

Meiobenthic assemblage of the grey mangrove (*Avicennia marina*) along the Saudi Arabian coast of the Red Sea with emphasis on free-living nematodes

by

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Abstract

Spatial variability in the population density of meiofauna and the assemblage of free-living marine nematodes was studied at 20 mangrove sites located along the Saudi Arabian coast of the Red Sea. The total abundance of meiofauna varied between the locations and ranged from 119 to 1380 ind. 10 cm⁻². A total of seven main taxa were recorded. Nematodes dominated (64.3%) in all sediment samples. They were followed by harpacticoid copepods (13.2%) and polychaetes (12.9%) with significant differences in their density between the locations surveyed ($p < 0.001$). The Pearson correlation analysis showed significant positive correlations between the sand fraction and nematodes, harpacticoid copepods and turbellarians. Twenty-five genera of free-living nematodes belonging to 15 families were recorded in the study area. Microlaimidae were the most abundant family, while Xyalidae, Desomodridae and Chromidoridae were the most diverse families. *Microlaimus*, *Halalaimus* and *Terschellingia* were the most frequent genera. ANOSIM values obtained for the distribution of different nematode genera in various habitats showed no significant differences. Feeding types of different nematode genera were also documented and the epistrate feeders along with the deposit feeders were found to be the common feeding types in the present study.

Key words: Meiofauna, nematodes, distribution, diversity, mangrove, Red Sea, Saudi Arabia

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Introduction

Mangrove forests occupy large areas of the world's tropical coastline and play an important role in the coastal food webs (Alongi 1989; 1990a; Armenteros et al. 2006; Abrantes & Sheaves 2009; Morrisey et al. 2010). The mangroves are mainly inhabited by a great variety of benthic invertebrates and fish populations and thereby act as nursery and feeding grounds for many organisms (Robertson & Duke 1987; 1990; Polidoro et al. 2010; Barbier et al. 2011). Meiofauna is considered to be the most abundant group within invertebrates, intensively grazed by juveniles of marine organisms such as shrimps, crabs, polychaetes, gastropods and fish (Gee 1989; Ólafsson & Moore 1990; Nagelkerken et al. 2008; Schratzberger & Ingels 2018). Meiofauna can occupy different habitats with varying sediment structure, especially in estuarine sediments, where it play an important ecological role through close association with physicochemical properties of the sediment (Barnes et al. 2008; Ferrero et al. 2008; Semprucci et al. 2014). Many studies have addressed meiobenthic assemblages in different mangrove regions all over the world, providing extensive information on the meiobenthic fauna (e.g. in Africa: Dye 1983a,b; Dye & Lasiak 1986; Vanhove et al. 1992; Ólafsson 1995; Ólafsson et al. 2000; in India: Ansari et al. 1993; Chinnadurai & Fernando 2006; 2007; Kumary et al. 2008; Sahoo et al. 2013; in Brazil: Netto & Galucci 2003; Pinto et al. 2013; in Malaysia: Gee & Somerfield 1997; Somerfield et al. 1998; in Vietnam: Xuan et al. 2007; Mokievsky et al. 2011; in Cuba: Lalana-Rueda & Gosselck 1986; Armenteros et al. 2006; and in Australia: Hodda & Nicholas 1985; 1986; Alongi 1987a,b; Nicholas et al. 1991; Alongi & Christoffersen 1992; Gwyther 2000; Abdullah & Lee 2017). Free-living nematodes, the most abundant metazoans in marine benthic ecosystems, play an important role in the biogeochemistry of mangrove habitats worldwide (Coull 1999; Kathiresan & Bingham 2001; Sajan et al. 2010).

The Red Sea coastline of Saudi Arabia stretches for about 1700 km and covers almost 4/5 of the entire eastern part of the Red Sea and is generally considered as a region that provides favorable conditions for the growth of mangroves (Saifullah 1996). Mangroves on the Saudi Arabian coast of the Red Sea, which cover an area of about 135 km² are the longest mangrove stand in West Asia and the Arabian regions (Almahasheer et al. 2017). These mangroves are found in both the tropical and subtropical zones, where environmental conditions are extreme in terms of higher water temperature and salinity (Edwards 1987; Khalil 2015). Despite the importance of mangrove vegetation as a special habitat that occupies a characteristic niche

in the Red Sea, research focusing on meiofaunal communities that affect the productivity and food web dynamics of these ecosystems is mostly neglected. Quite a few studies have been carried out in the Red Sea, including mostly the western coast, e.g. Pusceddu et al. (2014) who studied the meiofaunal diversity at a single mangrove location in South Sinai, the northern Red Sea, and El-Serehy et al. (2015) who investigated the composition and distribution of benthic meiofaunal assemblages along the Egyptian Red Sea coast in the vicinity of mangrove stands. In addition, Sabeel & Vanreusel (2015) focused on the potential effect of mangrove tree clearance on the nematode density in the Sudanese coast of the Red Sea. Considering all this, it is clear that the eastern coast of the Red Sea has rarely witnessed benthic studies that focused on meiofaunal assemblages. The main objective of the current study is to define meiobenthic communities and different abiotic parameters that affect their spatial distribution in different mangrove regions along the Saudi Arabian coast of the Red Sea. Furthermore, this study provides new insights into the genus composition of nematodes, which can be considered as a preliminary study for this particular region.

Materials and methods

Study area

Twenty different sites, representing various mangrove ecosystems with the grey mangrove (*Avicennia marina*) along the 1500 km coast of the Saudi Arabian Red Sea, were selected for the present study (Table 1 and Fig. 1). The sites are located between 16°30' & 25°30'N and 36°10' & 42°20'E, which covers a stretch of coast from Jazan in the south to Duba in the north (Fig. 1). All sampling sites were located in the leeward part of the subtidal zone. Of the five sites in the Jazan region, two of them (sites II and III) contain a dense population of dead mangrove trees, and another one (site IV) is located near the outlet of a sewage treatment plant. Four sites were selected in the Al-Birk region, with site VI located near a fish farm outlet. The Jeddah region was represented by one site (XI) located near a sewage treatment plant, and the Rabigh region was also represented by one site located near a fish farm effluent (XVI). Both the sewage treatment plant and the fish farm usually discharge the effluent into the coastal areas, after proper treatment and settlement. Al-Wajh and Duba regions comprise the most pristine mangroves in the Red Sea and they were represented by three different sites.

