-	-	-	M	L	L	-	-	-	-	-	25	0.72	0.72
Phanodermatidae	Phanoderma	1b	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.03	0.03
Anticomidae	Anticoma	1b	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	5	0.21	015
	Odontanticoma	2a	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	5		0.06
Ironidae	Syringolaimus	2a	-	-	-	-	-	L	-	-	-	-	-	-	-	-	L	-	-	-	-	-	10	0.93	0.09
	Thalassironus	2a	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	L	-	-	10		0.20
	Trissonchulus	2a	-	-	-	L	-	-	-	-	-	-	L	L	M	L	L	-	-	-	-	-	30		0.62
Oxystominidae	Halalaimus	1a	-	L	-	M	L	L	-	-	-	L	L	-	M	L	L	-	-	-	-	L	50	1.15	0.85
	Oxystomina	1a	-	L	-	-	-	-	-	-	-	L	-	L	-	-	L	-	-	-	-	L	25		0.28
Onchalaimidae	Oncholaimus	2b	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	2.22	0.05
	Oncholaimellus	2b	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	5		0.06
	Prooncholaimus	2b	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	5		0.11
	Viscosia	2b	M	L	-	L	L	L	-	-	-	M	L	L	L	-	L	-	-	-	-	H	55		1.99
Enchelididae	Eurystomina	2b	-	L	-	-	-	-	-	L	-	-	-	L	L	-	L	-	-	-	-	-	25	0.31	0.31
Triplyaididae	Bathylaimus	1b	L	-	-	-	M	M	-	L	-	M	-	-	-	-	L	L	-	L	-	-	40	2.59	2.47
	Tripyloides	1b	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	5		0.09
Rhabdodemaniidae	Rhabdodemanina	1b	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	5	0.11	0.11
Trefusidae	Rhabdocoma	1a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	5	1.01	0.29
	Trefusia	1a	-	-	-	-	-	-	-	-	-	-	-	-	H	-	-	-	-	L	-	-	10		0.71
Chromadioridae	Atrochromadoira	2a	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	7.43	0.01
	Chromadora	2a	-	L	-	-	-	L	-	-	-	-	-	-	-	L	-	-	-	L	-	-	20		0.39
	Chromadorella	2a	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	5		0.11
	Chromadorina	2a	M	L	-	-	-	-	-	-	-	-	-	M	-	L	-	-	-	-	-	-	20		0.76
	Chromadorita	2a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	5		0.04
	Dichromadora	2a	M	M	-	L	L	L	-	-	-	L	-	M	L	L	M	-	-	L	L	-	60		2.50
	Hypodontolamus	2a	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	5		0.05
	Neochromadora	2a	H	L	-	L	L	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	25		0.49
	Endeolophos	2a	-	L	-	-	-	-	-	-	-	H	-	-	M	-	-	-	-	-	-	-	15		1.48
	Prochromadorella	2a	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	5		0.21
	Ptycholaimellus	2a	-	-	-	-	-	L	-	-	-	-	-	L	-	L	L	-	-	-	-	-	20		0.79
	Spiiphorella	2a	-	-	-	-	L	-	-	-	-	-	-	-	-	L	L	-	-	L	-	-	20		0.44
	Tirochamus	2a	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5		0.06
Comesomatidae	Comesa	2a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	5	6.17	0.04
	Dorylaimopsis	2a	-	H	-	-	L	L	L	-	-	-	-	-	-	-	-	-	L	-	-	-	25		1.51
