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Discussions

Structural and functional study of the nematode community from the Indian western continental margin with reference to habitat heterogeneity and oxygen minimum zone

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Abstract

We studied patterns of nematode distribution along the western Indian continental margin to determine the influence of habitat heterogeneity and oxygen minimum on the community's taxonomic and functional structure. A single transect, perpendicular to the coast at 14° N latitude was sampled from 34 to 2546 m depth for biological and environmental variables during August 2007. Nematodes were identified to species and classified according to biological/functional traits. A total of 110 nematode species belonging to 24 families were found along the transect. Mean nematode density was higher on the shelf (176 no 10 cm^{-2}, 34 m depth) than on the slope (12 + 10 cm^{-2}) or in the basin 6 c.9 nd 10 cm^{-2}). Across the entire study area, the dominant species were *Terschellingia longicaudata*, (15.2 %) *D* smodora sp 1, *Sphaerolaimus gracilis*, and *Theristus ensifer*; their maximum density was at shelf stations. Multidimensional scaling ordination (nMDS) of the nematode species abundance data indicated the effect of different zones (ANOSIM; Global $R = 0.607$; $P = 0.028$), but it was not the same in case of functional traits. Only seven species were found exclusively in the oxygen minimum zone: *Pselionema* sp 1, *Choanolaimus* sp 2, *Halichoanolaimus* sp 1, *Cobbia dentata, Daptonema* sp 1, *Trissonchulus* sp 1, and *Minolaimus* sp 1. Moreover, in our study, species diversity was higher on the shelf than on the slope or in the basin. The distinctive features of all three zones as based on nematofaunal abundance were also reflected in the functional traits (feeding types, body shape, tail shape, and life history strategy). Correlation with a number of environmental variables indicated that food quality (measured as the organic carbon content and chlorophyll content) and oxygen level were the major factors that influenced the nematode community (structural and functional).

1 Introduction

The continental margin exhibits extreme topographical heterogeneity in terms of geomorphological features (e.g., shelf, slope, rise, marginal highs) and their related environmental conditions (e.g., depth, pressure, temperature, salinity, light, dissolved oxygen, sediment characteristics) (Levin et al., 2001). This heterogeneous environment is of great ecological interest because of its wide range of gradients of living conditions and the high faunal diversity it supports on local, regional, and global scales (Vanreusel et al., 2010). The heterogeneous habitat leads to the complexity, which plays an important role in structuring the benthic community (Gooday et al., 2010). The western Indian continental margin, located in the eastern Arabian Sea of the northern Indian Ocean, includes a series of complex environments including shelf, slope, and a permanent oxygen-depleted zone. In general, oxygen minimum zones (OMZs) are defined as layers of the water column where dissolved oxygen (DO) concentrations fall below $0.5\,mL\,L^{-1}$. Oxygen minima are common in the world oceans (Kamykowski and Zentara, 1990) and are found at intermediate depths in the Arabian Sea, off western Mexico, and off Peru and northern Chile. The Arabian Sea OMZ is one of the strongest and most intense in the world, having oxygen concentrations $< 2\,\mu M$ in its core (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009; Zettler et al., 2009). Although the Arabian Sea covers only 2 % of the surface area of the World Ocean, it is one of the most biologically productive regions (Ryther and Menzel, 1965).

At small scales, OMZs create heterogeneous environments that influence the structure of the surrounding communities and the dynamics of the meiobenthic populations. A good knowledge of the ecology and adaptations of the benthic fauna living in these areas is therefore essential.

The entire western Indian continental margin (shelf to slope) supports a high benthic biodiversity (Ingole et al., 2010). Free-living nematodes are prominent members of the meiobenthos along the ocean continental margin, often constituting > 90 % of all metazoa (Vincx et al., 1994). Moreover, they are more tolerant than macro- and meiofauna

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of anoxic conditions (Giere, 1993; Moodley et al., 1997). Previous workers like Jensen (1987) and Murrell and Fleeger (1989) investigated low-oxygen conditions in sandy sediments at shallow depths and from the Gulf of Mexico, respectively. They found that nematode abundance was unaffected by oxygen concentration. Cook et al. (2000) studied nematodes from the Arabian Sea OMZ and concluded that nutrient input is more important than the oxygen concentration. Moreover Levin et al. (1991) also found no evidence that low oxygen affects nematode abundance and suggested that food supply or biological interactions between the larger organisms and meiofauna might be more important.

Most of these studies, however, investigated meiofauna and Nematoda at higher taxonomic levels. Furthermore, nematode community structure from the continental margin (including the OMZ) of the Arabian Sea remains undescribed. Despite the dominance and importance of nematodes, studies of their community from the OMZ of the Arabian Sea have not been conducted. An exclusive study from the Indian western continental margin with reference to nematode tolerance in the OMZ is therefore important. Moreover, nematode community analyses, deriving diversity and community structure from species abundance data, can provide important basic information on marine ecology, but studies that required information on nematode ecology have used a functional-group approach (Thistle and Sherman, 1985). One possible approach to determining the role of biodiversity in ecosystem functioning is the functional/biological-trait approach (Chalcraft and Resetarits, 2003). Species in functional groups share several morphological traits (Chalcraft and Resetarits, 2003), and use of these traits may provide additional information on changes in biodiversity and also facilitate better comparison with other geographical regions (Bremner, 2008). Various biological traits play important roles in ecological functioning. Giere (1993) showed that a classification based on buccal structures of marine nematodes had applications in a variety of marine habitats. Thistle and Sherman (1985) found that nematode tail shape formed an important biological trait especially in locomotion and reproduction. Furthermore, body size is known to influence many traits of an animal, such as its life history, physiology, and

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energy requirements, whereas species morphotype represents adaptations to life in oxygen-poor and sulphide-rich sediments (Vanhove et al., 1995). Bongers et al. (1991) classified the genera (along a scale of 1 to 5) from r-selected "colonisers" to K-selected "persisters", according to their life history, to assess the condition of terrestrial and freshwater habitats but also of marine environments from the shelf.

In the study reported here, we therefore examined the nematode community structure along a habitat gradient using traditional diversity measures, taxonomic properties, and the functional-group concept based on biological traits so as to answer the following questions.

Does heterogeneous environment affect marine nematode community structure both structurally and functionally?

What are the patterns and drivers of variation in nematode composition and diversity (structural and functional) along the western Indian margin; i.e., are oxygen levels the main driver, or are other factors (sediment, productivity, etc.) more important?

2 Materials and methods

2.1 Study area

A single transect was selected perpendicular to the coast of the Arabian Sea at 14° N latitude (Fig. 1). In this region, the shelf break is located about 105 km from the coast (120 m depth). Beyond it is a 116 km wide shelf-margin basin.

2.2 Sampling

A detailed benthic sampling was performed on board ORV *Sagar Kanya* during August 2007 (cruise no. SK 237). Eight stations were sampled, at water depths of 34, 48, 102, 525, 1001, 1524, 2001 and 2546 m, by means of a spade box corer (50 cm × 50 cm × 50 cm size). According to Rao and Veerayya (2000) the transect can be divided into five regions – shelf (34, 48, and 102 m), upper slope (525 m), mid slope

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(1001 m), lower slope (1524 m), and basin (2001–2546 m). For our purposes, however, all three slope depths were considered a single region; the study area was therefore divided into only three depth zones – shelf, slope, and basin (Ingole et al., 2010). On the basis of oxygen concentration, the OMZ was defined as extending from 102 to 1524 m. For nematode assemblages, a PVC core (5.7 cm dia.) was used for sub-sampling. All these samples were preserved in 5 % formaldehyde–Bengal rose solution. Separate sub-cores were collected for organic carbon (C_{org}), sediment chlorophyll a (Chl a) measurements, and texture (grain size) analysis and were frozen at −20 °C. Bottom-water DO measurements were taken with a DO sensor attached to the CTD for depths down to 1524 m. Below this depth, water collected in Niskin bottles was used for DO and Chl a analysis.

2.3 Laboratory analysis

In the laboratory the samples were processed for environmental-parameter and community analysis. Dissolved oxygen was analyzed by Winkler's method (Strickland and Parsons, 1968). Chl a was estimated by means of an acetone extraction method (Holm-Hansen and Riemann, 1978). Total-carbon analyses were carried out in freeze-dried sediments with an NCS 2500 (Model-EA/NA1110) CNS analyzer. Inorganic carbon was analyzed with a CO_2 Culometer analyzer, and the percentage of $CaCO_3$ was calculated. Percentage of C_{org} was calculated by subtraction of inorganic from total carbon. Sediment texture was determined by Malvern Laser Analyzer (Model – Hydro 2000MU).