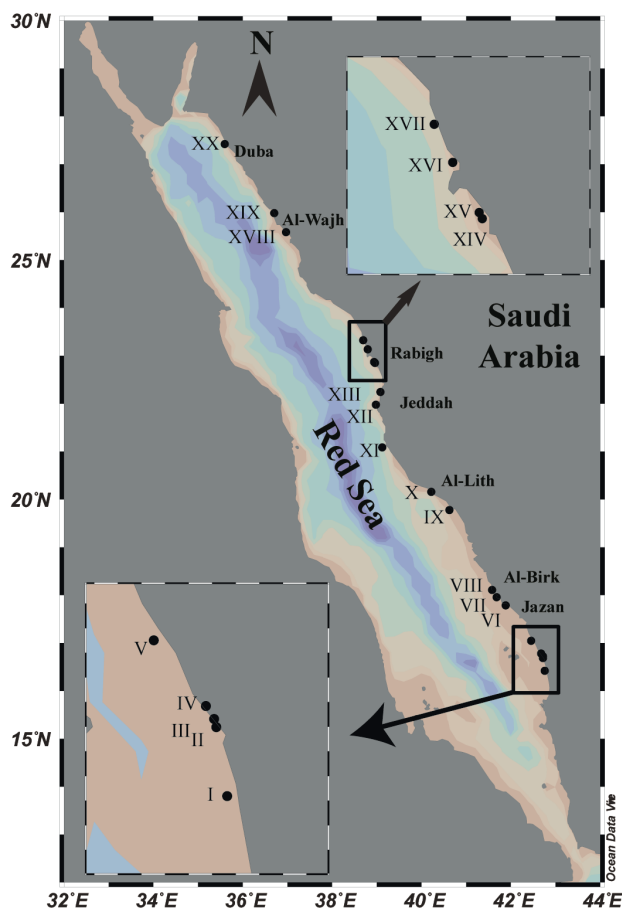


Figure 1
Map showing the study sites along the Saudi Arabian coast of the Red Sea

Sampling, sample processing and laboratory analysis

All field sampling work was carried out in February–March 2017 at low tide using a plastic corer with a length of 10 cm and a diameter of 7 cm. At each site, three replicates of sediment samples were collected for the meiofaunal studies and another three for analyzing the grain size as well as other abiotic parameters. The collected meiofaunal samples were immediately fixed with 4% neutral formalin in plastic bottles. In the laboratory, sediment samples were washed with tap water to remove the excess formalin and the meiofaunal organisms were sorted out using the documentation and illustration technique (Platt & Warwick 1983). The floating content was then sieved through a 40 µm mesh and the organisms retained on the sieve were collected in Petri dishes for sorting and later preserved in 70% ethyl alcohol along with 5% glycerol (Tolhurst et al. 2010). Small drops of Rose Bengal were also added to this solution to facilitate the counting process. All meiofaunal organisms were sorted into main groups and counted using a stereomicroscope. Nematodes were mounted on glass slides following the methodology of Somerfield & Warwick (1996). Identification of nematodes up to the genus level was carried out following the standard protocols of Platt & Warwick (1983, 1988) and Warwick et al. (1998). Clustering of nematodes based on their feeding status was carried out following the procedures of Wieser (1953). They were mainly classified into four feeding types: selective deposit

Table 1

Coordinates of different study sites along the Saudi Arabian coast of the Red Sea

Location	Site No.	Latitude N	Longitude E	Remarks
Jazan	I	16°25'6.85"	42°45'49.08"	Fringing reef
	II	16°41'54.15"	42°43'1.78"	Inland lagoon (dead mangrove)
	III	16°43'54.71"	42°42'29.12"	Inland lagoon (dead mangrove)
	IV	16°47'3.69"	42°40'23.07"	Fringing reef (near a sewage outlet)
	V	17°3'3.16"	42°27'8.85"	Fringing reef
Al-Birk	VI	17°48'0.89"	41°53'21.16"	Inland lagoon (fish farm outlet)
	VII	17°57'9.17"	41°41'10.91"	Fringing reef
	VIII	18°7'11.42"	41°34'52.77"	Fringing reef
	IX	19°47'30.24"	40°37'52.13"	Fringing reef
Al-Lith	X	20°9'56.94"	40°12'50.01"	Inland lagoon (fish farm outlet)
Jeddah	XI	21°16'8.74"	39°7'34.40"	Fringing reef (sewage plant outlet)
	XII	21°58'57.73"	38°58'44.60"	Inland lagoon
	XIII	22°15'11.33"	39°4'50.23"	Fringing reef
Rabigh	XIV	22°52'50.29"	38°56'33.66"	Inland lagoon
	XV	22°51'3.09"	38°57'35.99"	Inland lagoon
	XVI	23°8'10.01"	38°47'47.27"	Inland lagoon (fish farm outlet)
	XVII	23°19'47.25"	38°41'37.06"	Inland lagoon
Al-Wajh	XVIII	5°34'39.25"	36°58'13.98"	Inland lagoon
	XIX	25°59'27.67"	36°42'39.29"	Fringing reef
Duba	XX	27°25'52.30"	35°36'9.54"	Inland lagoon

feeders (1A), non-selective deposit feeders (1B), epigrowth (epistrate) feeders (2A) and omnivores/predators (2B).

In the laboratory, sediment samples were air dried in an oven at 80°C until constant weight and then mechanically sieved through a set of sieves with 2, 1, 0.5, 0.250, 0.125 and 0.063 mm mesh size and granulometric characteristics were determined following Morgans (1956). Total organic carbon (TOC) of dried subsamples was determined according to Parker (1983) by calculating the difference between the dry weight of the sediment (60°C, 24 h) and the residue remained after combustion at 550°C for 4 h. Seawater temperature and salinity were measured using a multi-parameter water quality analyzer (Horiba U50). Electrical conductivity EC (mS cm^{-1}) was measured in 1:2.5 soil:water extract and soil pH (saturated soil paste) as explained by Richards (1954).

Statistical analysis

Different univariate and multivariate tests were performed to find out the possible relations and interactions between the meiofaunal assemblages and other environmental parameters. One-way ANOVA was performed to determine significant differences

within the study sites for different aspects such as meiofaunal abundance, nematode feeding habits, as well as for biodiversity indices using SPSS V23. Values of the Pearson correlation coefficient (r) were also determined to analyze significant correlations between meiofaunal assemblages and environmental parameters. Principal component analysis (PCA) was applied to provide detailed information on the interaction between the environmental variables and various meiofaunal taxa using the PAST software (V3). Analysis of the similarity (ANOSIM) test was carried out to determine the similarity of nematodes among different mangrove habitats. Furthermore, the nematode diversity indices were calculated based on the Shannon-Wiener index (H'), Pielou's evenness index (J') and Margalef's species richness index (d). The Bray-Curtis similarity index and group average linkage were used to perform the multidimensional scaling (MDS) ordination of the abundance of different meiofaunal groups as well as the nematode genera. All these multivariate analyses (except PCA) were performed using the PRIMER 6.0 software (Clarke & Gorley 2006) and the data were transformed to square root prior to each analysis.

