Hydrobiologia **426:** 57–64, 2000.
G. Liebezeit, S. Dittmann & I. Kröncke (eds), Life at Interfaces and Under Extreme Conditions.

Meiobenthos of hypersaline tropical mangrove sediment in relation to spring tide inundation

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Key words: hypersaline, mangrove, tidal cycles, meiofauna, nematode assemblage

Abstract

Tropical intertidal sediments often contain porewater of relatively high salinity, especially in areas exposed to longer periods without seawater inundation and high evaporation. Such an area exists on the west coast of Zanzibar: a high intertidal mangrove plateau, flooded only during spring high tides, with sediment porewater salinities commonly exceeding 100 ppt. A field survey was conducted in this area to examine variations in population density of major meiofaunal taxa and the assemblage structure of free-living marine nematodes during spring-neap tidal cycles. Samples were taken on seven occasions for two months, starting from the end of the rainy season. Porewater salinity remained high throughout the sampling period, ranging from 89 to 160 ppt. Neither spring tide inundation nor heavy rains lowered the salinity markedly. The meiofauna consisted only of four taxa, present on all sampling occasions: nematodes, harpacticoid copepods, plathyhelminthes and chironomids. Densities in surface sediments (0–5 cm) were low compared to other mangrove areas, ranging from 271 to 656 animals 10 cm^{-2} with nematodes dominant on all sampling occasions (58–87%). Density fluctuations could not be explained by the effects of spring tide inundation, but the meiofauna showed significant correlations with grain size and organic material. Despite the wide range of salinity, only the numbers of chironomids were negatively correlated with increased salinity. Nematode species diversity was low in all samples, although altogether 28 species were recorded in the samples. Four species occurred in more than 50% of the samples (*Microlaimus* sp. (100%), *Metalinhomoeus* sp. (76%), *Daptonema* sp.l (56%), *Chromadorina* sp. (56%)) while 12 species were found only in one or two samples. Multidimensional scaling ordination (MDS) of the nematode species abundance data indicated little effects of spring tide inundation on the assemblage structure, but rather a successive change from wet to dry season with a reduction in species diversity and increased numbers of the dominant nematode species *Microlaimus* sp.

Introduction

In physically harsh environments, such as exposed sandy beaches or hypoxic sediments, the abundance and species diversity of benthic macrofauna is often greatly reduced and sometimes this group totally disappears. By contrast, benthic meiofauna may survive in such environments, often in relatively high abundance, although diversity is usually limited to a few specialised species (e.g. Ólafsson, 1991; Vopel et al., 1996; Modig & Ólafsson, 1998).

Mangrove forests occupy large areas of the world's tropical coastlines. These forests occur at all intertidal levels and may, therefore, exhibit large variations in temperature and salinity. Longer periods without inundation, together with characteristics of tropical areas such as high evaporation and periods of little rainfall, result in high water losses from the sediment. Thus, combined with limited ground water flow, excessive accumulation of salt in the porewater can occur. High salinity areas may be recognised by dwarfed trees and bare patches devoid of trees (Alongi, 1989; Wolanski et al., 1992).

In a survey of the mangroves of Zanzibar, Ólafsson (1995) described the meiobenthos in a hypersaline habitat where sediment salinities exceeded 100 ppt. In these extreme conditions, no marine macroinfauna were found and the meiofauna was restricted to three taxa in relatively low numbers. Apart from a brief account of meiofauna densities in extreme salinities (up to 135 ppt) (Alongi, 1988), the meiobenthos in hypersaline mangrove habitats has received no further attention.

The hypersaline area in Zanzibar is located at high intertidal level where the sediment is inundated only at spring high tides. This means that the sediment is exposed to incoming sea-water two times a day for ca. 4–6 days and then stays dry until the next spring tide after ca. 8–10 days. The meiofauna inhabiting this area may be affected by the tidal cycle in several ways. It is well known that meiofauna are rapid colonisers of intertidal sediments (e.g. Sherman & Coull, 1980; Savidge & Taghon, 1988), where hydrodynamic forces are relatively high, providing a quick dispersal via currents (see review by Palmer, 1988). Therefore, it is plausible that the area may be colonised at every spring tide by marine species that are not adapted to extreme saline conditions. This would presumably result in higher density and different species composition at, or just after, the spring tides compared to periods when the sediment is not flooded. Secondly, the flooding of the hypersaline sediment could act as a lifeline to those species present in the area by lowering the porewater salinity during critical periods in their life-cycle. Several meiofauna species, for instance, complete their life-cycle within hours or days (cf. Hicks & Coull, 1983; Heip et al., 1985). In the hypersaline area, we might therefore have species that thrive under the periods of flooding, while during the non-flooding periods only the most tolerant individuals will survive.

