Structure and function of nematode communities across the Indian western continental margin and its 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 low oxygen levels 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. The oxygen minimum zone extended from 102 m to 1001 m. Nematodes were (described and undescribed) identified to species and classified according to biological and functional traits. A total of 110 nematode species belonging to 24 families were found along the transect. Three depth zones were identified, the shelf (depth range 34–102 m; highest nematode mean density: 176.6 ± 37 ind/10 cm^2), the slope (525–1524 m; 124.3 ± 16 ind/10 cm^2), and the basin (2001–2546 m; 62.9 ± 2 ind/10 cm^2). Across the entire study area, the dominant species were *Terschellingia longicaudata*, *Desmodora* sp 1, *Sphaerolaimus gracilis*, and *Theristus ensifer*; their maximum density was at shelf stations. Nematode communities in different zones differed in species composition. *Chromadorita* sp 2 (2.78%) and *Sphaerolaimus gracilis* (2.21%), were dominant on the shelf, whereas *Terschellingia longicaudata* (4.73%) and *Desmodora* sp 1 (4.42%) were dominant on the slope, but in the basin, *Halalaimus* sp 1(1.11%) and *Acantholaimus elegans* (1.11%) were dominant. 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. The functional composition of nematodes was strongly linked to the organic carbon and dissolved oxygen concentration. 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. Correlation with a number of environmental variables indicated that food quantity (measured as the organic carbon content and chlorophyll content) and oxygen level were the major factors that influenced nematode community structure and function.

Key words: oxygen minimum zone, habitat heterogeneity, Nematoda, functional traits, deep sea, Arabian Sea, Indian continental margin.

1. Introduction

The continental margin exhibits great topographical heterogeneity in geomorphological features (e.g., canyons and seamounts, 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 in living conditions and the high faunal diversity it supports on local, regional, and global scales (Vanreusel 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, with oxygen concentrations < 2 µM in its core (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009; Zettler et al., 2009). The OMZ in the Arabian Sea is spread over 285,000 km^2 of the benthic area. The OMZ occupies approximately the 150–1000 m depth range and is the thickest of the three major OMZs of the open ocean (Banse et al., 2014). 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).

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 other meiofauna to anoxic conditions (Giere, 1993; Moodley et al., 1997). Studies like those of Jensen (1987) and Murrell and Fleeger (1989) reported effects of low-oxygen conditions on nematofauna in sandy sediments at shallow depths and from the Gulf of Mexico, respectively, and showed 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 oxygen concentration, but in another experimental study in the tidal flats, hypoxia caused a dramatic change in the nematode community composition, including reduction in diversity and abundance of all dominant nematodes except for genus *Odontophora* (Van Colen et al., 2008). Neira et al.

(2013) found that nematode generic and trophic diversity was lowest at the most oxygen-depleted site along a central Chile margin. De Troch et al. (2013), in a short incubation experiment, found that nematodes were not affected by anoxic conditions. They further concluded that responses to stress depend on the species and the frequency of the hypoxic periods. In contrast to several studies on the effects of anoxia on Nematoda at higher taxonomic levels, little is known about their response at the species level.

Several transitional settings in the western Indian continental margin, including the shelf, slope (long stretch of OMZ), and basin, provide multiple oxygen and other environmental gradients. These settings allowed us to investigate how oxygen and environmental factors affect and modulate the structure and function of nematode communities at the species level. An exclusive study from the Indian western continental margin with reference to nematode tolerance in the OMZ is therefore important. Furthermore, nematode community structure from the western Indian continental margin (including the OMZ) of the Arabian Sea remains unstudied. In general information on nematode species data is missing from the Arabian Sea and the present study can provide important basic information on nematode community structure.

Traditional taxonomy-based methods of nematode community analyses may not, however, fully account for nematodes' diverse roles in ecosystem function (Schratzberger et al., 2007), so the inclusion of functional analysis has been recommended (de Jonge et al., 2006).