The fixed nematode samples were carefully examined and sieved (mesh size 37 μm). Nematode samples were examined through a stereo-microscope, and all the nematodes that were present in the samples were picked and mounted on permanent glass slides for taxonomic identification. In all, 1798 nematodes were examined from the whole area. They were identified up to described and morphotype species level from the pictorial keys of Platt and Warwick (1983) and the NeMys database (Deprez et al., 2005). For identification to species level, each morphotype was sketched and mea-

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sured by means of a camera lucida so that all specimens of the same genus could be compared.

2.4 Nematode functional trait analysis

Nematode species and genera were classified according to their buccal morphology, tail shape, adult length, adult shape, and life history.

Feeding types: Individual nematode species were assigned to four feeding categories according to Wieser (1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A), and predators/omnivores (2B).

Tail shape: In addition to the feeding types, Thistle and Sherman (1985) developed a functional-trait scheme based on tail shape. Tail types are diverse and variable and suggested as an effective method of characterizing nematode communities (Thistle and Sherman, 1985). Nematodes were assigned to four tail-shape groups, which are common in free-living marine nematodes: short/round, elongated/filiform, conical, and clavate.

Total length and body shape: Total length and the maximum width for adult nematodes were measured, and from the results we calculated the length-width ratio. Soetaert et al. (2002) suggested three body-shape morphologies: stout, slender, and long/thin. Length-width ratio is a measure of a nematode's body shape; long/thin animals have high ratios, and stout animals low ratios. From measured length, each species was therefore assigned to one of four length groups (< 1, 1–2, 2–4, > 4 mm) and three shape categories (stout, with a length–width ratio < 18; slender, with a length–width ratio of 18–72; and long/thin, with a length–width ratio > 72).

Life history (C–P score): Nematodes were allocated to life-history groups according to Bongers (1990) and Bongers et al. (1991); genera are classified on a scale from 1 to 5 from colonisers (1, short life cycle, high reproduction rates, high colonisation ability, tolerance of various types of disturbance) to persisters (5, long life cycles, low colonisation ability, few offspring, sensitivity to disturbance).

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2.5 Statistical analysis

The similarity analysis at the species level was based on two types of similarity measures: the Bray–Curtis dissimilarity (Bray and Curtis, 1957), based on the relative abundances of nematode genera, and the similarity matrix, based on presence-absence data.

Differences between the sets were visualized by means of non-metric multidimensional scaling (nMDS) plots. The SIMPER module of the PRIMER software (Anderson et al., 2008; Clarke and Gorley, 2006) was used to quantify the contribution of individual species to the between-zone dissimilarity (Clarke, 1993). Diversity was expressed in terms of the expected number of species in a sample, EG (51). The other diversity indices were calculated by means of Margalef's index (Margalef, 1968) for species richness (d), Pielou's index (Pielou, 1966) for species evenness (J'), and the Shannon–Wiener index (Shannon and Weaver, 1963) for species diversity (H' by using loge). A non-parametric Kruskal–Wallis test was used as the global significance test for differences in univariate parameters by means of the PAST program (Hammer et al., 2001). Analysis of similarities (ANOSIM) was used to test for significant differences between the zones and the similarity percentages.

Environmental variables were then normalized and subjected to principal-components analysis (PCA) for ordination. A lower triangular Euclidean distance matrix relating to the ordination was constructed (Clarke and Green, 1988). The relationships of taxonomic and functional traits with environmental variables were examined by mean of the BIOENV procedure (Clarke and Ainsworth, 1993), which calculates rank correlations between a similarity matrix derived from biological data and matrices derived from the environmental variables, thereby defining a set of variables that "best explain" the biotic structure.

To identify the species that would characterize the three zones compared (shelf, slope, and basin) we performed the Indicator Species Analysis or IndVal (Dufrêne and Legendre, 1997) using multi-level pattern analysis (De Caceres et al., 2010) in

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the R environment (R. Development Core Team, 2010) with the "indicspecies" function. The statistical significance of the relationship between the species and site was tested by means of Monte Carlo randomizations with 1000 permutations. The details of the method are described by Dufrêne and Legendre (1997). All the analyses were performed with the procedures in the R software (R Development Core Team, 2010; Dimitriadou et al., 2014) and the PERMANOVA+ module of the PRIMER v6 software (Anderson et al., 2008; Clarke and Gorley, 2006).

3 Results

3.1 Environmental parameters

The sediment texture was variable, as the shelf region and upper slopes (525 m) were characterised by silty and sandy facies, whereas the sediments at the mid slope (1001 m), lower slope (1524 m), and basin were characterised by clayey silts. The salinity of the bottom water varied little, but temperature was decreased with depth. The bottom-water DO ranged from 0.08 to 2.3 mL L^{-1}. The lowest near-bottom oxygen levels were recorded on the upper slope and mid slope (0.08 and 0.28 mL L^{-1}, respectively), hereafter defined as the OMZ. Oxygen values began to increase at the lower slope, defining the base of the OMZ. Higher values of DO were observed in the basin (Table 1). The OMZ as defined above extended from 102 to 1525 m in the study area; its core was located at 525 m, where the lowest DO value was recorded (Ingole et al., 2010).

The OMZ was also characterised by higher values of sediment Chl *a* and organic carbon (Table 1) than were the shelf and basin. A PCA ordination constructed from the eight environmental factors (DO, sediment chlorophyll, C$_{org}$, CaCO$_3$, C : N ratio, clay, silt, and sand (Fig. 2)) showed that the first two components accounted for about 81 % of the variability of the data (Fig. 2) (PC1 explained 43.5 %, PC2 33.3 %). Two shelf stations were characterised by high coarse sand and CaCO$_3$ content, whereas one

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(at depth 102 m) clustered mainly with the slope stations, largely because of higher organic-matter content and was clearly separated from the others on the basis of its higher silt content. Basin samples were characterised by higher DO level (Fig. 2).

3.2 Nematode density and community structure

A total of 110 nematode species belonging to 24 families were found along the transect (Table 2). Nematode density was higher at the shelf stations than on the slope or in the basin. The mean nematode density in the slope region was 124 ind 10 cm^{-2}, and the lowest density was observed on the upper slope (37.64 ind 10 cm^{-2}); the highest average nematode density (176 ind 10 cm^{-2}) was observed at shelf depth (34 m). Average density in the basin was 62.9 ind 10 cm^{-2} (Fig. 3).

Non-metric multidimensional scaling (nMDS) based on nematode species abundance (Bray–Curtis) and presence/absence data clearly suggested that the communities of the three benthic zones differed. Multidimensional scaling ordination of the nematode species-abundance data indicated the effects of zones (ANOSIM; Global $R = 0.607$; $P = 0.028$). The nMDS plot based on the Bray–Curtis similarity measure indicated three groups of samples (Fig. 4). The larger group included the slope stations and the deepest shelf station – those stations that form the OMZ (Fig. 4) – but the nMDS based on presence/absence separated only the slope and basin. The stations on the shelf were distributed randomly (Fig. 5), but ANOSIM tests confirmed a significant effect of benthic zone – shelf, slope, and basin – on nematode assemblages (Global $R = 0.615$; $P < 0.05$).

Thirty-eight species were identified that were found only in the shelf region. Of these, *Chromadorita* sp 2 (13.8 %), *Sphaerolaimus gracilis* (11.0 %), and *Setosabatieria* sp 1 (10.2 %) were dominant. *Dolilaimus* sp 1 (33.2 %), *Oxystomina affinis* (31.1 %), and *Epicanthion* sp 1 (22.0 %) dominated the slope, and *Axonolaimus* sp 2 (30.2 %), *Halanchus* sp 1 (23.0 %), and *Dolicholaimus* sp 1 (15.1 %) dominated the basin. Across the entire study area, however, the dominant species were *Terschellingia longicaudata*,

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(15.2 %), *Desmodora* sp 1 (14.5 %), *Sphaerolaimus gracilis* (11.7 %), and *Theristus ensifer* (9.1 %); their maximum contributions came from shelf stations.