Materials and methods

Study area

Unguja island is the largest island of Zanzibar and supports six major mangrove stands of approximately 6000 hectares (Ngoile & Shunula, 1992; Shunula & Whittick, 1996). This study took place in the Muwanda mangrove forest (05° 55′ S, 39° 13′ E), the second largest mangrove stand, situated on the north-west coast of Unguja. The forest is up to 1 km wide and covers an area of about 520 hectares. A description of the zonation of mangrove vegetation is given in Shunula & Whittick (1996). *Avicennia marina* dominates the mid and high intertidal forest and is the only species extending landwards (Shunula & Whittick, 1996).

The field sampling was confined to a plateau in the high intertidal zone of the forest. The *Avicennia marina* grow there as small shrubs, occurring scattered over the plateau. Large patches (hundreds of m^2) occur as bare sediment without trees. Porewater salinity is generally very high here, typically over 100 ppt and the local residents use parts of the plateau for salt extraction.

Field sampling

A sampling station, ca. 25 m^2, was located at a site approximately 3.7 m above chart datum, 80 m from land in a part of the plateau, where the sediment appeared smooth, without trees, pneumatophores or visible crab holes. Sampling was carried out on seven occasions from the end of May to middle of July 1996. This included four spring tide samplings; June 4 (S2), June 18 (S4), July 2 (S5) and July 16 (S7) and three sampling occasions during neap tides; May 24 (N1), June 11 (N3) and July 9 (N6). No sampling was done during the neap tide between S4 and S5. Sampling was carried out at low tides during daytime. The first sampling date was 1 day after the last heavy rains from the rainy period. The station was inundated at least at four high tides prior to sampling at spring tide while it had not been inundated for at least eight high tides prior to sampling at neap tides.

At each sampling occasion, a square frame of 1 m^2 was randomly located and samples retrieved as follows: one 5 cm deep core (8.5 cm^2) was pushed into the sediment at a fixed position within the frame for meiofauna sample and left in position. Only meiofauna cores were taken on the first sampling occasion. 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. Cores (8.5 cm^2) for organic content and grain size determination were taken down to 5 cm depth and finally the core for meiofauna was retrieved and fixed with 5% formalin. When possible, porewater was retrieved from the holes left by the sediment sampling and salinity measured with a refractometer. On some occasions, one had to dig deeper to get sufficient water for salinity measurements. The whole procedure was repeated 5 times, yielding 5 replicates of each variable.

In the laboratory, the meiofauna samples were washed through 500 and 40 μm sieves and meiofauna extracted from the 40 μm fraction using Ludox (colloidal silica polymer) at a specific gravity of 1.15. The meiofauna was enumerated and identified to major taxa in a Petri dish under a stereo dissecting microscope. The extracted samples were transferred to glycerine and mounted on slides for nematode identification under a high-power microscope. Nematodes were sorted to species, identified to genus level using the pictorial keys of Platt & Warwick (1983) and assigned to trophic groups according to the scheme of Wieser (1953). Grain size samples were oven dried at 85 °C for 24 h and subsequently sieved through a series of sieves (2, 1, 0.5, 0.25, 0.125 and 0.063 mm) and grain size determined on the basis of the weight of each size fraction (Giere et al., 1988). Organic content was determined by oven drying samples at 85 °C for 48 h and then combusting them at 550 °C for 12 h (Giere, 1993). Chlorophyll samples were fixed with 90% ($^{v}/_{v}$) acetone and kept in the dark, refrigerated for 24 h and analysed using a spectrophotometer according to Parsons et al. (1984). Temperature was measured at 3 cm depth in the sediment with a mercury thermometer. Due to technical problems, chlorophyll samples were not processed from the second sampling date (S2).

Statistics

Differences in density were investigated by means of one-way analysis of variance. Paired a posterior 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 apart from organic% data which were arcsine transformed. Cochran’s C test was used to check the assumption of homoscedasticity. Major taxa and nematode species abundance data were double square root transformed and subjected to non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure (Warwick et al., 1990a,b).