Many previous studies (e.g. Bremner et al., 2003; Boström et al., 2006) on macrobenthic invertebrates have shown that linking the taxonomic and functional aspects can reveal different relationships between assemblages, and for exploration of the relationship between biodiversity and ecosystem function, nematodes could be considered the ideal model organisms (Danovaro et al., 2008).

Nematode 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). 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 energy requirements, whereas species morphotype represents adaptations to life in oxygen-poor and sulphide-rich sediments (Jensen, 1987). Bongers (1990) and Bongers et al.

(1991, 1995) 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 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 a heterogeneous gradient like the shelf, slope, and deep basin of the western Indian continental margin affect the marine nematode community 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

The bottom topography of the Arabian Sea includes the Carlsberg Ridge is in the southern part, the Murray Ridge in the northern part, and an unsloped region in between (from 14° N to 21° N). The continental shelf is 120 km wide off the southern part, narrows to about 60 km off 11° N, and widens to about 350 km off the Gulf of Cambay (Shetye and Shenoi, 1988).

Surface circulation is controlled by the seasonal variation in various types of winds. During the SW monsoon, biological productivity in the Arabian Sea lies mainly around the centers of seasonal upwelling off the Arabian Peninsula, Somalia, and southwest India (Qasim, 1977). The Arabian Sea is characterised by a very pronounced midwater oxygen minimum zone (OMZ) between 150 and 1250 m; it is over 1000 m thick and extends vertically from the bottom of the euphotic layer (~100 m) to ~1000 m (Wishner et al., 1990). The variations in the intensity of the OMZ are related to upwelling intensity and thermocline ventilation by Indian Ocean water (Reichart et al., 1998). It is located directly beneath the productive upwelling region (de Sousa et al., 1996; Morrison et al., 1998).

2.2. Sampling

A single transect was selected perpendicular to the coast of the Arabian Sea at 14° N latitude (Fig. 1). 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 × 50 × 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 (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 m to 1001 m. For nematode assemblages, a PVC core (5.7 cm diameter) was used for sub-sampling. At each station, two sub-samples were sliced per centimetre down to 5 cm sediment depth and fixed in buffered 4% formalin. Separate sub-cores was collected for organic carbon (C_{org}) and sediment chlorophyll-*a* (Chl-*a*), and they were frozen at –20ºC. Bottom-water dissolved oxygen (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.

2.3. Laboratory analysis

Dissolved oxygen was analyzed by Winkler's method (Strickland and Parsons, 1968). Sample bottles are stored upright in an ice chest in a dark location and were analyzed after a period of 8–9 hours. Chl-*a* was estimated by means of an acetone extraction method using a fluorometer (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 granulometry was determined by a Malvern Laser Analyzer (Model—Hydro 2000MU).

Meiofauna samples were washed over a 500-µm mesh and then sieved on a 32-µm mesh, which retained the meiofauna fraction. This retained fraction was then elutriated by the centrifugation-flotation technique with LUDOX (Vincx, 1996; Heip et al., 1985). Nematodes were counted through a stereo-microscope and were picked and mounted on permanent glass slides for taxonomic identification. In all, 1798 nematodes were examined. They were identified up to described and morphotype species level from the pictorial keys of Platt and Warwick

(1983) and the NeMys database (Vanaverbeke et al., 2015). For identification to species level, each morphotype was sketched and measured 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 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: 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 characterising nematode communities. 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 body 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 mm, 1–2 mm, 2–4 mm, >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). The species belonging to the monhysterid family were assigned to the C–P 2 class ("general opportunists") as advised by Bongers et al. (1995) and later mentioned by Pape et al. (2013); no nematodes belonged to C–P class 1 ("enrichment opportunists").

A biological-traits matrix was constructed by assignment to each nematode species of its affinity to each trait category and the percentage (%) contribution of each species.

2.5. Statistical analysis

The similarity analysis at the species level was based on two types of similarity measures: the Bray-Curtis dissimilarity (standardised, square-root transformed) (Bray and Curtis, 1957), based on the relative abundances of nematode genera, and ordination using the Jaccard similarity index based on presence-absence (Clarke, 1993). Differences between the samples were visualised by means of non-metric multidimensional scaling (nMDS) plots.