Only seven species were found exclusively in the OMZ: *Pselionema* sp 1, *Choanolaimus* sp 2, *Halichoanolaimus* sp 1, *Cobbia dentata*, *Daptonema* sp 1, *Trissonchulus* sp 1, and *Minolaimus* sp 1. Only nine species were found exclusively in the basin: *Acantholaimus calathus, Acantholaimus mirabilis, Sphaerolaimus* sp 1, *Subsphaerolaimus* sp 1, *Pierrickia* sp 2, *Sabatieria praedatrix, Epicanthion* sp 1, *Longicytholaimus* sp 1, and *Oncholaimus attenuates*. The top 10 dominant species from OMZ from the remaining areas are given in Table 3.

The IndVal index produced a list of indicator species for each group of sites: four genera were indicative of the shelf area and five genera of the slope (Table 4). *Viscosia viscosia* ($P = 0.005$; stat value = 0.751) was a good indicator of the shelf, whereas *Choanolaimus* sp 2 was strongly and significantly ($P = 0.005$; stat value = 0.950) associated with the slope. *Acantholaimus mirabilis* ($P = 0.005$; stat value = 1.000) was significantly associated with the basin. In addition, a number of indicator species were highly significantly ($P = 0.005$) associated with the shelf, slope, or basin. Table 4 lists which species were associated with which zones. The conditional probability or positive predictive value of the species and the conditional probability of finding the species at sites belonging to any of the zones are shown in Table 4 for the relevant species, but those species with the highest IndVal value for the set of all the samples from the three zones (e.g., *Acantholaimus elegans, Acantholaimus filicaudatus, Anoplostoma blanchardi, Anoplostoma* sp 1, *Synonchiella* sp 1, *Desmoscolex* sp 1, *Tricoma* sp 1, and *Siphnolaimus ewensis*) were not amenable to statistical testing because of the lack of an external group for comparison.

SIMPER analysis revealed that the average value of dissimilarity between the shelf and slope stations was 57 %. The species that contributed most to this dissimilarity were *Chromadorita* sp 1 (2.53 %), *Terschellingia longicaudata* (2.50 %), and *Halalaimus* sp 1 (2.48 %). The average value of dissimilarity between the slope and basin stations was 75.84 %, and the species that contributed most to the difference were *Se-

tosabatieria (4.14 %), *Paralinhomoeus* sp 1 (2.71 %), and *Chromadorita* sp 1 (2.60 %). The average dissimilarity between shelf and basin regions was 76.19 %, and the highest contributors to this difference were *Halalaimus* sp 1 (3.61 %), *Longicytholaimus* sp 1 (2.42 %), and *Setosabatieria* sp 1 (2.41 %). Moreover, deep-basin samples were more homogeneous (average similarity was 86 %) then slope (75 %) or shelf stations (50 %). The three benthic zones differed significantly in the diversity indices (Margalef's d; Pielou's J' evenness; estimated total number of species, ES (51); and log2 Shannon–Wiener Index for species diversity, H') of nematode assemblages (Kruskal–Wallis test: $P < 0.05$). The average values of diversity indices in each zone are given in Table 5.

3.3 Functional traits

Functional attributes of nematode communities in the Arabian Sea are listed in Tables 6 and 7. Assemblages collected at the eight stations differed both taxonomically and functionally, but the nMDS ordinations of taxonomic groups did not match the ordinations based on functional groups (Fig. 5). This geographic separation was less pronounced in the ordinations derived from functional characteristics of nematode communities, although the basin clumped in one group. ANOSIM revealed insignificant differences between the functional assemblages of the three benthic zones (Global $R = 0.694$, $P = 0.021$). The results were confirmed by the nMDS plot (Fig. 6).

Assemblages were dominated by non-selective deposit feeders (1B) and predators (2B), whereas proportions of selective deposit feeders (1A) and epigrowth feeders (2A) were comparatively low (Table 6). The shelf area was dominated by non-selective deposit feeders (1B) and predators (2B), whereas the slope area (OMZ) stations showed the highest proportions (29–48 %) of the predators/omnivores (group 2B). The shelf and basin areas were dominated by deposit feeders (mainly the non-selective 1B group).

Conical and clavate were the most prevalent tail shapes at the majority of stations (Table 6); the average proportion of conical tails was higher on at the slope (OMZ) stations (33–49 %). Clavate tails dominated at all stations, but slightly less so in the

OMZ than on the shelf and in the basin area. Average adult lengths of nematodes ranged from 1 to 4 mm, and the majority of all recorded individuals occurred in the two intermediate length classes (1–2 and 2–4 mm). The OMZ stations showed the highest proportion in the 1–2 mm category (36–62 %); the size 2–4 mm was the second dominant (28–39 %). Moreover, the basin was also dominated by these two length categories. Nematodes with a length in the range of 2–4 mm were significantly correlated ($P < 0.05$) with slender body shape at shelf stations. A significant correlation ($P < 0.05$) between conical tail shape and long/thin body shape was also observed.

The majority of the nematodes were slender, and the proportion decreased with depth (from 83 % in the shelf to 41 % in the basin), whereas stout animals accounted for between 8 and 11 %. Long/thin animals continuously decreased with increasing depth until the lower slope, but they were more abundant (46–51 %) in the basin than were those of slender or stout shape. Slender nematodes were recorded more often in the shelf region (71–83 %). Over 76 % of all identified individuals attained a coloniser-persister (C–P) score of 2 to 3. The shelf, slope, basin regions harbored mostly colonisers in the range of 2–3. Extreme persisters (C–P score of 5) were absent (Table 7).

The information in a particular functional group was not a simple reflection of the information in species abundance. Ecological information captured by adult length, adult shape, and life-history strategy was less site-specific and thus differed notably from information contained in other taxonomic groups.

Moreover the trait matrix revealed several notable relationships between traits. For example, large body was generally correlated with slender to stout body shape and low C–P score, whereas smaller species had higher C–P scores. Equally, in contrast to the generally small selective deposit feeders, predators were usually large. Some other combinations occurs such as, non-selective feeders with clavate tail shape, category while predators followed the similar trend as was conical tail shape category. Moreover the traits matrix revealed some combinations of functional groups to which not many species belonged (e.g. epigrowth feeders with rounded tails).

Our schematic model represents the exact combinations of each functional trait. For example, the shelf region favors the dominance of clavate tail shape, epigrowth feeding, slender body shape, and coloniser life style with length in the range of 1–2 mm. Similarly the OMZ shows an increasing pattern of some traits like conical tail shape, long/thin body, and greater prevalence of omnivores and deposit feeders. Coloniser life style and length ranges were similar in pattern, however, except in the basin, even when the sediment characteristics changed from silty sand to clay. Feeding habit and tail shape also differed in the basin (Fig. 7).

3.4 Influence of abiotic parameters

Results of BIOENV analysis revealed several notable relationships with environmental parameters. For example feeding types have the best correlation with C_{org}, sediment chlorophyll, and silt. Body size was well correlated with DO, clay, and C_{org}, whereas tail shape was correlated with clay, DO, and silt, and body length with sand, clay, and C : N ratio. C–P status was related to clay and DO (Table 8).

Analysis with distance-based linear models (DistLM) indicated that the six abiotic variables related to the variation in nematode community structure explained 54 % of its total variation, although not all variables were significant. The DistLM analysis allowed the identification of those abiotic variables that were best correlated with the observed distribution patterns of taxonomic and functional traits of nematode species (Table 9). Results based on the abundance and presence/absence data were virtually identical; therefore, only the results based on the abundance data and functional traits are reported (Table 9). Variables such as the near-bottom oxygen content, C_{org}, and sediment Chi *a* showed the highest correlations ($P < 0.05$) with the composition of nematode assemblages, whereas the functional traits were mainly explained by with total organic carbon input and sediment Chl *a* ($P < 0.05$).

4 Discussion

4.1 Nematode density and community structure

Nematode density was higher in the shelf regions than on the slope or in the basin, but the lowest density was observed in the basin (2001–2546 m), where oxygen content was highest. Generally, depth can have a major influence on nematode community composition (Giere, 2009), and moreover the basin was covered by only two stations.