Table 2

Differences in abiotic parameters of seawater (temperature – T and salinity – S) as well as sediment [pH, electrical conductivity – EC (mS cm^{-1}); total organic carbon – TOC; and MD – mean grain size] observed at different sites along the Saudi Arabian coast of the Red Sea

Site	Seawater		Sediment					
	T (°C)	S (PSU)	pH	EC (mS cm^{-1})	TOC (%)	MD (μm)	Sediment type	Sorting Index
I	28.9	38.56	8	6.9	3.5	353	medium sand	poorly sorted
II	28.5	43.1	8	5.3	3	296	medium sand	poorly sorted
III	31.1	40.3	7.05	22	3	356	medium sand	poorly sorted
IV	27.9	38.2	7.77	6.79	1	96	very fine sand	moderately sorted
V	28.9	40.1	7.6	10.26	3.7	208	fine sand	poorly sorted
VI	29.4	42.9	7.91	8.09	2.9	451	medium sand	poorly sorted
VII	28.7	41.5	6.75	9.95	3.3	243	fine sand	poorly sorted
VIII	28.5	39.3	7.45	10.1	2.5	229	fine sand	poorly sorted
IX	32.1	43.6	7.3	9.9	3	150	fine sand	poorly sorted
X	32.4	40.1	7.78	7.31	3.5	441	medium sand	poorly sorted
XI	29.3	43.1	7.82	10.1	1.8	156	fine sand	poorly sorted
XII	28.1	41.3	7.65	10.19	2.8	366	medium sand	poorly sorted
XIII	29.8	41.1	7.91	8.9	2	350	medium sand	poorly sorted
XIV	31.5	41.1	8.01	2.31	1.1	747	coarse sand	moderately sorted
XV	31.2	42.1	7.61	11.65	1.9	183	fine sand	poorly sorted
XVI	31.1	41.1	7.95	10.19	1.9	232	fine sand	moderately sorted
XVII	33.2	41.3	7.87	6.79	1.3	224	fine sand	moderately sorted
XVIII	36.2	42.1	7.91	6.49	1.7	197	fine sand	poorly sorted
XIX	35.1	43.5	7.85	6.8	1.6	249	fine sand	poorly sorted
XX	29.2	40.8	8.08	7.76	2.5	232	fine sand	poorly sorted

Results

Abiotic factors

All abiotic factors at the study sites are presented in Table 2. The minimum seawater temperature and salinity were recorded at site IV (27.9°C and 38.2, respectively), while the maximum temperature (36.2°C) was measured at site XVIII and the maximum salinity (43.6) at site IX. The lowest pH value was determined at site VII (6.75), while the highest (8.08) at site XX. The EC values varied considerably at the surveyed sites and ranged from 2.31 and 22 mS cm⁻¹ at sites XIV and III, respectively, with an average of 8.89 mS cm⁻¹ (Table 2). Regarding the sediment characteristics, the sand fraction dominated at all sites, ranging from 88.1 (site II) to 99.2% (XIV). The contribution of the silt-clay fraction was considerably low and ranged between 0.76 and 11.96% at sites XIV and II, respectively. Values of the mean grain size ranged from 96 µm at site IV to 747 µm at site XIV, with an overall average of 288 µm (Table 2). Furthermore, the sediment sorting index showed that a total of 16 sites were characterized by poorly sorted texture, while four sites – by moderately sorted texture (Table 2). The total organic carbon content was generally low (average 2.4%) and ranged between 1% and 3.7% at sites IV and V, respectively (Table 2).

Meiofaunal composition and abundance

The meiofaunal abundance fluctuated between 119 and 1380 ind. 10 cm⁻² with an average value of 643 ± 462 ind. 10 cm⁻² (Fig. 2). Higher abundance of meiofauna was determined at six sites (I, VI, XII, XIII, XVI and XVII – 1370, 1008, 1350, 1110, 1350 and 1380 ind. 10 cm⁻², respectively; Fig. 3a). On the other hand, site XV showed the lowest abundance of 119 ind. 10 cm⁻² (Fig. 3a). A total of seven main taxa were identified in the sediment samples of mangrove stands (Fig. 2). The largest number of taxa (6) was observed at sites XIII and XVI, while the smallest number (1) was reported from site V (average: 4 ± 1 SD). Free-living nematodes, harpacticoid copepods and polychaetes were the most abundant taxa, accounting for almost 90.4% of the total meiofaunal abundance. Nematodes were the most abundant group (average abundance 413 ind. 10 cm⁻²) and accounted for about 64.3% of the total meiofauna. Their abundance varied between 72 and 1100 ind. 10 cm⁻² at sites II and XVII, respectively (Fig. 3b). Their contribution ranged between 29 and 100% of the total meiofaunal abundance recorded at each site. In terms of abundance, harpacticoid copepods were the next most dominant group and accounted for 13.2% of the total meiofaunal abundance at 14 sites, where it was present with an average of 85 ind. 10 cm⁻². Their abundance varied

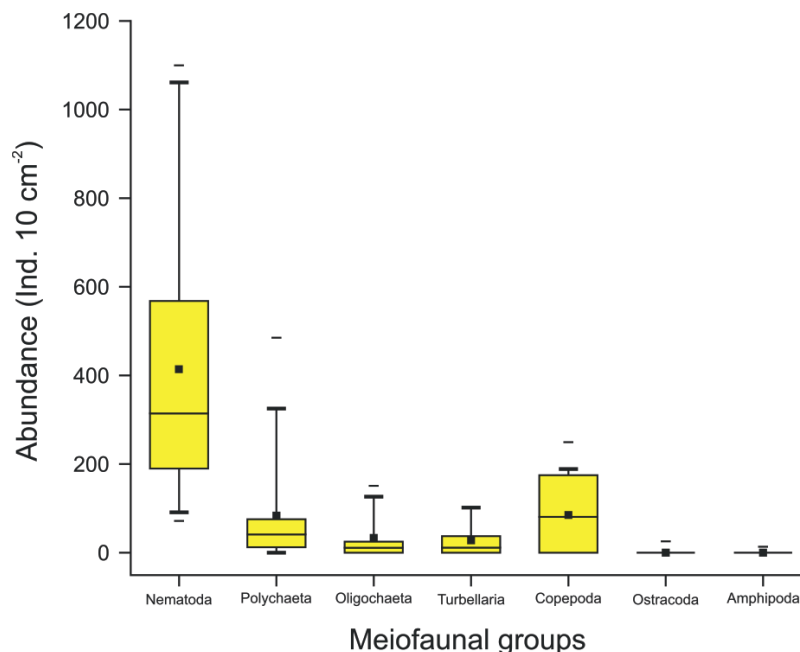


Figure 2

Box and whisker plot of different meiofaunal groups (ind. 10 cm⁻²) along the Saudi Arabian coast of the Red Sea. The bottom and the top of the boxes are the first and third quartiles, the band inside the boxes indicates the median, while the black square inside the box indicates the mean and the end of the whiskers expresses the range of abundance.

greatly at different sites, with particularly high abundance recorded at sites: XVII, XIII, VI, VII and XVI (Fig. 3c). Polychaetes were yet another relevant group, which accounted for about 12.9% of the total meiofaunal abundance. They were observed at 15 sites with an average abundance of 83 ind. 10 cm^{-2} . Their abundance was relatively higher at some sites (I, XII, XIII and XVI; Fig. 3d) with a maximum of 485 ind. 10 cm^{-2} at site XIII, which in turn represented almost 43.7% of

the total meiofauna obtained from that particular site. The contribution of oligochaetes and turbellarians to the total meiofauna was only 5.1 and 4.1% with mean counts of 33 and 27 ind. 10 cm^{-2} , respectively. Their maximum abundance was observed at site XVI with densities of 153 and 104 ind. 10 cm^{-2} , respectively (Fig. 3e-f). Other groups, such as ostracods and amphipods, were recorded at only one site with very low abundance.