	Paracomesoma	2a	-	-	-	-	-	L	L	L	L	-	-	-	-	L	L	-	M	M	-	-	40		3.70
	Sabatieria	1b	-	-	-	-	M	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	10		0.87
Elthmolaimidae	Ethmolaimus	2b	-	-	-	-	-	-	-	-	-	-	H	-	-	-	-	-	-	-	-	-	5	1.64	0.50
	Gomphionema	2b	-	-	-	-	-	L	-	-	L	-	-	-	-	L	-	-	M	-	-	-	20		1.12
Cyatholaimidae	Kraspedonema	2a	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	L	-	-	10	5.20	0.20
	Longicyatholaimus	2a	-	L	-	-	L	-	-	-	-	-	-	-	-	M	L	-	-	-	-	-	20		1.22
	Marylynnia	1b	-	-	-	-	-	L	L	L	L	-	-	-	-	L	-	-	L	-	-	-	30		1.26
	Paracanthonchus	2a	L	-	-	-	-	-	-	-	L	-	-	-	-	L	-	-	-	-	-	H	20		0.50
	Paracyatholaimus	2a	-	-	-	-	-	-	-	-	-	-	L	H	L	-	-	-	-	-	-	-	15		1.56
	Paralongicyatholaimus	2a	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	L	10		0.23
	Pomponema	2a	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	5		0.12
Selachinematidae	Gammanema	2b	-	-	L	-	-	L	-	-	-	-	L	-	-	-	L	-	-	-	-	-	20	0.95	0.14
	Halichoanolaimus	2b	-	L	-	-	L	L	-	-	-	L	-	-	L	-	-	-	L	-	-	-	30		0.80
Desmodoridae	Chromaspirina	2a	-	-	-	-	-	L	L	L	-	-	-	-	-	-	-	-	-	L	-	-	20	37.29	0.61
	Demodora	2a	H	L	L	H	L	M	L	H	L	M	-	L	-	-	-	-	L	H	-	M	70		9.31
	Leptonemella	1a	-	-	-	-	L	M	H	H	L	L	-	-	-	L	M	-	L	M	L	-	55		5.60
	Metachromadora	2a	M	-	H	M	M	L	L	H	L	M	-	-	-	-	M	-	M	L	L	L	75		6.41
	Molgolaimus	2a	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5		0.28
	Spinnia	2a	M	H	-	L	H	H	H	H	H	M	-	L	L	M	H	-	H	H	-	L	80		14.74
Epsilonematidae	Epsilonema	1a	-	-	-	-	-	-	-	-	-	-	-	-	M	-	-	-	-	-	-	-	5	0.23	0.22
Microlaimidae	Microlaimus	2a	M	-	-	H	L	H	M	H	L	H	H	L	L	H	H	H	H	M	H	-	85	14.64	14.50
Leptolaimidae	Comacolaimus	2a	-	-	-	L	-	L	-	-	-	L	-	M	-	-	-	-	-	L	-	-	25	1.92	0.77
	Leptolaimidae gena	1a	-	-	-	-	-	-	-	-	-	L	-	-	L	-	-	-	-	-	-	-	10		0.09
	Leptolaimus	1a	-	L	L	M	L	-	-	-	-	-	-	L	-	L	L	-	-	-	L	L	45		0.63
	Leptolaimoides	1a	-	-	-	-	-	-	-	-	-	-	H	-	-	-	-	-	-	-	-	-	5		0.36
	Onchum	2a	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	5		0.05
Haliplectidae	Haliplectus	1a	-	-	-	-	-	-	-	-	-	L	-	H	M	-	-	-	-	-	-	-	15	1.72	1.71
Aegialoctaimidae	Aegiolaimus	1a	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	5	0.27	0.15
	Diplopeltoides	1a	-	-	-	-	L	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	10		0.11
Ceramonematidae	Dasynemoides	1a	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.06	0.06
Desmoscolecidae	Desmoscolex	1a	-	L	-	M	-	-	-	-	-	-	-	-	L	-	-	-	L	-	-	-	20	0.36	0.25
	Tricoma	1a	-	L	-	L	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	15		0.11
Monhysteridae	Monhystera	1b	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.12	0.12
Xyalidae	Daptonema	1b	L	H	L	L	L	L	L	-	L	-	-	-	-	L	L	-	L	L	-	-	60	6.65	1.98