Nematode abundance decreased from the shallow to the deeper region of the shelf, but in the slope area the density was highest inside the OMZ (525 m) and decreased to its lowest value in the lower part of the OMZ (1524 m). The nematode density we report was lower than those reported by Cook et al. (2000) and Neira et al. (2001) for the bathyal Oman margin. Levin et al. (1991) found the highest densities of nematodes (190 ind 10 cm^{-2}) in the center of the OMZ; we found 120 ind 10 cm^{-2}). The role of DO is crucial in structuring meiofaunal communities, and oxygen limitation might directly control meiofauna composition within the OMZ (Neira et al., 2001). Moreover in general, for the benthic community, the distribution and community structure of benthic populations are greatly influenced by the presence of OMZs (Arntz et al., 1991; Levin, 2003). In our study the combined OMZ stations showed higher density than non-OMZ stations, perhaps as a result of the ability of some species to tolerate low-oxygen conditions to take advantage of abundant food (Levin et al., 1991; Cook et al., 2000). Nematodes are known for their higher tolerance range, which is widely accepted to be the result of their ability to tolerate low-oxygen conditions (Cook et al., 2000; Giere, 1993; Levin et al., 1991). Of the eight stations presented here, four are true OMZ stations, where DO contents are less than 0.5 mL L^{-1}. As reported earlier, and as we also found, sediments in the OMZ regions are much richer in organic matter and accumulated remnants of primary production than are other stations (Veit-Köhler et al., 2009), but these stations did not show markedly higher nematode density. Veit-Köhler et al. (2009) found, however, that nematode abundance decreased with increasing oxygen level. Moreover, a comparative study by Netto et al. (2005) of meiofauna from shelf and deep-sea sites

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off the south-east coast of Brazil found that the relative abundance of nematodes in the meiofauna increased with depth. Similarly in our study the nematode density did not follow any particular gradient, though the deep-basin stations showed the lowest density, which was well correlated with increasing bottom DO content and decreasing availability of organic carbon and sediment chlorophyll *a* in the basin beneath the lower slope. This pattern indicates that the overall decrease in nematode abundance with increasing water depth is related to the decreasing supply of organic matter. Neira et al. (2001) stated that oxygen limitation can play a direct role in structuring meiofauna communities at higher taxonomic level, but other authors, like Levin et al. (2002) and Veit-Köhler et al. (2009) stressed the combination macrofaunal predation and presence of food (Cook et al., 2000).

The nMDS based on nematode species abundance separated the three zones, and the difference was confirmed by the ANOSIM test. SIMPER also confirmed the huge dissimilarity among the three zones. Group 1 comprised the stations of the shelf region, with the exception of the deepest shelf station, which was clumped with the slope area to form the OMZ stations, where opportunistic species such as *Pselionema sp 1, Choanolaimus sp 2, Halichoanolaimus sp 1, Cobbia dentata, Daptonema sp 1,* and *Trissonchulus* sp 1 were found. Both Desmoscolecidae and *Richtersia* sp 1 and *Desmodora* sp 1 were most abundant at this lowest shelf station, where the DO concentration was low (< 0.5 mL^{-1}).

In addition to the seven species found exclusively in the OMZ a number of species were found exclusively outside it: *Diplolaimelloides* sp 1, *Halalaimus gracilis, H.* sp 1, *H.* sp 2, *H.* sp 3, *Viscosia* sp 1, *Meyersia* sp 1, *Prooncholaimus* sp 1, *Metalinhomoeus longiseta, Paralinhomoeus* sp 2, *Axonolaimus* sp 2, *Araeolaimus* sp 1, *A.* sp 2, *Bathyeurstomina* sp 1, *Theristus heterospiculum, T. interstitialis,* and *Sabatieria ornata*. Eight species were commonly found in all three zones: *Acantholaimus elegans, A. filicaudatus, Anoplostoma blanchardi, Anoplostoma* sp 1, *Synonchiella* sp 1, *Desmoscolex* sp 1, *Tricoma* sp 1, and *Siphnolaimus ewensis.* Large-scale comparisons of nematode community structure in other ocean basins indicate that continental-shelf

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nematode communities differ significantly from slope communities, in agreement with our study (Vanreusel et al., 2010). The dominant taxa on the slope – *Dolilaimus* sp 1, *Oxystomina affinis,* and *Epicanthion* sp 1 – also dominated the shelf and deep-basin communities but were less prominent at the deeper stations in our study. *Axonolaimus* sp 2 (30.2 %), *Halanchus* sp 1 (23.0 %), and *Dolicholaimus* sp 1 (15.1 %) were found in deeper sediments, suggesting that nematode assemblages are specific to certain habitats in the deep sea.

Nematode species that were dominant in shelf-OMZ regions, like *Tricoma* sp 1, *Desmoscolex* sp 1, *Viscosia abyssorum,* and *V. glabra* were found to have special features. The Desmoscolecidae and *Richtersia* sp. share the presence of cuticular protrusions, which might be viewed as protective coverings. The Desmoscolecidae are characterised by so-called desmen, ring-like expansions that are often reinforced with sediment grains (Decraemer, 1985). Furthermore, oncholaimid nematodes (*Viscosia abyssorum, V. glabra*) are known to transport themselves actively and rapidly to suitable new habitats (Fonseca-Genevois et al., 2006), but these species were found in each of the three benthic zones, and they were not exclusively dominant. The dominant species like *Terschellingia longicaudata*, *Desmodora* sp 1, and *Sphaerolaimus gracilis*, however, have been recognised extensively as tolerant (Schratzberger et al., 2006). Adaptations in *Terschellingia* sp and *Sphaerolaimus* sp – the presence of dark, often multilayered intracellular globules in the intestinal cells – are often pointed out. Moreover, the deposition of insoluble metal sulphides in intracellular inclusions in *Terschellingia longicaudata*, has been suggested to be a mechanism of detoxification of sulfide (Nicholas et al., 1987).

Several nematode species have proven to be cosmopolitan, inhabiting a variety of deep-sea habitats and different oceans. The IndVal index reaches its maximum (100 %) when individuals of the target species are observed at all the sites of one group and at no sites of any other (Dufrêne and Legendre, 1997). For those species that were found in equal proportions in each of the three zones, the association with the set of all the sites cannot be statistically tested, because no external group is available for

comparison, so these species cannot be treated as indicators of a particular habitat but can be considered cosmopolitan. Most species can use a variety of deep-sea habitats (Vanreusel et al., 2009).

Even though the majority of the species identified in our study were common and recorded from each of the three benthic zones, the IndVal index identified some species that can serve as indicators of the shelf, slope, and basin. The IndVal index is an important tool for ecosystem monitoring and assessments because it expresses a value for species or genera that can characterize the particular environment (Dufrene and Legendre, 1997). The genus *Acantholaimus* is quite typical of the deep sea and is rarely found in shallow water; only one species has been described from intertidal sediments (Platt and Zhang, 1982). Moreover, *Viscosia viscosia* often inhabits the surface layers of sediment and is apparently capable of floating (Fonseca-Genevois et al., 2006).

As is clear from the presence of very few dominant species within the OMZ, not all nematode species can tolerate low oxygen levels. Moreover, in our study, species diversity was higher on the shelf than on the slope or in the basin, in contrast to the results of an earlier study on macrofauna from this area by Ingole et al. (2010). SIMPER also confirmed that the basin (86 %) and slope stations (75 %) were more homogenous then the shelf stations (50 %). The more heterogeneous habitat can, in turn, support a higher number of taxa (see, e.g., Levin et al., 2010; Vanreusel et al., 2009).

Differences in diversity appear to be partly due to the bottom-water DO gradient, which includes values that are below the oxygen tolerance of many species. Therefore very few species were present on the slope, especially inside the OMZ. Moreover, the results of a macrofauna study from this area have shown that different physiographic provinces and an oxygen gradient have a greater influence on the species composition and diversity than do other oceanographic conditions (Ingole et al., 2010). The species number and diversity were positively correlated to DO and negatively correlated with Chl *a* and C_{org}. Species diversity is not always correlated with the organic enrichment of the sediment; Schratzberger and Warwick (1998) observed a decrease in species richness possibly due to anoxia and the release of toxic substances under high input of

organic loading. The lower species diversity of the nematode community under hypoxic conditions is accompanied by high dominance of a very few highly abundant species.

Levin et al. (2001) suggested, however, that the availability of oxygen and sediment heterogeneity, disturbance, and bottom current flow are key factors regulating species richness of local communities.

The reduction in species diversity, suggesting a very limited functional diversity, risks underestimating the true functional complexity of nematode communities (see, e.g., Gutierrez et al., 2000; Levin et al., 2000). Nematode species especially from OMZs seem able to develop some functional adaptations, as they must have a certain tolerance for sulphidic and/or anoxic conditions.

4.2 Functional traits

Marine organisms are often challenged by fluctuations in the aquatic environment, which they must survive, regulate, tolerate, or resist (Odiete, 1999). The different gradient of biological, chemical, and physical properties in the aquatic environment makes it more complicated. Among them one of the major challenges is the depletion of DO, but some organisms are able to cope by means of extreme changes in their body morphology and physiology (Schneider and Bush-Brown, 2003). In our study the distinct features of all three zones, as based on nematofaunal abundance, were also reflected in the functional-trait approach.