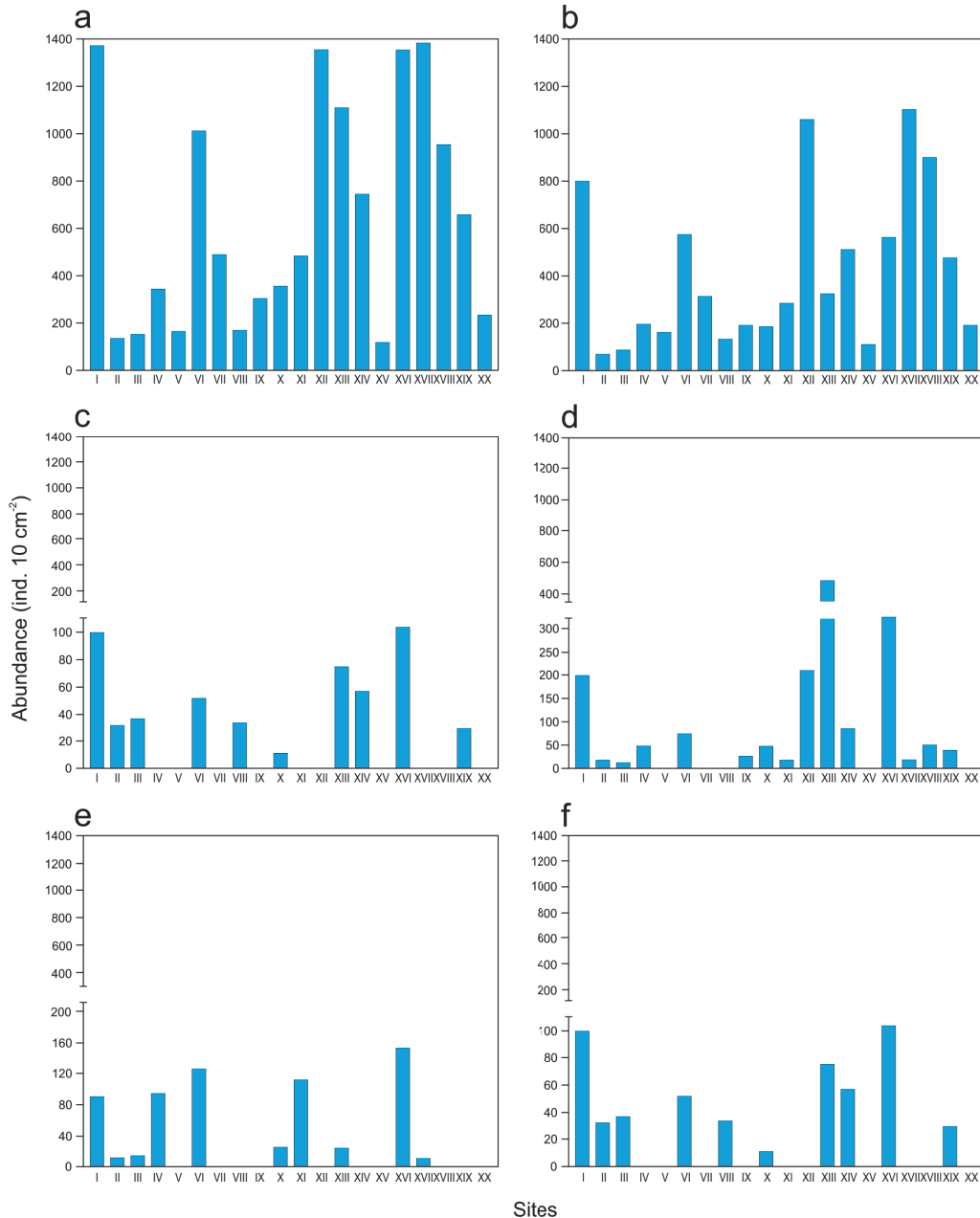


Figure 3

Spatial variations in abundance (ind. 10 cm^{-2}) of: a) total meiofauna, b) nematodes, c) harpacticoid copepods, d) polychaetes, e) oligochaetes, and f) turbellarians observed at different sites along the Saudi Arabian coast of the Red Sea

Free-living nematode assemblage structure

A total of 25 genera belonging to 15 families and three orders were recorded from the study area (Table 3). Chromadorida were the dominant order and were represented by 12 genera, which in turn accounted for 40.2% of the total nematode assemblages. They were followed, in terms of abundance and distribution, by Enoplida represented by five families and seven genera (accounting for 34.3% of the total nematode counts) and Monhysterida with two families and six genera (25.5% of the total nematode counts). Microlaimidae, Oxystominidae, Ironidae and Desmodoridae were the most abundant families and accounted for 19.8%, 16.2%, 15% and 14.7%, respectively (Table 3), while Xyalidae was the richest family (four genera), followed by Desmodoridae (three genera; Table 3). Interestingly, about 42% of all these nematode genera were observed only once during the entire study period. *Microlaimus* had the highest relative abundance, accounting for 17.4% of the total identified nematodes, followed by *Halalaimus* with the relative abundance of 16.2%. Both *Syringolaimus* (14%) and *Terschellingia*

(10.3%) were also present with considerable relative abundance (Table 3), making these four genera the most dominant ones, which together contributed about 58% to the total abundance of nematodes recorded in this study. Concerning the trophic structure of nematode assemblages, epistrate feeders were the dominant group (52.1%), followed by deposit feeders (44.4%), while predators/omnivores were represented by only 3.5% of the total nematode community. Epistrate-feeding (epigrowth) nematodes were significantly abundant at sites I, II, IV, V, VIII, X, XI, XVIII and XIX (Fig. 4). While selective deposit feeders dominated, in terms of abundance, at sites III, VI, IX, XIV, XV, XVI and XX, non-selective feeders showed greater abundance at sites VII, XIII and XX (Fig. 4).