Continued on p. 53

Table 3. Continued..

Family	Genus	Feeding group	Maruhubi					Chucwani					Chwaka Bay					Muwanda					frq.	Family	Genus
			1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	%	%	%
	Unident.gen	1b	-	-	-	-	-	-	-	-	-	-	-	M	L	L	M	-	L	M	-	-	30		2.16
	Steineria	1b	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	5		0.05
	Stylotheristus	1b	L	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10		0.09
	Thesistus	1b	L	-	-	-	-	-	L	-	-	L	L	L	M	-	-	M	L	-	H	H	50		2.22
	Trichothesistus	1b	-	-	-	L	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10		0.09
Sphaeroloimidae	Metasphaerolaimus	2b	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	5	0.67	0.04
	Parasparolaimus	2b	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5		0.14
	Sphaerolaimus	2b	-	L	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	10		0.13
	Subsphaerolaimus	1b	-	L	-	-	L	-	-	-	-	-	-	-	-	L	L	-	-	-	-	-	20		0.35
Linhomoeidae	Desmolaimus	1b	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	5	5.18	0.04
	Eleutherolaimus	1b	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	5		0.04
	Linhomoeus	2a	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	L	-	-	L	15		0.27
	Megadesmolaimus	1b	-	L	-	L	M	M	-	-	-	-	-	-	-	-	L	-	-	-	-	-	25		1.14
	Metalinhomoeus	1b	L	L	-	-	-	L	-	-	L	-	-	-	L	L	M	-	M	L	-	-	45		1.77
	Teschellengia	1a	L	-	-	-	M	L	-	-	L	L	L	L	-	M	M	-	-	-	-	-	45		1.88
Axonolaimidae	Ascolaimus	1b	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.16	0.03
	Axonolaimus	1b	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	10		0.13
Diplopeltidae	Southeniella	1b	-	-	L	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	10	0.05	0.05
Secerneutea	Rhabditis	1b	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	5	0.04	0.04
Unident family	Genus a		-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	L	-	-	-	10		0.31
	Genus b		-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5		0.06
	Genus c		-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5		0.07
	Genus d		-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	5	0.12	
	Genus e		-	-	-	-	-	-	-	-	-	-	-	-	M	-	-	-	-	-	-	-	5		0.19
	Genus f		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	5		0.20
	Shannon-Wiener (H)		3.60	3.43	0.94	3.49	3.95	4.09	3.09	3.16	2.08	3.61	2.55	3.27	3.96	3.92	4.25	0.49	3.65	3.42	1.31	2.84			
	Simpson (D)		0.88	0.87	0.26	0.89	0.90	0.91	0.85	0.86	0.55	0.89	0.76	0.84	0.92	0.89	0.93	0.16	0.90	0.87	0.47	0.81			
	Pielou (J)		0.84	0.77	0.32	0.87	0.84	0.84	0.79	0.81	0.53	0.84	0.71	0.77	0.89	0.82	0.87	0.31	0.86	0.79	0.51	0.82			
	Richness (S)		14.3	13.4	5.0	13.3	17.1	17.8	10.8	10.8	9.4	13.6	8.6	12.9	16.2	17.2	18.7	2.6	13.5	12.9	4.7	9.7			

Table 4. Average number per 10 sq. cm and standard error of the ten most abundant nematode genera at three water levels. Diversity values and the results from 1-way ANOVA and Tukey tests are also presented.

	Low water N=9		Mid water N=4		High water N=7		ANOVA	
	Avg	SE	Avg	SE	Avg	SE	Sign.	Tukey
Spirinia	418	89	50	38	37	21	***	LW>MW,HW
Microlaimus	284	84	18	15	218	95	**	MW<LW,HW
Desmodora	245	124	17	10	56	31	NS	
Metachromadora	141	38	77	70	36	18	NS	
Leptonemella	174	41	0	0	5	4	***	LW>MW,HW
Paracomesoma	118	59	0	0	0	0	***	1)
Daptonema	56	36	3	3	15	15	NS	
Dichromadora	46	18	30	16	25	15	NS	
Bathylaimus	57	25	0	0	28	21	NS	
Theristus	5	4	29	29	68	27	**	HW>MW,LW
Richness - S	14.22	1.17	11.97	2.41	9.48	1.71	NS	
Simpson - D	0.85	0.04	0.74	0.16	0.69	0.10	NS	
Shannon-Wiener - H'	3.51	0.22	2.95	0.68	2.52	0.45	NS	
Pielou - J'	0.79	0.03	0.71	0.13	0.69	0.08	NS	

1) Kruskall-Wallis test employed, *** = $P<0.001$, ** = $P<0.005$, NS = not significant

abundant and frequent genera were *Microlaimus* and *Spirinia*, followed by *Desmodora* and *Metachromadora* (Table 3).

The multidimensional scaling ordination (MDS) of the nematode genera clearly separates samples taken from low water stations from other stations (Fig. 3). There was a significant difference among low water