We applied PERMANOVA designed with two factors—“station” (all stations in the zone combined) nested in “zones” (shelf, slope, and deep basin)—to detect the statistical significance of differences in pair-wise comparisons of nematode communities from different zones (PERMANOVA, Anderson, 2005; Anderson et al., 2008).

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).

Environmental variables were then subjected to principal-components analysis (PCA) for identification of the spatial patterns based on environmental data. A lower triangular Euclidean distance matrix relating to the ordination was constructed (Clarke and Green, 1988). Before calculation of the Euclidean distance resemblance matrix, the data were checked for uniform distribution and normalised (by subtraction of the mean and division by the standard deviation, for each variable) before analysis.

Analysis of collinearity was tested by means of draftsman plot and the associated standard product moment correlation coefficients between all pairs of variables, and those with correlations $r^2 > 0.9$ were omitted from the model. If distribution of residuals was skewed, natural logarithm transformation was applied to the response variable until assumptions were met by the best model. The relationships of taxonomic and functional traits with environmental variables were examined by means 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. We performed RELATE and a stepwise distance-based linear model permutation test (DistLM, McArdle and Anderson, 2001) to identify which set of environmental variables predicted the multivariate variation in nematode species assemblages. The adjusted R^2 was used as a selection criterion to permit the fitting of the best explanatory environmental variables in the model. Euclidean distance was used as the resemblance measure in all DISTLM procedures. Results were visualised with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008).

To identify the species that would characterise 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 Cáceres et al., 2010) in 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 randomisations 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., 2011) and the PERMANOVA+ module of the PRIMER v6 software (Clarke and Gorley, 2006; Anderson et al., 2008). A schematic diagram was prepared from the taxonomic and functional dataset that represented the pattern in the benthic zones of western Indian continental margin.

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 clayish silts. The salinity of the bottom water varied little, but temperature decreased with increasing 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), defined as the OMZ. Oxygen values began to increase at the lower slope. Higher values of DO were observed in the basin (Table 1). The core of the OMZ was located at 525 m, where the lowest DO (0.08 ml l^{-1}) value was recorded.

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 (PC1 explained 43.5%, PC2 33.3%). Two shelf stations were characterised by high coarse sand and $CaCO_3$ content, whereas one (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. Nematode density was higher at the shelf stations than on the slope or in the basin. The lowest average density was observed in the basin: 62.9 ± 2 ind/10 cm^2. The mean nematode density in the slope region was 124.3 ± 16 ind/10 cm^2, and the lowest density was observed on the lower slope (98.1 ind/10 cm^2), whereas the upper slope station near the shelf was represented by a density of 155.2 ind/10 cm^2, but the mid slope density was 120.0 ind/10 cm^2. The highest average nematode density 176.6 ± 37 ind/10 cm^2 was observed at shelf depth.

nMDS based on nematode species abundance (Bray-Curtis) and presence/absence data illustrates clearly the extent to which the three zones differ (Fig. 3 and 4). The nMDS plot based on the Bray-Curtis similarity measure indicated three groups of samples (Fig. 3). The largest group included the slope stations and the deepest shelf station—those stations that form the OMZ. The PERMANOVA community results indicated significant differences between the three zones (p = 0.03), but the nMDS based on presence/absence separated only the slope and basin. The stations on the shelf were distributed randomly (Fig. 4), and the PERMANOVA community results confirmed nonsignificant differences between the zones (p = 0.12). In pair-wise PERMANOVA, comparisons between shelf and deep basin nematode assemblages differ significantly, .p = 0.046, whereas the pairwise comparisons between slope and shelf and between slope and basin were not significant (Table 2).

Thirty-eight species were identified that were found only in the shelf region. Of these, *Chromadorita* sp 2 (2.78%) and *Sphaerolaimus gracilis* (2.21%) were dominant. *Terschellingia Longicaudata* (4.73%) and *Desmodora* sp 1 (4.42) dominated the slope, and *Halalaimus* sp 1 (1.11%) and *Acantholaimus elegans* (1.11%) dominated the basin. Across the entire study area, however, the dominant species were *Terschellingia longicaudata*, (15.2 %), *Desmodora* sp 1 (14.5%), *Sphaerolaimus gracilis* (11.7%), and *Theristus ensifer* (9.1%); their maximum contributions came from shelf stations (Table 3).