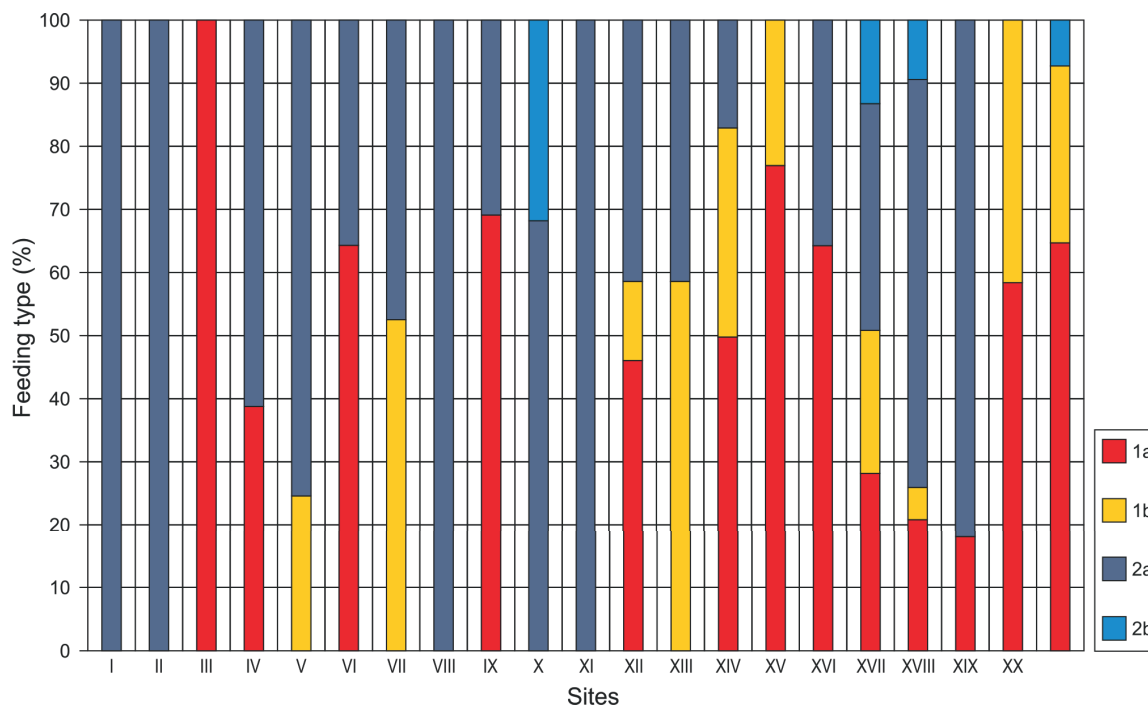
Statistical analysis

One-way ANOVA showed significant differences between the sites in the total abundance of meiofauna as well as other individual groups ($p < 0.001$). Based on nematode feeding habits, one-way ANOVA also revealed significant differences between the

Table 3

Total count, relative abundance (%) and feeding types of different nematode genera recorded in mangrove sediments along the Saudi Arabian coast of the Red Sea. 1A – selective deposit feeders; 1B – non-selective deposit feeders; 2A – epigrowth feeders; 2B – predators/omnivores

Order	Family	Genus	Total count	Relative abundance (%)	Feeding type
Enoplida	Ironidae	<i>Syringolaimus</i>	1155	14.0	2a
		<i>Dolicholaimus</i>	86	1.0	2b
	Oxystominidae	<i>Halalaimus</i>	1336	16.2	1a
	Oncholaimidae	<i>Viscosia</i>	85	1.0	2b
		<i>Oncholaimus</i>	71	0.9	2b
Triplyoididae	<i>Bathylaimus</i>	40	0.5	1b	
Aegialoalaimidae	<i>Aegialoalaimus</i>	59	0.7	1a	
Chromadorida	Chromadoridae	<i>Spilophorella</i>	91	1.1	2a
		<i>Metachromadora</i>	63	0.8	2a
	Cyatholaimidae	<i>Paralongicyatholaimus</i>	135	1.6	2a
	Selachinematidae	<i>Synonochium</i>	49	0.6	2b
	Desmodoridae	<i>Desmodora</i>	745	9.0	2a
		<i>Molgolaimus</i>	29	0.4	2a
		<i>Spirina</i>	447	5.4	2a
	Leptolaimidae	<i>Leptolaimus</i>	48	0.6	1a
	Microlaimidae	<i>Microlaimus</i>	1442	17.4	2a
		<i>Bolbolaimus</i>	198	2.4	2a
Desmosolecidae	<i>Desmosolezia</i>	17	0.2	1a	
Haliplectidae	<i>Haliplectus</i>	63	0.8	1a	
Monhysterida	Xyalidae	<i>Stylotheristus</i>	49	0.6	1b
		<i>Theristus</i>	196	2.4	1a
		<i>Paramonhystrea</i>	201	2.4	1b
		<i>Daptonema</i>	722	8.7	1b
	Linhomoeidae	<i>Metalinhomoeus</i>	90	1.1	1b
		<i>Terschellingia</i>	849	10.3	1a

**Figure 4**

Relative abundance of each trophic status of nematodes at different study sites along the Saudi Arabian coast of the Red Sea. 1A – selective deposit feeders; 1B – non-selective deposit feeders; 2A – epigrowth feeders; 2B – predators/omnivores

sites ($p < 0.001$). Pearson's correlation (r) analysis revealed some significant correlations between the meiofaunal groups and various nematode genera with changing environmental parameters. The sand fraction showed significant positive correlation with the total meiofauna ($r = 0.675$, $p < 0.01$) and with different meiofaunal groups such as nematodes ($r = 0.59$, $p < 0.01$) and harpacticoid copepods ($r =$

0.61 , $p < 0.01$) (Table 4). Turbellarians showed a negative correlation ($r = -0.502$, $p < 0.05$) with the percentage of the very fine sand fraction (Table 4). Some nematode genera like *Paralongicyatholaimus* ($r = 0.73$, $p < 0.01$), *Dolicholaimus* ($r = 0.57$, $p < 0.01$) and *Metachromadora* ($r = 0.57$, $p < 0.01$) are significantly positively correlated with temperature, while *Halalaimus* ($r = 0.43$, $p < 0.05$) and *Microlaimus*

Table 4

Values of Pearson's coefficient of correlation (r) indicating possible relationships between meiofaunal groups and different environmental parameters (Meio – total meiofauna; Nema – nematodes; Poly – polychaetes; Oligo – oligochaetes; Turb – turbellarians; Cope – copepods; Ostr – ostracods and Amph – amphipods)

Parameter	Meio	Nema	Poly	Oligo	Turb	Cope	Ostr	Amph
Sand (%)	0.675**	0.591**	0.39	0.29	0.34	0.614**	0.24	0.06
VC sand	-0.13	-0.11	0.03	-0.30	0.13	-0.22	-0.26	0.12
CS sand	0.32	0.24	0.26	0.00	0.39	0.37	-0.10	0.10
M sand	-0.08	-0.08	-0.08	-0.09	-0.10	0.06	0.07	0.01
F sand	0.38	0.34	0.09	0.40	0.13	0.38	0.492*	-0.17
VF sand	-0.448*	-0.35	-0.23	-0.09	-0.502*	-0.573**	-0.28	0.01
Silt-clay	-0.675**	-0.591**	-0.39	-0.29	-0.34	-0.614**	-0.24	-0.06
pH	0.39	0.33	0.31	0.32	0.35	0.12	0.16	0.13
EC	-0.28	-0.29	-0.11	-0.06	-0.01	-0.25	0.02	-0.03
OC (%)	-0.38	-0.39	-0.19	-0.19	-0.01	-0.23	-0.13	-0.11
Temperature	0.17	0.31	-0.10	-0.25	-0.09	0.08	0.06	-0.08
Salinity	-0.02	0.03	-0.13	-0.11	-0.21	0.10	-0.02	-0.02

* Correlation is significant at the 0.05 level (2-tailed); ** Correlation is significant at the 0.01 level (2-tailed)