Results

Environmental variables

During the course of the study, the environmental factors fluctuated considerably (Figure 1). Porewater salinity was on average higher at neap tides than at spring tides (Figure 1 and Table 1). Mean grain size varied also significantly ($p < 0.00l$) being higher in the beginning of the study compared to later dates.

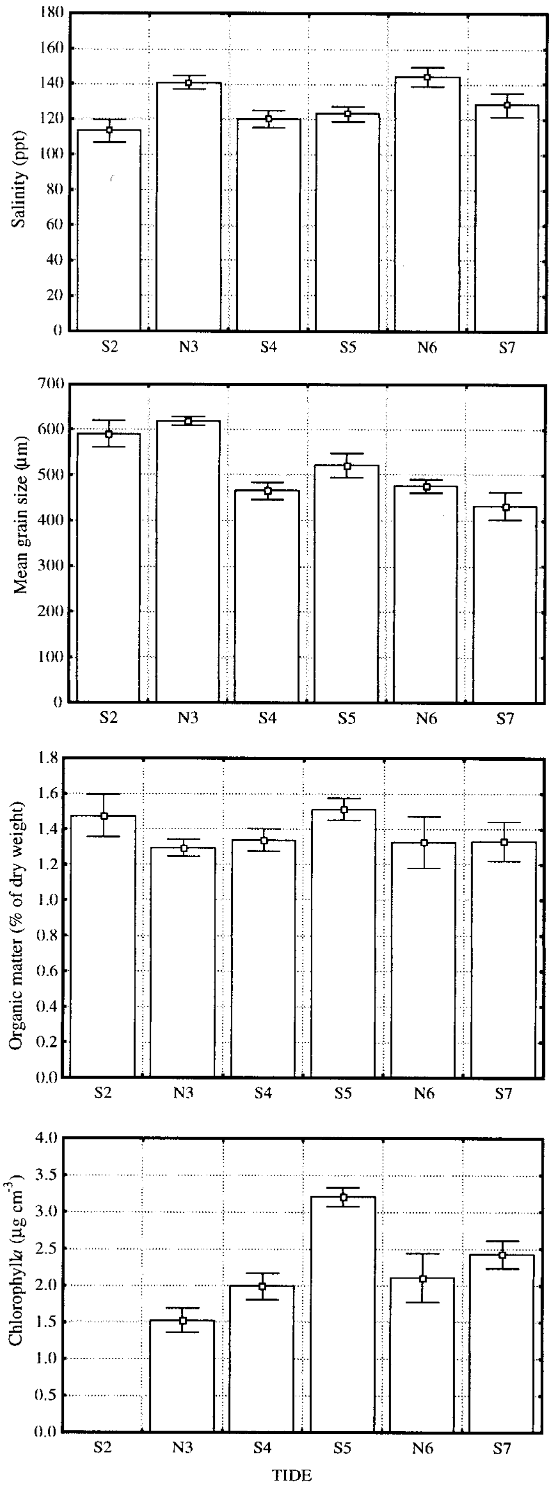

Figure 1. Average values ($n = 5$) of environmental factors from six sampling dates (S: spring tide, N: neap tide, numbers: sampling occasion). Error bars represent standard error.

Table 1. The results of one-way ANOVA and Tukey a posteriori tests on meiofauna and environmental data. NS = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (S: spring tide, N: neap tide, numbers represent sampling occasions)

	ANOVA	Tukey
Meiofauna		
Nematoda	*	NS
Harpacticoida	**	N1>S4, S5, N6, S7
Chironomida	NS	
Plathyhelminthes	***	N3<S2, S4, S5, N6, S7; S2, S4<N6, S7
Environmental factors		
Salinity	**	S2<N3, N6
Grain size	***	S2>S4, N6, S7; N3>S4, N6
Chlorophyll *a*	**	N3<S5, S7; S5>S4, N6
Organic matter	NS	

There was no significant difference in organic content of the sediment among dates (Figure 1, Table 1), while chlorophyll *a* varied significantly (Figure 1, $p < 0.01$). Temperature in the sediment was similar on all sampling occasions varying from 29 to 33 °C.

Meiofauna taxa

Altogether, four taxa were recorded on all sampling occasions. Densities in surface sediments (0–5 cm) were low compared to other mangrove areas, ranging from 271 to 656 animals 10 cm^{-2}. Nematodes were most abundant in all samples, constituting between 58% and 87% of the total meiofauna. Harpacticoid copepods were usually the second most abundant group with 6–34% of total meiofauna. Chironomids (Diptera larvae) and plathyhelminthes were also found in all samples and composed between 3–9% and <1–12%, respectively, of the total fauna.