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, Epacanthion* sp 1, *Longicyatholaimus* sp 1, and *Oncholaimus attenuateus*. The top 10 dominant species from OMZ and from the remaining areas are given in Table 4.

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 5). *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 5 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 5 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 *Siphonolaimus ewensis*) were not amenable to statistical testing because of the lack of an external group for comparison.

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 (PERMANOVA: $p < 0.05$). The average values of diversity indices in each zone are given in Table 6.

3.3. Functional Traits

Functional attributes of nematode communities in the Arabian Sea are listed in Tables 7 and 8. The geographic separation was less pronounced in the ordinations derived from functional characteristics of nematode communities, although the basin and slope samples were clumped into groups but shelf stations were randomly distributed (Fig. 5). As shown by the results of pair-wise PERMANOVA, three zones containing nematode assemblages (shelf vs deep basin; slope vs deep basin) differed significantly. Assemblages were dominated by deposit feeders (1B, 1A) followed by predators (2B), whereas proportions of epigrowth feeders (2A) were comparatively low (Table 7). The shelf area was dominated by non-selective deposit feeders (1B) and predators (2B), whereas the slope stations showed the highest proportions (29–48%) of predators/omnivores (group 2B). Similarly the dominance of predators (2B) was seen in OMZ stations, from 102 to 1001 m. The shelf and basin areas were dominated by deposit feeders (mainly the non-selective 1B group).

Clavate and conical were the most prevalent tail shapes at the majority of stations (Table 7); the average proportion of conical tails was higher on the slope and at the OMZ stations (33–49%). Clavate tails dominated at all stations, but slightly less on the slope and inside the OMZ (1001 m) 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.

The majority of the nematodes were slender, although their proportion decreased with depth (from 82% in the shelf to 76% in the basin), whereas stout animals accounted for between 2 and 13%. Long/thin animals continuously decreased with increasing depth until the lower slope (at the core of OMZ), but they were more abundant (17–24%) in the basin than were those of slender or stout shape. Over 76% of all identified individuals attained a 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) and colonisers were completely absent (Table 8).

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

Moreover the biological trait matrix revealed no particular notable relationships between traits. Certain trends were observed, however; for example, 1–2 and 2–4 mm lengths were generally correlated with slender and colonisers (C-P score 2–3), whereas nematodes of length > 4 mm had higher C-P scores and long/thin body shape. Some other combinations occurred, such as non-selective feeders with clavate tail shape, whereas predators followed a trend similar to that of the conical tail-shape category (Table 9).

The schematic model represents the exact trend of each functional trait at each benthic zone. The relative abundance of each trait was plotted as an area graph, and a schematic figure was prepared to show the pattern according to the zones. 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 a higher abundance of some traits, like round tail shape, stout body shape, 2–4 mm length, and greater prevalence of omnivores and deposit feeders. Coloniser life style (C-P 2–3) was more frequent, whereas persisters (C-P 4) decreased to lower numbers in the OMZ. In the basin, however, the sediment characteristics changed from silty sand to clay. Feeding habit and tail shape also differed in the basin (Fig. 6).

3.4. Influence of abiotic parameters on structure and function of the nematode community

The RELATE analyses indicated that patterns based on environmental variables were significantly related to the patterns inherent in nematode community structure both taxonomically ($r = 0.37$, $p = 0.01$) and functionally ($r = 0.41$, $p = 0.01$). Results of BIOENV analyses revealed several notable relationships of species abundance data and biological traits with environmental parameters. For example feeding types have the best correlation with C_{org}, sediment Chl-*a*, 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 score, however, was significantly correlated with clay and DO (Table 10). Moreover in the case of species abundance data, bottom water DO, clay, and C_{org} were proved to be the best correlated ($r = 0.712$, $p =0.02$). Of the 10 environmental parameters, 6 were retained for further analysis on the basis of collinearity analysis (Draftsman plot). Only 4 variables—salinity, temperature, water Chl-*a*, and C:N ratio) with correlation r^2 values 0.9 (considered redundant) were omitted for the DISTLM procedures; the remaining variables and their pair-wise spearman correlations are shown in Table 11.