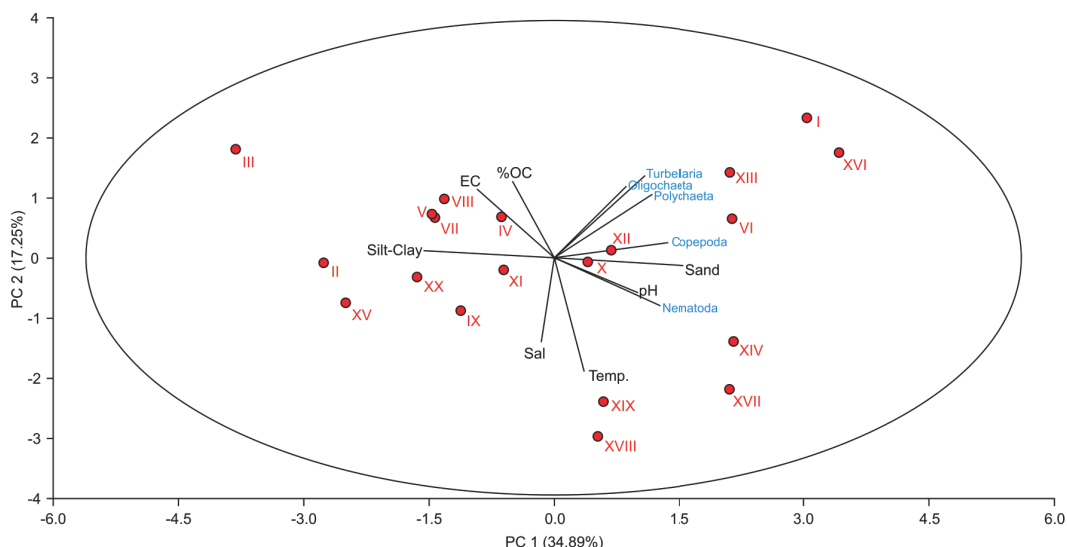


Figure 5

Principal component analysis (PCA) of normalized environmental variables and meiofaunal groups showing the main environmental gradient and relations along the surveyed sites

($r = 0.45, p < 0.05$) – with the percentage of sand. PCA ordination (based on correlation) of environmental variables and meiofaunal groups showed that the first two components accounted for 52.14% of the total variance (PC1: 34.89% and PC2: 17.25%). The main environmental variables that define PC1 were sand, silt/clay, pH and EC along with all meiofaunal taxa, while PC2 was mainly represented by TOC, salinity and temperature (Fig. 5). Most of the meiofaunal groups were positively correlated with sandy substrate and pH, but negatively correlated with such factors as silt-clay fraction, EC and TOC (Fig. 5). ANOSIM values obtained for the distribution of different nematode genera in various habitats clearly indicate that there are no significant differences between habitats ($p > 0.05$). The largest number of nematode genera (S) was determined at three sites (XII, XVII and XVIII; Table 5). Margalef’s species richness index (d) varied between 0.27 and 2.15 at sites I and XVII, respectively (average 0.65 ± 0.63), while values of Pielou’s evenness index (J’) showed a considerable variation between the sites ($F = 4.41, p < 0.05$; Table 5). The Shannon diversity index (H’) fluctuated between 0.66 and 2.37 without any significant variation among the sites ($F = 3.95, p > 0.05$; Table 5). The multidimensional scaling ordination (MDS) based on the Bray-Curtis similarity of the meiofaunal group abundance showed a 40% similarity between different sampling sites and two main groups (60% of similarity; Fig. 6a). The generic structure of nematodes also produced four main clusters with 40% similarity (Fig. 6b).

Table 5

Biodiversity indices of nematodes determined for different sites along the Saudi Arabian coast of the Red Sea: the total number of genera (S), richness (D), Pielou’s evenness index (J’) and Shannon-Wiener index (H’)

Site	S	d	J'	H' (log)
I	2	0.27	0.95	0.66
II	1	0.00	0.00	0.00
III	1	0.00	0.00	0.00
IV	3	0.63	1.00	1.10
V	2	0.35	0.95	0.66
VI	3	0.54	1.00	1.10
VII	3	0.59	0.99	1.09
VIII	1	0.00	0.00	0.00
IX	2	0.34	0.97	0.67
X	4	0.91	0.98	1.36
XI	2	0.32	0.97	0.68
XII	10	1.96	0.98	2.26
XIII	2	0.31	0.99	0.69
XIV	3	0.55	0.98	1.08
XV	2	0.37	0.94	0.65
XVI	4	0.80	0.91	1.26
XVII	11	2.15	0.98	2.36
XVIII	10	2.00	0.98	2.25
XIX	5	1.03	0.99	1.59
XX	2	0.34	0.99	0.69

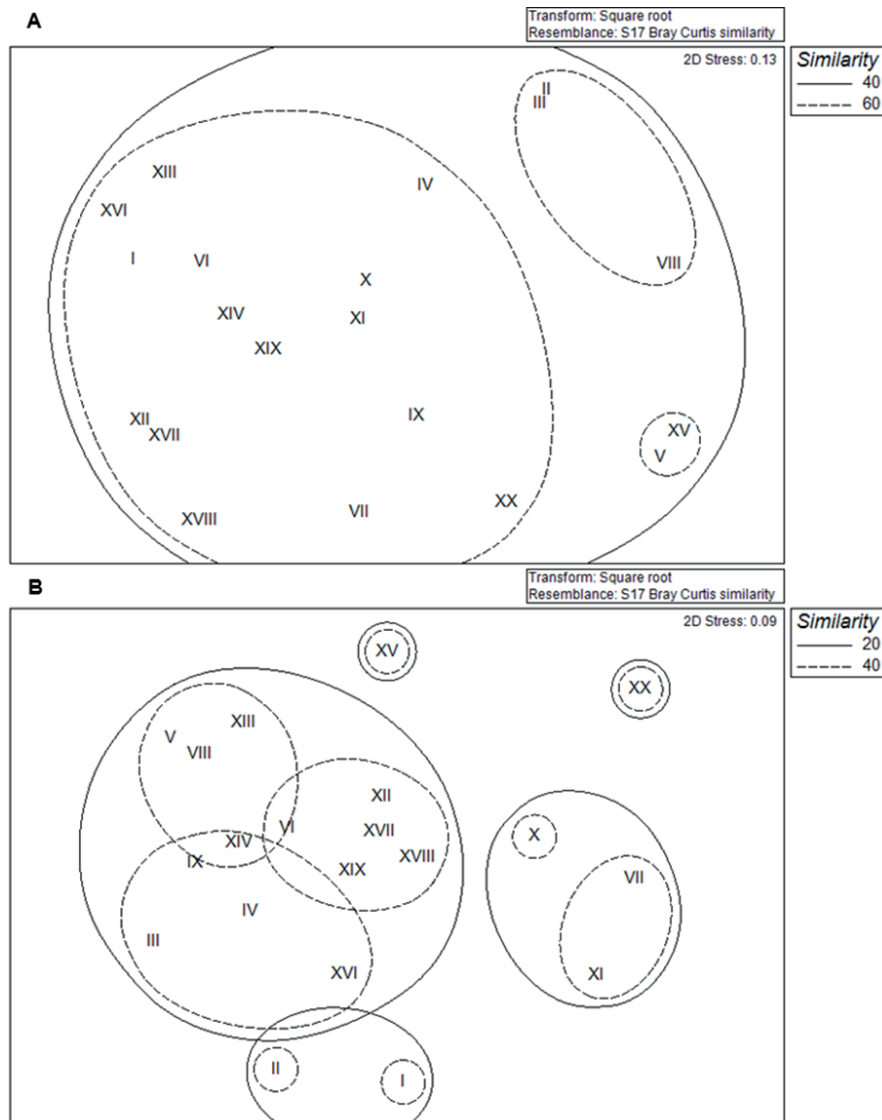


Figure 6

Multidimensional scaling (MDS) ordination based on the Bray-Curtis similarity indices of: A) different meiofaunal groups and B) nematodes