Deposit feeders were more abundant in shelf and basin areas than at most of the slope-area (OMZ) stations, where predators/omnivores were most abundant. Epigrowth feeders were more abundant at lower shelf stations and at some stations of the OMZ region, probably because of the higher organic content of the sediment; OMZ sediments were characterised by large, filamentous sulphur bacteria. *Thioploca* and *Beggiatoa* (Jørgensen and Gallardo, 1999) are often conspicuous features of the sediment surface there (Levin et al., 2000). Several previous workers have predicted that *Thioploca* mats represent a significant source of food for the OMZ faunas of the Peru–Chile margin (Gallardo, 1977; Arntz et al., 1991; Levin et al., 2000). Epigrowth feeders

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have been found to feed on microbiota by scraping them off solid surfaces or mucus threads with their teeth. Higher organic matter enriched the growth of diatoms and ciliates in the OMZ, which can contribute significantly to food for epigrowth feeders, but in general the proportion of predators/omnivores and epigrowth feeders was low in the our study. Gambi et al. (2003) suggested that the low prevalence of predatory and omnivorous nematodes can be attributed to the absence of freshly dead organisms.

The dominance of the deposit feeders in silty sediments of the basin is in agreement with most previous deep-sea studies (Tietjen, 1984; Jensen, 1988; Netto et al., 2005). Jensen (1988) found that the deep sea fauna in the Norwegian Sea was dominated by deposit feeders and had few predators and scavengers. Deposit feeders were also the dominant group in the Puerto Rico trench and the Hatteras abyssal plain The selective deposit feeders (microvores) are the main consumers of deep sea bacteria (Ingels et al., 2010) because deposit-feeding nematodes have minute buccal cavities, restricting them to small particulate food or dissolved organic matter. The relative proportion of each of the four Wieser feeding types in a community depends on the nature of the available food, which may perhaps explain their prominence on exposed substrata (Platt and Warwick, 1980). Thus BIOENV analysis found that feeding types correlated well with C_{org}, sediment chlorophyll, and silt, which represent the substratum condition and feeding content.

In nematodes, the tail plays an important role in locomotion, which in turn depends on sediment type (Riemann, 1974). Our BIOENV analysis revealed that tail type in nematodes was significantly correlated with sediment texture and C_{org}. The clavate tail shape dominated in the sandy shelf region, the conical tail shape in the fine sand and muddy sediments of the slope, and the long tail shape on the shelf and in the basin region. Nematodes with clavate tail shape dominated at each depth, although to a greater degree in the shelf and slope regions (Table 3). The dominance of clavate shape suggested the adaptability of the nematofauna, as Riemann (1974) considered this type of tail morphology to be typical of the inhabitants of the interstitial spaces in sand. The conical tail shape was observed more frequently in slope regions than on

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the shelf; again Riemann (1974) suggested conical tail could be a special adaptation to fine sand and muddy sediments, where only an incomplete interstitial system exists. Long-tail shape nematodes were found more often in the shelf and deep-basin regions than on the slope, where they were much less similar to round tail shape, but the scant availability of data on this aspect prevents comparison and any generalised conclusion.

Vanhove et al. (1995) and Soetaert et al. (2002) noted that length and width are important functional attributes for describing chemical stress, metabolic rate, the ability to move or migrate, and vulnerability to predation. In fact, size of animals is an integrative feature strongly correlated with their morphology, locomotion, feeding mode, and other characteristics. Most authors have related nematode length and width to granulometry, as the results of BIOENV analysis revealed that body shape was significantly correlated with sand and clay.

In our case, slender nematodes were dominant in the shelf region, and their lengths were mainly in the ranges of 2–4 mm and 1–2 mm. The slope area harbored more long/thin nematodes, as was the case in earlier studies (Jensen, 1987). Pronounced body elongation in nematodes and greater surface–volume ratio in thiobiotic species are adaptive characters related to low oxygen partial pressure and epidermal uptake of dissolved organic matter (Jensen, 1987). Further, increased length under suboxic or anoxic conditions reflects increased mobility. The increasing trends of long/thin nematodes from shelf to deeper stations possibly signify that large body size could facilitate easy burrowing through the sediment, but below the OMZ, the long/thin nematodes were even more abundant, suggesting the relationship with fine clay and silt sediments where only an incomplete interstitial system exists. In general comparison, however, the oxygenated organisms are found to be of size and shape a different from those of organisms from the OMZs (Schneider and Bush-Brown, 2003).

Consequently, the small-bodied nematodes appeared to be more abundant in the communities inhabiting the OMZ. This pattern may be explained by physiological constraints. Small organisms are better able to satisfy their metabolic demands because they have a higher surface–volume ratio.

Some "hard" traits, usually less accessible but with direct functional roles (Hodgson et al., 1999) like life history, are widely used in freshwater and terrestrial habitats (Bongers, 1990). Over 75 % of all identified individuals attained a C–P score of 2 to 3. Animals from the OMZ represented a higher contribution to this range. Under eutrophic conditions, colonisers are more numerous, whereas the number of persisters remains constant, but persisters (scores 3–4) were more often seen in deeper waters, perhaps because most deep-water nematodes are deposit feeders, which often score 3–4 on the C–P scale (Bongers et al., 1991).

The trait matrix revealed that some combinations of functional groups were significantly correlated. Stout body shape was positively correlated with clavate, long tail and non-selective feeding type because these traits showed the same increasing trend from shelf to basin (Fig. 4). A similar trend was evident for long/thin tail shape with 4 mm and clavate shape with non-selective feeding, which showed very high positive correlation (0.8). In general, large organisms were more prominent at eutrophic sites, whereas smaller organisms become more dominant in oligotrophic environments (Thiel, 1975). This pattern clearly explains the abundance of long/thin nematodes in the slope region of the Arabian Sea. The analysis of a combination of biological traits seems to be a more reliable approach for assessing the functional structure of nematode communities than was relying on single functional groups (Schratzberger et al., 2007). Our schematic model presented the trait responses in different zones (Fig. 4). The outcome confirmed that functional-trait analysis is of additional ecological importance, and the information captured by the biological-trait matrix was not a simple reflection of the information contained in taxonomy. They differ in their abilities to respond to environmental stresses and disturbance, thereby conferring resilience on the community. Environmental conditions thus influence the importance of functional complementarity in structuring communities (Hooper et al., 2005).

4.3 Environmental parameters and their impact on the nematode community

The thickness of the OMZ is strongly influenced by circulation and by the oxygen content of the ocean region. The Arabian-Sea OMZ spreads over $285\,000\,km^2$ and is the second most intense OMZ in the world tropical ocean (Kamykowski and Zentara, 1990); oxygen depletion is nearly total at depths from 200 to 1000 m (see, e.g., Morrison et al., 1998).In this region oxygen concentrations and organic matter are inversely correlated (Levin and Gage, 1998), and this condition represents a major challenge for the adaptation of many species in OMZs. The DistLM analysis indicated that DO concentration and organic content were the only parameters that were significantly correlated with nematode species and functional data. Moreover, results of BIOENV analysis revealed the importance of C_{org}, sediment chlorophyll, and silt content for feeding strategy. Organic enrichment is an important ecological process in marine sediments (Kelly and Nixon, 1984), and it is related to the presence of fine sediment, a low hydrodynamic regime, and low DO (Snelgrove and Butman, 1994). Nematode assemblages were dominated by deposit-feeding organisms, which can make full use of both particulate organic matter and the associated bacterial biomass. Moreover the content of organic matter can partially explain the spatial patterns of distribution of free-living nematodes in some habitats (see, e.g., Ólafsson and Elmgren, 1997; Schratzberger et al., 2006). Body size was well correlated with DO, clay, and C_{org}, whereas tail shape was correlated with clay, DO, and silt and body length with sand, clay, and C : N ratio. This pattern shows the properties of sediment-related factors, which are also important for morphological characteristics of species. The highest values of sediment C_{org} on the slope are probably due to the diverse topographic features there, and the associated hydrodynamic processes play an important role in the enrichment of C_{org} (Rao and Veerayya, 2000).

Several authors have pointed out that nematode species can successfully cope with anoxic conditions by developing appropriate physiological and behavioural mecha-

nisms (e.g., symbiosis with bacteria, which we also observed, and migration to "oxygen islands," sensu Reise and Ax (1979) and Wetzel et al. (1995).