There was a significant temporal difference in abundance of nematodes, harpacticoids and plathyhelminthes (Figure 2, Table 1). These density variations did not show patterns reflecting the spring or neap tides. For the nematodes, there was an increase in overall density during the latter part of the study as was the case for the plathyhelminthes (Figure 2). The harpacticoids were, however, found in more than three times higher densities at the first sampling occasion compared to the other occasions. There was no significant difference in the density of chironomids among dates ($p > 0.05$).

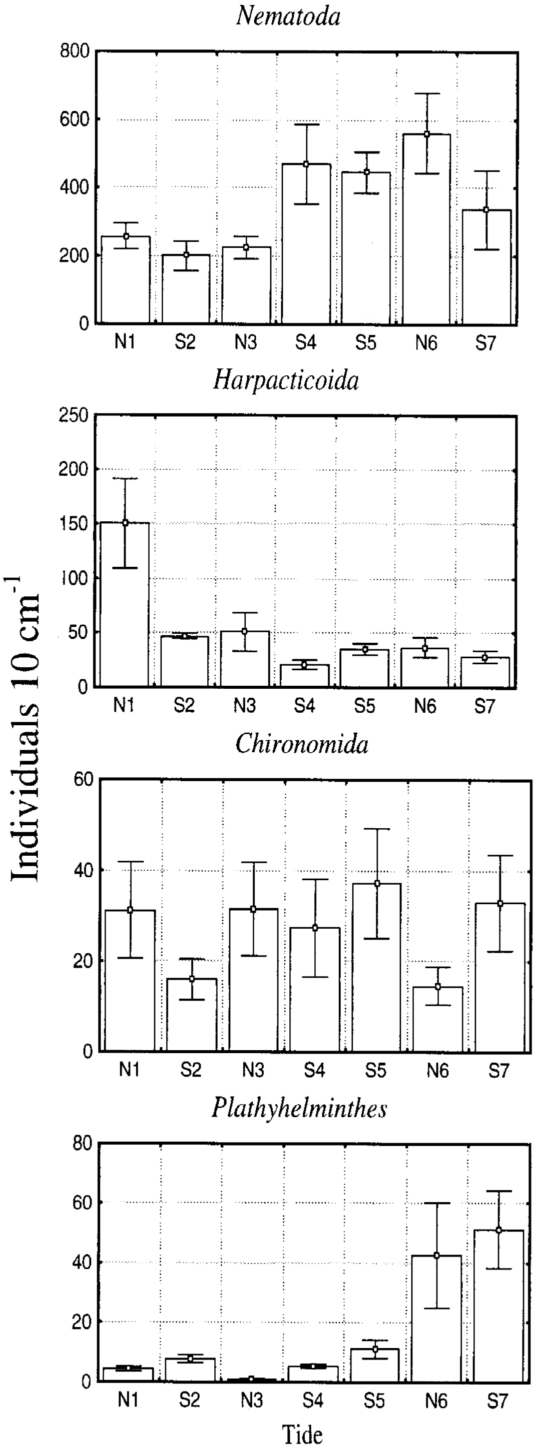

Figure 2. Average number ($n = 5$) per 10 cm^2 of individuals of the meiofauna taxa from all sampling dates (S: spring tide, N: neap tide, numbers: sampling occasion). Error bars represent standard error.

Table 2. Nematode species found in current study. Family, feeding group status (according to Wieser (1953), percentage frequency occurrence and percentage of total abundance is also presented (1a: selective deposit feeders, 1b: non-selective deposit feeders, 2a: epistrate feeders, 2b: predators/omnivores)