Analyses with distance-based linear models (DistLM) indicated that the six abiotic variables related to the variation in nematode community structure explained 97% of its total variation, although not all variables were significant. Similarly for the functional traits of the eight variables, six were used by the DISTLM procedure to construct the best-fitting model, together explaining 96% of total variation. 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 11, 12). 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. Variables such as the C_{org} and near-bottom oxygen content showed the highest correlations ($p < 0.05$) with the nematode assemblages, whereas the functional traits were mainly explained by total organic carbon input ($p < 0.05$). Figs

7, 8 show the DISTLM results by means of a dbRDA plot, with the species abundance and biological traits superimposed. The vectors of the environmental variables retained by the DISTLM procedure as fitting the best explanatory model indicate the important role of OC in the slope area and Chl-*a* and sand in the shelf, whereas DO and clay were important in the basin.

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. Nematode densities and biomass along the regular slope generally decrease with water depth, surface primary productivity, and distance offshore (Soltwedel, 2000).

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). Of the eight stations presented here, three are true OMZ stations, where DO contents are less than 0.5 ml l^{-1}. Nematode abundance was highest in the center of the OMZ (525 m) and decreased to its lowest value in the lower part of the OMZ (1001 m). Total metazoan meiofauna, and more specifically nematode densities, often reach maximum values at the lowest oxygen concentrations within OMZs (reviewed in Levin, 2003).

In our results, nematode densities were lower than those reported by Cook et al. (2000) for the bathyal Oman margin (range: 494–2495 ind/10 cm^2). Moreover they found the highest abundances inside the OMZ (700 m) not in its center (400 m), but Levin et al. (1991) found the highest densities of nematodes (190 ind/10 cm^2) in the center of the OMZ (at 745 m), where high concentrations of organic carbon and pigments were found. 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). Although data do not exist to identify which, if any, of the factors shapes the nematode community assemblages, we note that C_{org} ($r^2 = 0.734$, $p < 0.05$) and near-bottom oxygen content showed the highest correlations ($r^2 = 0.464$, $p < 0.05$). Similarly many previous OMZ investigations have noted a correlation between food quality and meiofaunal abundance and the absence of oxygen. For example, Cook et al. (2000) reported a strong positive correlation between nematode density and food quality, measured as the hydrogen index, along a transect through the Oman margin OMZ. Meiofaunal densities were correlated only with sediment Chl-*a*, and not with oxygen or other sediment parameters along a similar OMZ transect on a seamount off Mexico (Levin et al., 1991).

Moreover, in general, nematode abundance did not follow any particular gradient though it was lowest at the deep basin stations. Generally, depth can have a major influence on nematode density (Soltwedel, 2000; Udalov et al., 2005). The pattern of quantitative distribution of nematode abundance has been described for intertidal and upper subtidal (<50 m) zones. The average world-wide nematode density is 1530 ind/10 cm^2; for continental slope (1000–2500 m) it drops to 430 ind/10 cm^2, for lower slope (2500–3500 m) to 360 ind/10 cm^2, and for abyssal and hadal depths (>5000 m) it is still lower (140 ind/10 cm^2) (Soltwedel, et al., 2003; Mokievsky et al., 2004). Large-scale comparisons of nematode community structure in other ocean basins indicate that continental-shelf nematode communities differ significantly from slope communities (Vanreusel et al., 2010).