4.4 Interesting findings in the OMZ

The greatest numbers of specimens of *Desmodora* sp were found with the epibionts.
Some species were observed to have structural modifications.
Some species were observed to have unidentified blackish gut content.
A nematode was found in the gut of the *Metalinhomoeus* sp 1, which has a very small buccal cavity.

5 Conclusions

Free-living nematodes are an abundant and diverse component of the meiofauna in the western continental margin of Arabian Sea. They follow the general trends of decreasing nematode abundance and diversity with increasing depth observed among other benthic taxa along the continental shelf and in the deep sea. We aimed to determine the nematode community structure and functional traits in the Indian western continental margin, including the OMZ. The effects of heterogeneous environments were more evident in taxonomic groups than in functional traits. Although numerous factors could be important for the formation and persistence of nematode communities, the presence of the OMZ seems to be paramount. Along with organic content, DO plays a vital role in structuring nematode communities and certain functional adaptations among different species may play an important role in determining the ecosystem function. From our study, no single parameter can be determined to cause the observed patterns in the three benthic zones. Our results support the previous finding that, among the meiofauna, nematodes are the taxon most tolerant of environmental variation but that within the nematode community only a few species can tolerate oxygen minima. Our study has provided the first insight into the ecosystem functional diversity from

coastal to deep-sea nematode fauna from the Arabian Sea, but only further work will reveal whether this pattern is broadly applicable.

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Table 1. Location and depth of sampling stations and sediment texture.

Depth	34	48	102	525	1001	1524	2001	2546
Lat (°N)	13°54.26′	13°59.88′	14°00.29′	14°00.24′	14°00.25′	14°00.30′	14°00.09′	13°59.55′
Long (°E)	74°18.97′	74°00.03′	73°29.94′	73°13.97′	73°08.11′	72°57.22′	71°13.21′	70°48.40′
Temperature, °C	23.2	20.84	18	10.7	7.85	5	–	–
Salinity (psu)	35.8	35.5	35.1	35.3	35.2	35	–	–
DO, mL L^{-1}	0.69	0.56	0.38	0.08	0.28	1.35	2.3	2.3
Sediment Chl – µg^{-1}	1.4	0.2	0.6	0.7	2.1	0.6	0.6	0.2
C_{org} (%)	1.9	0.8	1.5	3.8	4.4	2.2	0.3	0.9
C : N	11.0	–	10.3	10.8	8.9	8.2	4.6	4.9
Clay (%)	8.3	9.8	3.0	12.9	13.2	8.7	15.1	15.6
Silt (%)	75.6	39.7	38.5	53.6	84.5	89.4	79.2	71.7
Sand (%)	16.0	50.5	58.5	33.5	2.3	1.9	5.7	12.7
Texture	Clayey silt	Silty sand	Silty sand	Sandy silt	Clayey silt	Clayey silt	Clayey silt	Clayey silt
CaCO$_3$	26.8	69.2	65.1	44.5	28.3	24.5	49.3	53.7

Table 2. List of species and their presence in and absence from each habitat.

	Shelf	Shelf	Shelf	Upper slope	Mid slope	Lower slope	Basin	Basin
	34 m	48 m	102 m	525 m	1001 m	1524 m	2001 m	2546 m
CHROMADORIDAE								
Acantholaimus calathus	−	−	−	−	−	−	+	+
Acantholaimus elegans	+	+	+	+	+	+	+	+
Acantholaimus filicaudatus	+	+	+	+	+	+	+	+
Acantholaimus mirabilis	−	−	−	−	−	−	+	+
Actinonema sp 1	+	+	+	−	−	−	−	−
Actinonema sp 2	+	−	−	−	−	−	−	−
Actinonema sp 3	+	+	+	−	−	−	−	−
Chromadora sp 1	−	−	+	+	−	+	+	+
Chromadorita sp 1	−	−	+	+	−	+	+	+
Chromadorita sp 2	−	−	+	+	+	+	+	+
AEGIALOALAIMIDAE								
Aegioloalaimus sp 1	+	+	+	−	−	−	−	−
AXONOLAIMIDAE								
Axonolaimus sp 1	+	+	−	−	−	+	−	−
Axonolaimus sp 2	+	−	−	−	−	−	+	+
Axonolaimus sp 3	+	−	−	−	−	−	−	−
ANOPLOSTOMATIDAE								
Anoplostoma blanchardi	+	+	+	+	+	+	+	+
Anoplostoma sp 1	+	+	+	+	+	+	+	+
Anoplostoma sp 2	−	+	+	+	+	+	−	−
DIPLOPELTIDAE								
Araeolaimus sp 1	+	+	−	−	−	−	+	−
Araeolaimus sp 2	+	−	−	−	−	−	+	+
Campylaimus sp 1	+	−	−	−	−	−	−	−
Southerniella sp 1	+	−	+	+	+	+	−	−
ENCHELIDIIDAE								
Bathyeurstomina sp 1	+	−	−	−	−	−	+	+
CERAMONEMATIDAE								
Ceramonema yunfengi	+	+	−	−	−	−	−	−
Cermonema attenuatum	+	+	−	−	−	+	−	−
Pselionema hexalatum	+	−	+	+	+	+	−	−
Pselionema sp 1	−	−	+	+	+	+	−	−
Pterygonema sp 1	+	+	−	−	−	−	−	−
Pterygonema sp 2	−	+	+	+	+	+	−	−
SELACHNEMATIDAE								
Cheironchus sp 1	+	−	−	−	−	−	−	−
Choanolaimus sp 2	−	−	+	+	+	+	−	−
Gammanema sp 1	+	+	−	−	−	−	−	−
Halichoanolaimus chordiurus	+	+	−	−	−	−	−	−
Halichoanolaimus robustus	+	+	+	+	+	+	−	−
Halichoanolaimus sp 1	−	−	+	+	+	+	−	−
Halichoanolaimus sp 2	−	+	+	+	+	+	−	−
Richtersia sp 1	+	+	−	−	−	−	−	−
Synonchiella sp 1	+	+	+	+	+	+	+	+
XYALIDAE								
Cobbia dentata	−	−	+	+	+	+	−	−
Cobbia sp 1	−	+	−	−	−	−	−	−
Cobbia sp 3	+	+	+	+	+	+	−	−
Cobbia sp 2	+	+	+	−	−	+	+	−
Daptonema circulum	+	+	+	+	+	−	+	+
Daptonema sp 1	−	−	+	+	+	+	−	−
Daptonema sp 2	+	−	+	+	−	−	−	−
Theristus ensifer	−	−	+	+	+	+	−	+
Theristus heterospiculum	+	+	−	−	−	−	+	+
Theristus interstitialis	+	+	−	−	−	−	+	−

Table 2. Continued.