Discussion

Meiofauna represents an important component of the benthic mangrove ecosystems worldwide by playing an important role in the degradation of organic matter and nutrient recycling processes (Riera & Hubas 2003; Austen 2004; Woodward 2010; Nascimento et al. 2012; Schratzberger & Ingels 2018). The present study has revealed considerable variations in the spatial distribution of meiofaunal abundance among different sites. The differences in the total meiofaunal density observed in the present study were within the range documented from other mangrove areas around the world (Table 6), while they were

slightly higher compared to previous studies in the Red Sea mangroves (Pusceddu et al. 2014; Sabeel 2015; Table 6). These particularly high abundance values may be due to the sampling strategy of the current study, which covered almost the entire coast of the Saudi Arabia Red Sea. Moreover, our results also show much higher abundance than that recorded from the littoral sediments of the Red Sea (44–223 and 100–130 ind. 10 cm⁻²) by Hulings (1975) and Hanafy et al. (2011), respectively. This may result from the relatively high productivity of the mangrove ecosystem compared to the littoral zone. The particularly high abundance observed at some of the sites (I, VI, XII, XIII, XVI and XVII) is mostly due to the location of these sites inside

Table 6

Meiofaunal abundance determined in different mangrove sediments worldwide (mean values given in parentheses)

Area/Country	Densities (ind. 10 cm ⁻²) Minimum–Maximum (mean)	References
Hunter River, south-eastern Australia	63–12 057 (225)	Hodda & Nicholas (1985)
Hunter River, south-eastern Australia	1–9596 (110)	Hodda & Nicholas (1986)
Northeastern Australia	57–2454	Alongi (1987a,b)
Mangrove mudflats, Australia*	470–5000 (1830)	Nicholas et al. (1991)
Barwon estuary, Victoria, Australia	250–8622 (2170)	Gwyther (2000)
Mngazana estuary, South Africa	84–530 (246)	Dye (1983 a)
New Caledonia	70–5137	Della Patrona et al. (2016)
West and east coast of Zanzibar, Africa	205–5263 (1493)	Ólafsson (1995)
West and east coast of Zanzibar, Africa	271–656	Ólafsson et al. (2000)
Gazi Bay, Kenya, Africa	1986–6707	Vanhove et al. (1992)
Island of Santa Catarina, South Brazil	77–1589 (448)	Netto & Galucci (2003)
South Cuba	36–245	Lalana-Rueda & Gosselck (1980)
Gulf of Batabano, Cuba	5–594 (109)	Armenteros et al. (2006)
West coast of Malaysia	407–1109 (700)	Sasekumar (1994)
Southeast coast of India	234–890	Chinnadurai & Fernando (2007)
Northern Red Sea, Egypt	(343)	Pusceddu et al. (2014)
Sudanese coast of the Red Sea**	(288)	Sabeel (2015)
Western side of the Red Sea, Egypt	18–193 (109)	El-Serehy et al. (2015)
Saudi Arabian coast of the Red Sea	119–1380 (643)	Present study

* In the top 1 cm of *Av. marina* sediment; ** Intact mangrove

Table 7

Nematode abundance (mean in parenthesis), percentage of total meiofauna, richness and dominant genera recorded in different mangrove sediments worldwide

References	Area/Country	Densities (ind. 10 cm ⁻²) Minimum–Maximum (mean)	% of total meiofauna	Number of families	Number of genera
Hodda & Nicholas (1985)	Hunter River, south-eastern Australia	63–11892	87–100	23	55
Alongi (1987b)	Cape York, north-east Australia	3–987	–	–	(205 sp.)
Nicholas et al. (1991)*	Mangrove mudflats, Australia	113–451	–	26	38
Dye (1983a)	Mngazana estuary, South Africa	62–411	80.4	–	–
Vanhove et al. (1992)	Gazi bay, Kenya	–	54–95	–	–
Ólafsson (1995)	West-east coast of Zanzibar, Africa	131–5210	64–99	30	94
Ólafsson et al. (2000)	West-east coast of Zanzibar, Africa	271–656	58–87	13	28
Netto & Galucci (2003)	Island of Santa Catarina, South Brazil	196–811	85–94	28	86
Pinto et al. (2013)	Pernambuco state, Northeastern Brazil	–	–	25	73
Armenteros et al. (2006)	Gulf of Batabano, Cuba	5–591 (104)	33–100 (88)	–	–
Ali et al. (1983)	Bay of Bengal, India	35–280	50–67	–	–
Chinnadurai & Fernando (2007)	Southeast coast of India	234–890	86–93	20	36
Bhadury et al. (2015)	Central west coast of India	–	–	13	20
Ansari & Bhadury (2017)	Sundarbans, India-Bangladesh	–	–	29	84
Somerfield et al. (1988)	North-western coast of Malaysia	(122)	–	32	85
Sasekumar (1994)	West coast of Malaysia	374–885	80–93	–	17
Sabeel (2015)	Sudanese coast, Red Sea	10–370	40–98	20	35
El-Serehy et al. (2015)	Western side of the Red Sea, Egypt	8–162 (73)	42–84 (67)	–	–
Present study	Saudi Arabian coast of the Red Sea	72–1100	29–100	15	25

* In the top 1 cm of *Av. marina* sediment

sheltered or protected lagoons and near fish farm effluents. Multivariate analysis (PCA) further confirmed the particular dominance of these sites based on the abundance of meiofauna. It is well documented that tidal oscillation has a negative impact on meiofaunal communities (Alongi 1987a; Alongi & Christoffersen 1992; Ólafsson 1995; Dernie et al. 2003) and the lagoons are likely those places where tidal currents have only minor effects, which we assume is a possible cause of the higher abundance observed at these sites. Moreover, the high density of meiofauna observed near the fish farm effluents is consistent with the study of Della Patrona et al. (2016). They observed that the effluent-receiving mangrove usually exhibits a twofold increase in the abundance and biomass of meiofauna due to the availability of organic matter and other nutrients. The relatively higher content of organic carbon in the sediments determined at some of these sites may have had an impact on the meiofaunal assemblages, even though no significant correlation was found in the statistical analysis.