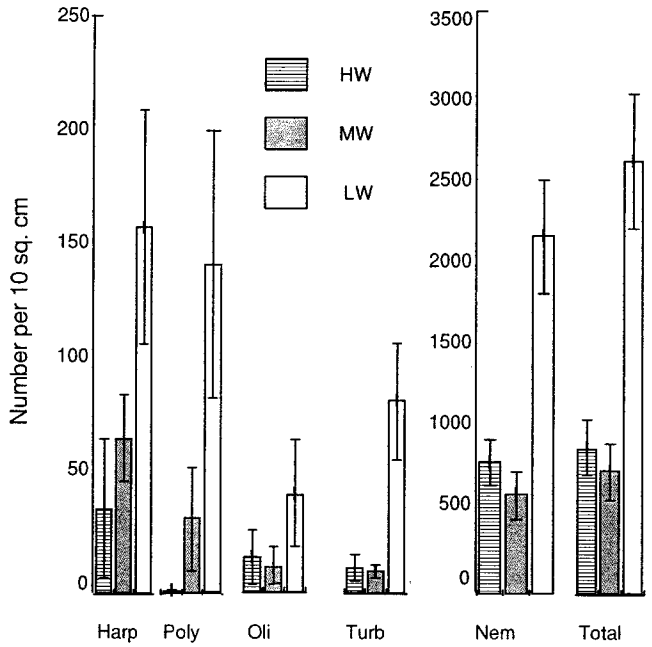

Fig. 2. Average number per 10 cm^2 (+ 1SE) of major meiofaunal taxa at high (solid bars, $N=7$), mid (hatched bars, $N=4$) and low (open bars, $N=9$) water level (Harp = Harpacticoida, Poly = Polychaeta, Oli = Oligochaeta, Turb = Turbellaria, Chir = Chironomidae, Nem = Nematoda).

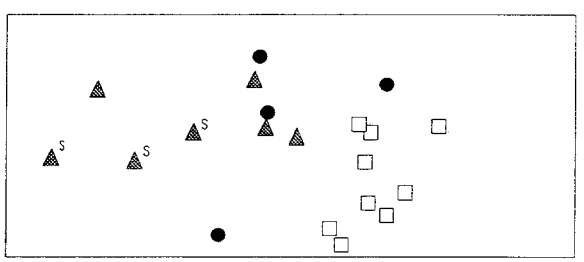

Fig. 3. Multi-dimensional scaling ordination for nematode genera abundance from three tidal levels. Triangle: High water station, Circle: Mid water station, Square: Low water station. Triangles marked with S represent samples taken from hyper saline sediments.

stations and high (ANOSIM, $P<0.001$) and medium water (ANOSIM, $P<0.05$) stations in pairwise comparisons but no significant difference was detected among high and medium water stations (ANOSIM, $P>0.05$).

Of the ten most abundant genera, five showed significant differences in densities between water levels (Table 4). The most abundant genus *Spirinia* was found in about 10 times higher numbers at the low water stations compared to high and mid water stations (Table 4, ANOVA $P<0.001$) and the abundant genera *Paracomesoma* and *Leptonemella* were almost exclusively found at low water stations (Table 4). On average the number of *Theristus* increased landwards (Table 4). Of all the genera 32, 10 and 6 were confined to low, high and mid water stations respectively. Diversity values were on average highest at the low water stations and lowest at high water stations, but this difference was not significant (Table 4). The analysis of similarities among low water stations and high and mid water stations showed that low water stations were more similar to each other than mid and high water stations, average Bray-Curtis similarity being 44 and 27 respectively. The genera contributing most to the dissimilarity among water levels are presented in Table 5. A number of genera were responsible for the observed difference in the nematode assemblage structure. Of the ten genera that contributed most to the dissimilarity, eight were among the ten most abundant genera (Table 4, Table 5).

At all water levels the trophic structure of the nematode assemblage was numerically dominated by epistrate feeders followed by non-selective deposit feeders, selective deposit feeders and predators/omnivores. The higher abundance of nematodes at the low water stations, compared to mid and high water stations, was mainly due to the higher abundance of non-selective deposit feeders and epistrate feeders (ANOVA, $P<0.001$ and $P<0.05$ receptively, Fig. 4). Epis-

Table 5. Average abundance of nematode genera at low water (n=9) and high and mid water (n=11) stations per 10 cm^2. Genera are ranked according to average Bray-Curtis dissimilarity ($\bar{\delta}$) between samples from different water levels. Mean values representing the contribution of each genus (i) to $\bar{\delta}$ are given ($\bar{\delta}_i$) and also shown as percentage contribution to $\bar{\delta}$ ($\bar{\delta}_i$%) and cumulative percentage ($\sum \bar{\delta}_i$%). A cut-off to the genera list was applied at $\sum \bar{\delta}_i\% = 50\%$