	Shelf	Shelf	Shelf	Upper slope	Mid slope	Lower slope	Basin	Basin
	34 m	48 m	102 m	525 m	1001 m	1524 m	2001 m	2546 m
LEPTOLAIMIDAE								
Dagda sp 1	+	+	+	−	−	−	+	+
DESMOSCOLECIDAE								
Desmoscolex sp 1	+	+	+	+	+	+	+	+
Tricoma sp 1	+	+	+	+	+	+	+	+
MONHYSTERIDAE								
Diplolaimella sp 1	−	+	−	−	−	−	−	−
Diplolaimelloides sp 1	−	+	−	−	−	−	+	−
IRONIDAE								
Dolicholaimus sp 1	+	+	−	−	−	−	−	−
Trissonchulus sp 1	−	−	+	+	−	−	−	−
SPHAEROLAIMIDAE								
Dolilaimus sp 1	−	−	−	−	−	−	+	+
Metasphaerolaimus sp 1	−	−	−	−	−	−	+	+
Metasphaerolaimus sp 2	−	−	+	+	−	+	+	+
Parasphaerolaimus sp 1	+	+	+	+	+	+	−	−
Sphaerolaimus balticus	+	+	−	−	−	−	−	−
Sphaerolaimus gracilis	+	−	+	+	+	+	−	−
Sphaerolaimus sp 1	−	−	−	−	−	−	+	+
Subsphaerolaimus sp 1	−	−	−	−	−	−	+	+
COMESOMATIDAE								
Actarjania sp 1	+	+	−	−	−	−	−	−
Dorylaimopsis sp 1	+	−	−	−	−	−	−	−
Dorylaimopsis sp 2	−	+	+	+	+	+	−	−
Hopperia sp 1	+	+	−	−	−	−	−	−
Pierrickia sp 1	+	−	−	−	−	−	−	−
Pierrickia sp 2	−	−	−	−	−	−	+	+
Sabatieria ornata	+	+	−	−	−	−	+	+
Sabatieria praedatrix	−	−	−	−	−	−	+	+
Sabatieria pulchra	+	−	−	−	−	−	−	−
Sabatieria punctata	+	+	−	−	−	−	−	−
Sabatieria sp 1	+	+	−	−	−	−	−	−
Sabatieria sp 2	+	−	−	−	−	−	−	−
Sabatieria sp 3	+	+	−	−	−	−	−	−
Setosabatieria sp 1	+	+	+	−	−	−	+	−
Vasostoma sp 1	+	−	+	−	−	−	−	−
THORACOSTOMOPSIDAE								
Epicanthion sp 1	−	−	−	−	−	−	+	+
Mesocanthion sp 1	+	−	−	−	−	−	−	−
OXYSTOMINIDAE								
Halalaimus gracilis	+	+	−	−	−	−	+	+
Halalaimus sp 1	+	+	−	−	−	−	+	+
Halalaimus sp 2	+	−	−	−	−	−	+	+
Halalaimus sp 3	+	−	−	−	−	−	+	+
Oxystomina affinis	+	+	+	−	−	−	−	−
Oxystomina sp 1	+	+	+	+	+	−	−	−
Wieseria sp 1	+	+	+	+	+	+	−	−
CYATHOLAIMIDAE								
Longicytholaimus sp 1	−	−	−	−	−	−	+	+
Marylynnia sp 1	−	+	−	−	−	−	−	−
Minolaimus sp 1	−	−	+	−	−	−	−	−

Table 2. Continued.

	Shelf 34 m	Shelf 48 m	Shelf 102 m	Upper slope 525 m	Mid slope 1001 m	Lower slope 1524 m	Basin 2001 m	Basin 2546 m
ONCHOLAIMIDAE								
Oncholaimus attenuatus	–	–	–	–	–	–	+	+
Oncholaimus mediterraneus	+	–	–	–	–	–	–	–
Viscosia viscosia	+	+	+	–	–	–	–	–
Viscosia sp 1	+	–	–	–	–	–	+	+
Viscosia sp 2	+	+	+	+	+	+	–	–
Viscosia sp 3	+	+	+	+	+	+	–	–
Meyersia minor	+	–	–	–	–	–	–	–
Meyersia sp 1	+	+	–	–	–	–	+	+
Meyersiaa sp 2	–	+	–	–	–	–	–	–
Prooncholaimus sp 1	+	+	–	–	–	–	+	–
LINHOMOEIDAE								
Metalinhomoeus longiseta	+	+	–	–	–	–	+	+
Metalinhomoeus sp 1	–	+	–	–	–	–	–	–
Terschellingia longicaudata	+	–	+	+	+	+	–	–
Paralinhomoeus filiformis	+	+	–	+	+	+	–	–
Paralinhomoeus lepturus	+	+	+	+	+	+	–	–
Paralinhomoeus sp 1	+	+	+	+	+	+	–	–
Paralinhomoeus sp 2	+	+	–	–	–	–	+	+
SIPHONOLAIMIDAE								
Siphnolaimus ewensis	+	+	+	+	+	+	+	+
TREFUSIIDAE								
Halanchus sp 1	–	+	–	–	–	–	–	–
MICROLAIMIDAE								
Microlaimus sp 1	+	+	+	–	–	–	+	+
DESMODORIDAE								
Desmodora sp 1	–	–	+	+	+	+	+	+

Table 3. The 10 most abundant species recorded from the oxygen minimum zone (OMZ) and from areas outside that zone.

Species	OMZ (%)	Species	Outside OMZ (%)
Terschellingia longicaudata	41.5	*Setosabatieria* sp 1	14.1
Desmodora sp 1	37.2	*Chromadorita* sp 2	11.2
Sphaerolaimus gracilis	27.6	*Sphaerolaimus gracilis*	8.9
Theristus ensifer	24.9	*Theristus heterospiculum*	8.3
Halichoanolaimus sp 1	15.3	*Synonchiella* sp 1	7.5
Pterygonema sp 1	14.2	*Metasphaerolaimus* sp 2	6.4
Daptonema sp 1	13.1	*Daptonema* sp 2	6.3
Parasphaerolaimus sp 1	12.1	*Siphnolaimus ewensis*	6.0
Halichoanolaimus robustus	11.5	*Axonolaimus* sp 3	5.8
Trissonchulus sp 1	11.5	*Parasphaerolaimus* sp 1	5.8

Table 4. List of indicator species calculated by IndVal index, number of genera associated with the shelf group = 4, number of genera associated to slope groups = 5, number of genera associated with the basin = 7.

	Association statistic	P value
Shelf		
Viscosia viscosia	0.978	0.005
Oxystomina affinis	0.976	0.005
Aegioloalaimus sp 1	0.973	0.005
Axonolaimus sp 1	0.950	0.045
Slope (OMZ)		
Choanolaimus sp 2	1.000	0.005
Cobbia dentata	0.973	0.041
Daptonema sp 1	0.951	0.041
Halichoanolaimus sp 1	0.942	0.042
Pselionema sp 1	0.941	0.042
Basin		
Acantholaimus mirabilis	1.000	0.005
Acantholaimus calathus	1.000	0.005
Sabatieria Ornata	1.000	0.005
Theristus heterospiculum	1.000	0.040
Setosabatieria sp 1	0.994	0.030
Metasphaerolaimus sp 2	0.994	0.030
Dagda sp 1	0.983	0.045

Table 5. Mean and standard error for diversity indices of the nematode communities at species level. d, Margalef's index for species richness; J', Pielou's index for species evenness; ES (51), estimated total number of species; H' (loge), log2 Shannon–Wiener Index for species diversity.

Zone	d	J'	ES(51)	H'(loge)
Shelf	13.53 ± 1.53	0.98 ± 0.01	40.54 ± 2.57	4.04 ± 0.10
Slope	7.89 ± 0.51	0.98 ± 0.01	31.69 ± 1.24	3.56 ± 0.06
Basin	7.49 ± 0.11	0.97 ± 0.0	28.16 ± 0.22	3.48 ± 0.01

Table 6. Functional trait matrix showing the percentages of all individuals belonging to four nematode feeding categories (1A, no buccal cavity or a fine tubular one, selective deposit (bacterial) feeders; 1B, large but unarmed buccal cavity, non-selective deposit feeders; 2A, buccal cavity with scraping tooth or teeth, epigrowth (diatom) feeders; 2B, buccal cavity with large jaws, predators/omnivores) and four tail-shape categories.

	Feeding type				Tail shape			
	1A	1B	2A	2B	Clavate	Round	Conical	Long
Shelf	18	49	5	28	62	10	16	12
Shelf	12	38	22	28	56	9	26	9
Shelf	16	40	15	29	64	1	33	2
Upper slope	15	15	22	48	48	2	46	4
Mid-slope	32	14	24	30	48	1	49	2
Lower slope	29	19	13	39	55	3	39	3
Basin	27	32	25	16	56	2	31	11
Basin	27	34	19	20	62	1	29	8

Table 7. Functional trait matrix showing the percentages of all individuals belonging to four body-length categories, three body-shape categories, and five life-history strategies (coloniser-persister score).

		Body length				Body shape			Life-history strategy (coloniser-persister score)				
	Depth	< 1 mm	1–2 mm	2–4 mm	> 4 mm	Slender	Stout	Long/thin	1	2	3	4	5
Shelf	34	10	35	51	4	83	8	9	14	50	28	8	0
Shelf	48	29	28	24	19	71	11	18	2	41	46	11	0
Shelf	102	15	46	31	8	66	7	27	0	63	24	13	0
Upper slope	525	21	36	40	3	68	6	26	0	38	42	20	0
Mid-slope	1001	25	37	35	3	68	4	28	0	39	37	24	0
Lower slope	1524	28	39	30	3	69	8	23	2	42	32	24	0
Basin	2001	25	35	27	13	41	8	51	0	32	45	23	0
Basin	2546	19	36	29	16	44	10	46	0	29	43	28	0

Table 8. Results from BIOENV analyses: Spearman rank correlation (rho) and significance level (P) between nematode biological traits and environmental variables. Values $P < 0.05$ are significant. DO, dissolved oxygen.