Family	Species	Feeding group	Frequency [%]	Abundance [%]
Oncholaimidae	*Viscosia* sp.	2b	15	1
Tripyloididae	*Bathylaimus* sp.	1b	3	<1
Trefusiidae	*Trefusia* sp.	1a	12	2
Chromadoridae	*Euchromadora* sp.	2a	6	<1
	Chromadora sp.	2a	18	3
	Chromadorina sp.	2a	56	9
	Chromadorita sp.	2a	15	1
	Ptycholaimellus sp.	2a	6	<1
Ethmolaimidae	*Gomphionema* sp.	2b	3	<1
Cyatholaimidae	*Marylynnia* sp.	2a	3	<1
Selachinematidae	*Halichoanolaimus* sp.	2b	3	<1
Desmodoridae	*Chromaspirina* sp.	2a	15	1
	Metachromadora sp.	2a	3	<1
	Spirinia sp.	2a	12	1
Microlaimidae	*Microlaimus* sp.	2a	100	50
Leptolaimidae	*Camacolaimus* sp.	2a	3	<1
	Leptolaimus sp.1	1a	24	2
	Leptolaimus sp.2	1a	3	1
Monhysteridae	*Monhystera* sp.	1b	9	1
Xyalidae	*Daptonema* sp.1	1b	56	10
	Daptonema sp.2	1b	6	<1
	Daptonema sp.3	1b	6	<1
	Paramonhystera sp.	1b	9	<1
	Promonhystera sp.	1b	9	<1
	Theristus sp.	1b	18	1
Linhomoeidae	*Linhomoeus* sp.	2a	12	1
	Metalinhomoeus sp.	1b	76	13

Several significant correlations were established between numbers of animals and environmental factors, when data from all sampling occasions were taken together. The correlations, however, were usually weak. Chironomida was the only taxon that showed significant correlation with salinity ($R = -0.41$, $p < 0.05$, $N = 30$). Significant negative correlations were detected between mean grain size and the number of nematodes ($R = -0.53$, $p < 0.01$, $N = 30$) and the number of plathyhelminthes ($R = -0.38$, $p < 0.05$, $N = 30$). A positive correlation was detected between grain size and harpacticoids ($R = 0.48$, $p < 0.01$, $N = 30$). Despite very small differences in the amount of organic material, there were significant correlations with the meiofauna. Nematodes were negatively correlated with organic material ($R = -0.55$, $p < 0.01$, $N = 30$), while there was a positive correlation for harpacticoids ($R = 0.38$, $p < 0.05$, $N = 30$).

Nematode assemblage

Altogether, 28 putative species of nematodes were recorded (Table 2). Of these, four species occurred in more than 50% of the samples (*Microlaimus* sp. (100%), *Metalinhomoeus* sp. (76%), *Daptonema* sp. (56%), *Chromadorina* sp. (56%)), while 12 were found only in one or two samples. The first three sampling dates *Microlaimus* sp. comprised on average 35% of the nematode population, but 60% for the last four sampling occasions. Multidimensional scaling ordination (MDS) of the nematode species abundance data indicated little effects of spring tide inundation

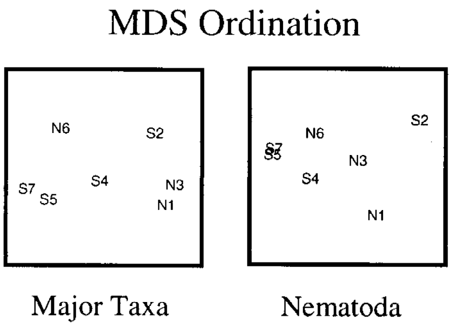

Figure 3. Non-metric MDS ordination of major taxa and nematode species abundance data based on average values ($n = 5$). (S: spring tide, N: neap tide, numbers: sampling occasion).

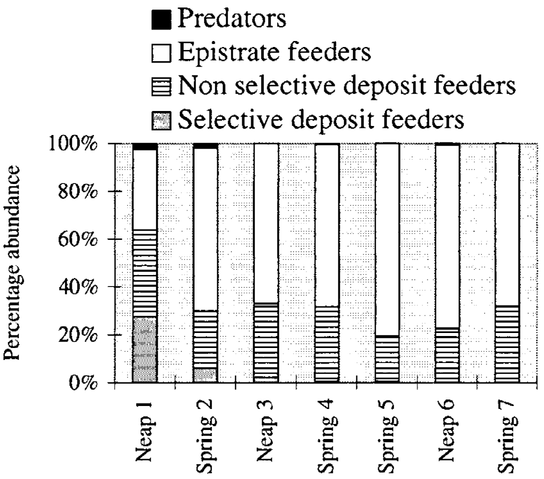

Figure 4. Percentage abundance of nematode trophic groups from each sampling occasion.

on the assemblage structure (Figure 3), but rather a successive change from wet to dry season. The number of species was far the highest on the first sampling date or 18 species (N1), but then gradually became lower i.e. 12 (S2), 12 (N3), 11 (S4), 6 (S5), 9 (N6) and 7 (S7). There was also a change in the trophic structure with time. Three species of selective deposit feeders were relatively abundant the first sampling dates but then this group totally disappeared by the end of the study (Figure 4).