	Low	Mid High	$\bar{\delta}_i$	$\bar{\delta}_i$%	$\sum \bar{\delta}_i$%
Leptonemella	174	3	3.57	4.90	4.90
Spirinia	418	42	3.36	4.61	9.50
Paracomesoma	118	0	2.94	4.03	13.53
Desmadora	245	42	2.49	3.41	16.95
Metachromadora	141	51	2.30	3.15	20.10
Microlaimus	284	145	2.11	2.89	22.99
Daptonema	97	29	2.07	2.83	25.82
Theristus	5	54	2.03	2.77	28.60
Metacyatholaimus	40	0	2.02	2.76	31.36
Metalihhomoeus	51	4	1.86	2.54	33.90
Bathylaimus	57	18	1.80	2.46	36.36
Viscosia	13	41	1.72	2.35	38.71
Dichromadora	46	27	1.68	2.30	41.01
Terschellengia	53	5	1.57	2.16	43.17
Dorylaimus	31	14	1.46	2.00	45.17
Gomphionema	36	0	1.34	1.84	47.01
Chromaspirina	19	0	1.34	1.84	48.85

trate feeders were most abundant at all water levels, but only significantly so for the high water stations (ANOVA, $P < 0.05$).

Numbers of selective deposit feeders were negatively correlated with average grain size ($R = -0.57$, $P < 0.01$, $N = 20$) and positively correlated with % of silt ($R = -0.49$, $P < 0.05$, $N = 20$). No significant correlations were found for other feeding types and the factors measured at each station.

At the hyper saline stations in Muwanda (stations 1 and 4) the nematode assemblage structure was different from most other stations (Fig. 3), particularly in having very low diversity values (Table 4). At these two stations only 3 + 6 genera were recorded, two of them being abundant at both stations i.e. *Microlaimus* and *Theristus*. At station 5 which was situated on the same plateau as the hyper saline stations it was impossible to dig to the ground water level. At this station diversity was also low. In this area, fiddler crabs were considerably slower to escape into their burrows when disturbed.

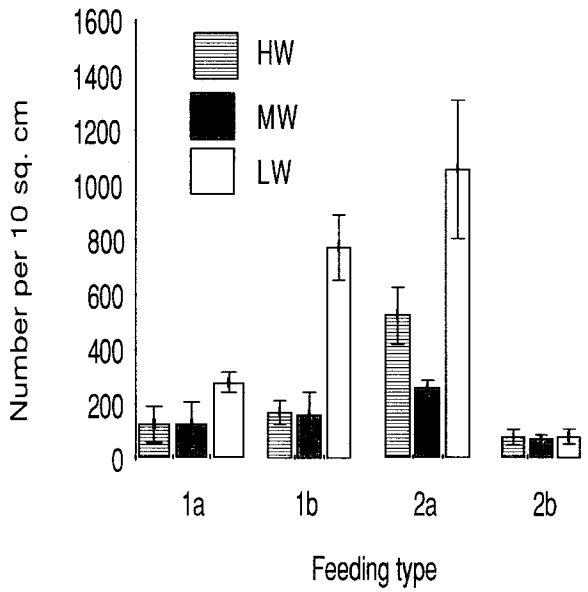

Fig. 4. Average number per 10 cm^2 (+ 1SE) of nematodes in each feeding category (1a = Selective deposit feeders, 1b = Non-selective deposit feeders, 2a = Epistrate feeders, 2b = Predators/Omnivores) from three intertidal areas (hatched bars: high water, $N = 7$; solid bars: mid water, $N = 4$; open bars: low water, $N = 9$).

Discussion

The density of major meiofaunal taxa in mangrove sediments varies considerably both on global and local scales (e.g. Lalana-Rueda & Gosselck, 1980; Hodda & Nicholas, 1985; Alongi, 1987a, b; Dye, 1983; Vanhove *et al.*, 1992). This variation is within the recorded range from other intertidal habitats. In this study it was clear that the height above sea-level was a major factor influencing density, i.e. the low water stations had in general higher density than mid and high water stations. Several authors have found significant differences in meiofaunal densities among intertidal positions in mangrove areas with highest abundance at low water stations (Hodda & Nicholas, 1985; Alongi, 1987b, 1990b; Nicholas *et al.*, 1991), although Dye (1983) found meiofauna in highest number at mid water level. Alongi (1987b, 1990b) concluded that physical factors (temperature, grain size, salinity) accounted for the difference he observed rather than biological variables. However it is difficult to attribute my findings to a single component, since the density of the major taxa showed no significant correlation with the environmental factors measured. In the case of the harpacticoids the negative correlation with the number of *Uca* spp. burrows was significant but rather weak.