Variable	Environmental parameters	Global test (Rho)	Significance level of sample statistics (%)
Species	DO, sediment chlorophyll	0.785	
Feeding types	TOC, sediment chlorophyll Clay, DO	0.44	3
Body size	Sand, Silt, C : N ratio	0.46	2
Tail shape	Clay, bottom DO	0.52	1
Body length	Sand, clay, C : N ratio	0.61	7
C–P value	Clay, bottom DO	0.53	8

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Table 9. Result of distance-based linear model (DistLM) analyses showing the influence of environmental parameters on nematode species data and on functional biological traits (Bray–Curtis similarity of square-root-transformed abundance.

Variable	R^2	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
Results with nematode species data							
DO, mL L^{-1}	0.4647	6420.3	5.209	0.007	0.4647	0.4647	6
Chl a µg^{-1}	0.40376	539.58	0.394	0.012	3.91E-02	0.50376	5
C$_{org}$ (%)	0.73435	3185.9	3.472	0.048	0.23059	0.73435	4
Clay (%)	0.827	1280	1.607	0.22	9.26E-02	0.827	3
Silt (%)	0.89849	987.83	1.409	0.34	7.15E-02	0.89849	2
Sand (%)	0.97481	1054.4	3.03	0.254	7.63E-02	0.97481	1
Results with functional biological traits							
Sed Chl a	0.14881	59.984	1.049	0.034	0.14881	0.14881	6
TOC	0.40413	102.91	2.142	0.049	0.25532	0.40413	5
Clay (%)	0.57135	67.404	1.56	0.242	0.16722	0.57135	4
Silt (%)	0.64021	27.759	0.574	0.669	6.89E-02	0.64021	3
Sand (%)	0.64021	−3.12E-13	0.76317	0.551	−7.73E-16	0.64021	3
DO, mL L^{-1}	0.85194	85.344	2.86	0.152	0.21173	0.85194	2

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Figure 1. Map showing location of the 8 sampling stations (in circle) in the coast of Arabian Sea along with depth contours and the positions of the sampling stations.

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Figure 2. Principal component analysis derived from the contribution of parameters in each benthic zone. PC 1 and 2 accounted for 81 % of the total variation present.
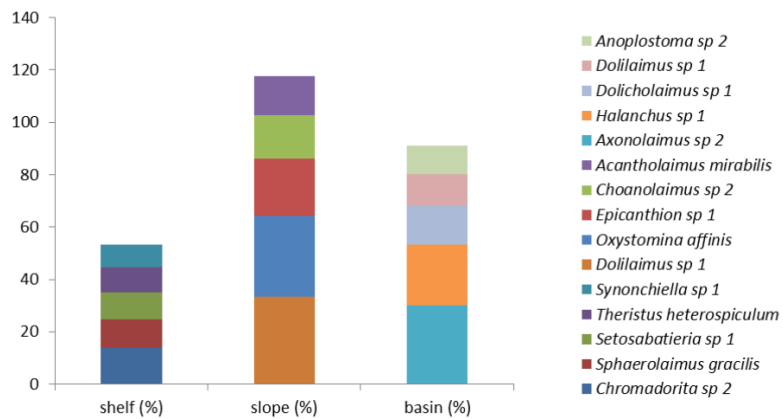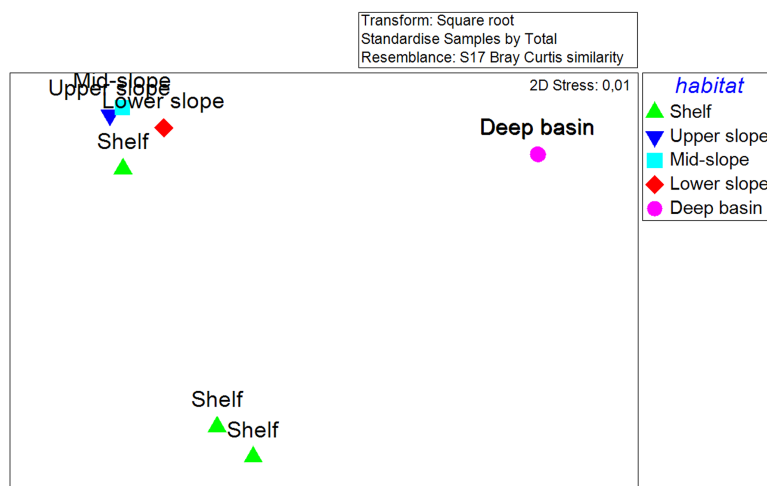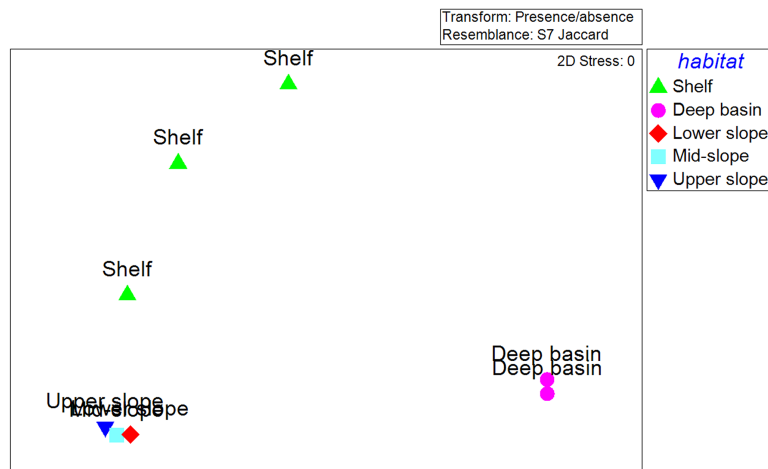
11580

Figure 3. Average relative abundances (%) of the most abundant species belonging to each of three benthic zones. Only the top 5 dominant species from each zone are presented.

Figure 4. nMDS ordination based on nematode species abundance using the Bray–Curtis similarity index.

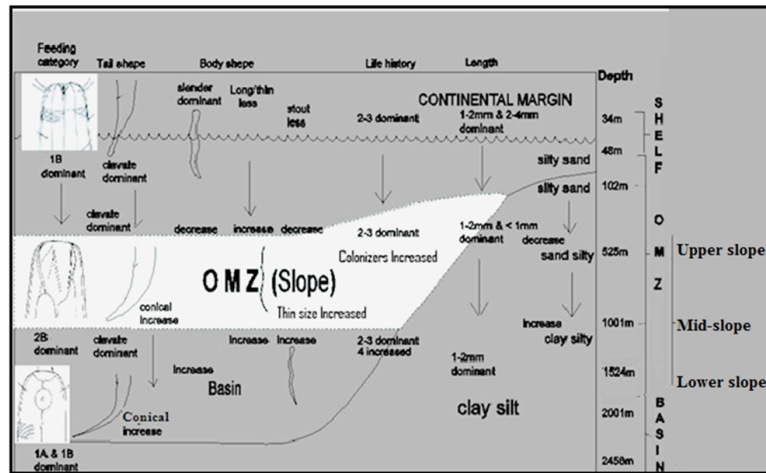**Figure 5.** nMDS ordination based on nematode species presence/absence.
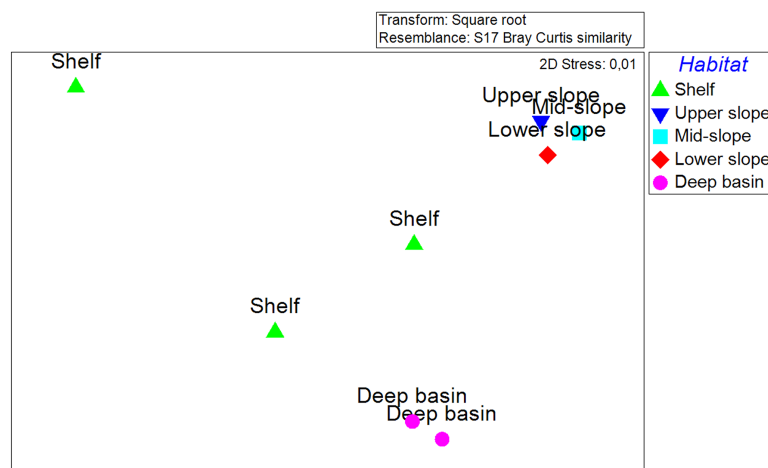
Figure 6. nMDS ordination based on nematode species biological traits using the Bray–Curtis similarity index.

Figure 7. Schematic model of all the biological traits at each benthic zone.