Discussion

Despite the existence of an abundant and species rich meiofauna assemblage lower on the shore, approximately 200 m away from our station (Ólafsson, 1995), this field survey strongly suggests that there is not a significant immigration of meiofauna from the lower shore into the hypersaline area during spring tide flooding. There was neither an increase in numbers for any of the taxa just after flooding, nor did we find any substantial change in species composition associated with the tidal cycle. Like most mangrove forests, this one is in a sheltered area and presumably the tidal currents are not strong enough to carry significant amount of meiobenthic animals from the lower shore.

To our surprise, the porewater salinity remained very high after flooding. This was also evident in a preliminary study carried out during the last days of the heavy rains where porewater salinity was well above 100 ppt, while freshwater pools were still on the sediment surface. This suggests that hypersalinity is a permanent condition and, therefore, it was not strange to note that none of the species appeared to be dependent on the incoming seawater. While the porewater salinity was higher during the neap tide sampling, the difference was relatively small from when the area had just been flooded, and perhaps not of a physiological importance for the species adapted to already high salinities. It is clear that the fauna living in or drifting to this habitat must be able to cope with extremely high porewater salinities. Apart from chironomids, the meiofauna seems to be unaffected by salinity variations (89–160 ppt) with respect to major taxa composition and densities. Other environmental factors may, therefore, be more important in regulating the meiofauna numbers within this habitat. For example, nematodes tend to be more abundant in finer sediments (Coull, 1988) and we found a negative correlation between nematode numbers and grain size. Though there was a significant difference in the mean grain size, the difference was little on average ranging from ca. 430 to 610 μm. The coarser sediment from the first sampling dates might result from flushing out of finer sediment particles by the heavy rains. We do not believe that this is an artefact as several samples were taken randomly within the same relatively small area at each sampling date.

While we could not link the tidal cycle to changes in the structure of the meiofauna assemblage, there was some indication that wet and dry seasons affected the infauna at this site. At the first sampling date, the rainy season had just ended with the last heavy rains only 1 day prior to sampling. It is obvious that the assemblage structure of the fauna was different both in terms of abundance, diversity and species composition at the first sampling dates. Input of dissolved and particulate organic matter through runoff as a result of heavy rains might have favoured, for instance, selective deposit feeders as these may utilise dissolved organic matter. This group of nematodes was abundant during the first sampling date and was present only in low numbers on subsequent sampling dates with none recorded on the last two sampling dates. The dominant species, *Microlaimus* sp., increased in numbers with time and was approximately four times higher in numbers during the last four sampling dates compared to the first three ones. This species can be classified as an epistrate feeder, where it presumably scrapes off bacteria and algae from sediment grains. It is plausible that the rain had drastic effects on the food resources this species depends on. Unfortunately, we can only offer circumstantial evidence here, as our laboratory experiments, designed to test whether salinity significantly altered meiobenthic assemblage structure, showed unacceptably high mortality of nematodes in control and treatment mesocosms. It appears that there is no distinct nematode assemblage characteristic of mangrove areas (Ólafsson, 1995; Somerfield et al., 1998). The nematode genera found in this study are commonly found in marine sediments all over the globe. Alongi (1988) recorded low numbers of nematodes during hypersaline conditions at a high intertidal mangrove station in tropical north-eastern Australia. The dominant species at that station was *Terschellingia longicaudata*, not found in the current study. In similarly high saline areas of the Red Sea, Gerdes et al. (1985) found only one nematode species, *Oncholaimus oxyuris*, present in the sediment, a genus not found in the hypersaline area of Muwanda. They also noted harpacticoids, plathyhelminthes and insect larvae as dominant groups of the benthos, which agrees with our current observations.

Conclusions

From this study, we draw the conclusion that in this hypersaline mangrove habitat, the meiobenthos is composed of four taxa, including a number of species, which are resident and able to cope with very high salinities. Immigration to the area appears to be low and the spring tide inundations do not appear to alter the community structure in terms of abundance or species numbers.

Acknowledgements

We thank J. Francis, 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. Special appreciation goes to M. Mwadini who skilfully assisted in the field and the laboratory. Salim M. Mohammed commented on the manuscript. This study was supported by SAREC (Swedish Agency for Research Co-operation with Developing Countries) grant no: SWE-94-057 and the Institution of Tropical Ecology in Uppsala under the Sida programme of Minor field studies.

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