In Australian mangrove areas Dye & Lasiak (1986) found that when fiddler crabs were excluded from sediments the abundance of meiobenthos increased 2- to 5-fold (98% nematodes). As the crabs are not known to ingest meiofauna the authors suggested that avoidance by downward migration and/or competition for food resources accounted for the increase. In salt marsh sediments both positive and negative effects of fiddler crabs on meiofaunal densities have been demonstrated (Hoffman *et al.*, 1984; DePatra & Levin, 1989).

The lack of significant correlations between environmental factors measured in this study and meiofauna taxa does not mean that these factors were not contributing to the density variations observed. They may indeed control the population densities of the major taxa differently and in different proportion at the various stations. An experimental approach where the factor of interest can be manipulated while fluctuations in all other variables kept to minimum may be more appropriate than simple correlation analyses, in evaluating the importance of community control mechanisms. Other factors, like food availability and sediment chemistry may also be of importance.

It is clear that with elevated intertidal height oscillations in physical parameters (salinity, temperature, water content etc.) become larger as well as more variable. If these factors are influencing the animal assemblages then we should expect more variable fauna within high intertidal areas compared with low. This seems to be the case in current study. The hypersaline stations in Muwanda certainly contributed to this variance. The salinity stress there clearly resulted in very poor fauna. At station 4 where salinity was over 100‰ the fauna was restricted to 3 nematode genera, *Microlaimus*, *Theristus* and *Bathylaimus*.

The dominance of epistrate feeders in the samples may be attributed to some extent to the sediment type. In the Australian mangroves deposit feeders usually outnumber other feeding guilds (e.g. Hodda & Nicholas, 1986; Alongi, 1987b) but there the sediment was much finer than in the current study. In general there is a trend for the proportion of epistrate feeders to be higher in sandier sediments and for deposit feeders to dominate in finer sediments (e.g. Wieser, 1959; Hopper & Meyers, 1967; Tietjen, 1969; Hodda & Nicholas, 1986). This is also in accordance with current finding that the numbers of selective deposit feeders were negatively correlated with average grain size.

Based on several studies (Hopper *et al.*, 1973; Fell *et al.*, 1975; Krishnamurthy *et al.*, 1984; Alongi, 1986, 1987b) Alongi (1987b) suggested that predatory nematodes are more abundant in the tropics than in other intertidal areas. The results of this study do not support the generalisation that predatory fauna is more abundant in tropical sediments. A number of samples from a sandflat on the eastern coast of Zanzibar also show low proportion of predatory nematodes (pers. observ.). It appears that the proportion of feeding categories is as variable in the tropical mangrove sediments as in other intertidal areas.

Investigations on nematode assemblage structure at the genus or species level in mangrove sediments are limited to eight studies, seven conducted in Australia (Decreamer & Coomans, 1978; Hodda & Nicholas, 1985, 1986; Alongi, 1987a, b, 1990b; Nicholas *et al.*, 1991) and one in India (Krishnamurthy *et al.*, 1984). From these studies it is clear that there is no distinct nematode assemblage confined to the mangrove areas i.e. there appear to be no numerically dominant species endemic (Alongi, 1987b) or common dominant genera among mangrove forests. However a dominance of Desmodoridae and Microlaimidae has also been reported in other mangrove areas (Decraemer & Coomans, 1978; Nicholas *et al.*, 1991) though not in all (Hodda & Nicholas, 1986). The most common genera found in this study are found in marine sediments all over the globe. That we do not have a well defined nematode assemblage in mangrove sediments may most likely be attributed to the heterogeneity of the environment, both in space and time. With only a handful of studies on meiofauna assemblage structure in mangrove sediments all generalisations regarding the structure and the control factors of meiobenthic assemblages in these diverse ecosystems must be regarded as tentative.

Acknowledgments

I thank Magnus Ngoile, the director of the Institute of Marine Sciences on Zanzibar for making facilities available and all the staff for helping in one way or another, Ron Johnstone for introducing me to the tropics. M. Mwadini, J. P. Shunula, S. M. G. Ndaro and O. Papakosta assisted in the field. Special appreciation goes to O. Papakosta who extracted and counted the meiofauna samples as well as preparing all nematode slides. Brian Bett and Ragnar Elmgren made valuable comments on an earlier draft of the manuscript and Magda Vincx is thanked for constructive criticism. This study was supported by the SAREC

(Swedish agency for research co-operation with developing countries) marine science programme in East Africa.

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