The abundance and diversity of meiofauna are usually affected by different environmental factors such as temperature, salinity, dissolved oxygen, sediment particle size, organic matter content and predator density (Coull 1999; Braeckman et al. 2011; Giere 2013), but the present study has shown a significant correlation only with the sand fraction of the sediment. Both the univariate (Table 4) and multivariate analysis (Fig. 5) provided further evidence for this correlation. The importance of granulometric parameters in determining the spatial variability of meiofauna was studied in various regions (Alongi 1987a,b; Ansari et al. 1993; Thilagavathi et al. 2011; Semprucci et al. 2015). The greater availability of space in the interstices of sand substrates allows organisms to use a variety of niches and thus increase their density and diversity (Dye 1978; Coull 1999; Mirto et al. 2002; Giere 2013). Furthermore, the sandy substrate provides a larger scope for specialization in their feeding habits in terms of the presence of attached materials as well as various biogenic materials like fragments of mollusk shells (McIntyre & Murison 1973; Anderson & Meadows 1978; Coull & Bell 1979; Rodríguez et al. 2003; Gheskiere et al. 2005). Although there are several parameters known to affect the variability of meiofauna, there are also quite a few studies that mention the absence or lesser impact of various environmental factors on the distribution of meiofauna (Ólafsson 1995; Netto & Gallucci 2003; Tolhurst et al. 2010; Abdullah & Lee 2017). Tolhurst et al. (2010) clearly demonstrated that microhabitat (separate niches within the same mangrove ecosystem) or other factors such as recruitment,

predation, food and competition have a much greater impact on the distribution of meiofauna than other environmental factors.

As in the previous studies carried out in the mangrove ecosystems around the world, nematodes were the dominant taxon also in the presented study. Their abundance determined in our study can be compared with those observed in mangroves in other parts of the world (Table 7). Nematodes were represented by 15 families and 25 genera, most of which were typical of intertidal sediments worldwide. The dominant families observed (Ironidae, Oxystominidae, Desmodoridae, Microlaimidae and Linhomoeidae) are considered to be common inhabitants of detritus-rich intertidal mangroves (Hopper et al. 1973; Alongi 1990b; Nicholas et al. 1991; Ólafsson 1995; Somerfield et al. 1998; Bhadury et al. 2015).

Despite the highest abundance, which can be compared to other temperate and tropical mangrove ecosystems, the composition of nematodes was less diverse (25 genera). This relatively small number can be explained either by the limited time of sampling, which covered only a specific season or by the oligotrophic nature of the Red Sea (Almahasheer et al. 2017), where the biodiversity is generally low. It has also been documented that tropical mangroves show basically lower diversity and density of meiofauna/nematodes compared to other temperate mangroves due to factors such as increased physical stress (Alongi 1987a,b; Armenteros et al. 2006), poor nutritional quality of mangrove-derived detritus (Tietjen & Alongi 1990; Alongi & Christoffersen 1992) and high tannin content in mangrove sediments (Alongi 1987c; Tietjen & Alongi 1990; Abdullah & Lee 2017). Although some of the sites were characterized by higher densities, the composition of nematodes did not show any particular pattern of dominance in different habitats studied. Furthermore, the study has also shown the absence of any characteristic genus for each specific habitat. This clearly shows that the composition of nematodes in the Red Sea follows a similar distribution pattern and does not appear to be affected by different habitats. ANOSIM, based on the pairwise test of nematode genera composition in different habitats, clearly proved the lack of significant differences between the habitats studied. Microlaimidae, Desmodoridae and Chromadoridae were the most abundant and diversified families, which is consistent with the studies by Bhadury et al. (2015) (the west coast of India), Nicholas et al. (1991) (Australia), Ólafsson (1995) (Zanzibar, Eastern Africa) and Sabeel & Vanreusel (2015) (Sudan), who observed similar trends. In the present study, we also observed the dominance of

certain nematode genera (*Microlaimus*, *Halalaimus*, *Syringolaimus*, *Terschellingia*, *Desmodora* and *Daptonema*) in mangrove sediments, which is similar to mangroves occurring across the temperate latitudes of South America, Australia as well as tropical mangroves (Hodda & Nicholas 1985; Nicholas et al. 1991; Ólafsson 1995; Netto & Gallucci 2003; Sabeel & Vanreusel 2015).

With regard to feeding types, it is well understood that the sandy substrate favors epistrate and non-selective feeders feeding on bacteria, benthic diatoms, protozoans and plant roots (Hodda & Nicholas 1986; Jensen 1987; Moens & Vincx 1997; Netto & Gallucci 2003), which was evidenced by the significant positive correlation obtained for some of the species (*Microlaimus* and *Halalaimus*) with the sand fraction. The sediment grain size is known to be the prime factor that determines the abundance and species composition of meiofauna, especially nematodes (Heip et al. 1985; Steyaert et al. 1999; Vanaverbeke et al. 2002; Semprucci et al. 2010; Fonseca et al. 2014), as it significantly affects the burrowing and interstitial behavior of benthic organisms (Vanaverbeke et al. 2011).

In the current study, two sites were characterized by low abundance and were inhabited by only one genus of nematodes (sites II and III). We hypothesize that this was primarily due to the presence of many dead mangrove trees, which eventually leach colloidal compounds from their fallen leaves, such as tannins that have the properties of inhibiting the growth of meiofaunal organisms (Alongi 1987c; Tietjen & Alongi 1990; Zhou et al. 2001). This was also evident in the total density of meiofauna determined at similar sites, which showed extremely small numbers compared to other regions. The dominance of other meiofaunal taxa in the present study (polychaetes and harpacticoid copepods) are in accordance with other studies conducted in the mangrove systems worldwide (e.g. Hodda & Nicholas 1986; Gwyther 2000; Netto & Gallucci 2003; Xuan et al. 2007; Chinnadurai & Fernando 2007; Mokievsky et al. 2011; Thilagavathi et al. 2011; Della Patrona et al. 2016). Sediment characteristics such as grain size, silt and clay content and organic matter availability (Alongi 1987b; Hsieh 1995; Pagliosa 2005; Sarkar et al. 2005) must have an impact on the distribution of these organisms in the Red Sea. Further research is needed to determine the exact impact of different sediment characteristics on meiofaunal assemblages in the Red Sea. It should focus on the relationship of meiofauna with sediment chemical properties, phaeopigments, dissolved oxygen, redox-potential, underground root biomass, and also tannin content in order to better understand the meiofaunal assemblages in mangroves.

Conclusions

The present study has focused mainly on the spatial distribution of meiofaunal communities along the mangrove ecosystem of the Saudi Arabian coastal waters of the Red Sea. The spatial distribution of meiofauna showed relatively higher abundance at the sites that seemed to be affected by anthropogenic impact. Different nematode genera observed were common inhabitants of tropical mangroves. This study presents an initial approach to research on meiofaunal communities, especially nematodes in mangrove ecosystems of this specific region. The future approach to studies of meiofauna in the Red Sea mangroves should give more attention to seasonal variations that may affect their distribution.

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