The nMDS based on nematode species abundance and presence-absence separated the three zones, and the difference was confirmed by PERMANOVA ($p = 0.03$). Group 1 comprised the stations of the shelf region, with the exception of the deepest shelf station, which was grouped 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, *Trissonchulus* sp 1, and *Minolaimus* sp 1 were found. The exculsive presence of these species in the OMZ may be the result of OMZ sediments that favor the success of nematode species that are tolerant (colonists) or adapted (endemics). In addition to the seven species found exclusively in the OMZ a number of species were found exclusively outside it. One might speculate that OMZs have isolated hypoxia-tolerant nematode species as a result of their different life strategies, small size, lower mobility, and lack of pelagic larval stage. Some species might therefore be able to tolerate the oxygen minima while others cannot. The exact mechanisms of adaptation to or preferences of species for the anoxic environment remains unclear, however. Several authors have pointed out that nematode species can successfully cope with anoxic conditions by developing appropriate physiological and behavioural mechanisms (e.g., symbiosis with bacteria, which we also observed, and migration to “oxygen islands,” sensu Reise and Ax (1979) and Wetzel et al. (1995). Mouthless and gutless nematodes carrying endosymbionts have been observed previously in deep-sea environments (Ingels et al., 2011).

Our study did not reveal that nematode species have developed any obvious adaptations, but they must have a certain tolerance for anoxic conditions. The dominant species in the OMZ, like *Terschellingia longicaudata*, *Desmodora* sp 1, and *Sphaerolaimus gracilis*, 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 as typical for sulphidic muds, but their significance is ambiguous, and their adaptive value for the thiobiotic life rather disputed. 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). Further, some specimens belonging to the OMZ showed some morphological differences, whereas others were observed to have epibionts, like the majority of specimens of *Desmodora* sp. Some species were observed to have unidentified blackish gut content. A small nematode was found in the gut of *Metalinhomoeus* sp 1, which has a very small buccal cavity.

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 characterise the particular environment (Dufrêne and Legendre, 1997). The genus *Acantholaimus (Acantholaimus mirabilis* significantly associated with basin, p = 0.005) 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). The genus *Acantholaimus* increased in relative abundance with increasing depth in many deep-sea areas (Soetaert and Heip, 1995). Moreover, *Viscosia viscosia* was a good indicator of the shelf because it often inhabits the surface layers of sediment and is apparently capable of floating (Fonsêca-Genevois et al., 2006).

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.

Species diversity was higher on the shelf than on the slope or in the basin. This difference appears to be partly due to the bottom-water DO gradient, which includes values that are below the oxygen tolerance of many nematode 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 by a very few highly abundant species. 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 gradients of biological, chemical, and physical properties in the aquatic environment complicate the situation. One major challenge 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 the three zones, 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. OMZs often support mats of large sulfur-oxidising bacteria, including *Thioploca*, *Beggiatoa*, and *Thiomargarita*, which are often conspicuous features of the sediment surface there (Levin, 2003). These bacterial mats have been observed previously at the Oman margin (Levin et al., 1997).

Several previous workers have speculated 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 have been found to feed on microbiota by scraping them off solid surfaces or mucus threads with their teeth. Higher amounts of 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 provided they acquire large teeth and are capable of ingesting other animals.

The dominance of the deposit feeders in silty sediments of the basin is in agreement with results from 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 included 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., 2011) 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). BIOENV analysis showed that feeding types were well correlated 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}. Nematodes with clavate tail shape dominated at each depth, although to a greater degree in the shelf and basin regions (Table 3). 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 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. The proportion of long-tail shape and round shape was much lower than that of the above-mentioned categories, 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, in concordance with the BIOENV analysis, which 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 organisms inhabiting the oxygenated environments are found to be of a size and shape different from those of organisms from the OMZs (Schneider and Bush-Brown, 2003).

Some biological 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). Bongers and Ferris (1999) also distinguished two types of opportunists: enrichment and general opportunists. The genus Monhystera (family Monhysteridae), which was represented by only two species (*Diplolaimella* sp 1, *Diplolaimelloides* sp 1) in the present study were classified as C-P class 2 (general opportunist) (Bongers, 1990).

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 presents 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. Nematodes with different functional characteristics differ in their abilities to respond to environmental stresses and disturbance, thereby providing resilience to 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 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). 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.

Results of BIOENV analysis revealed the best correlation between the functional trait and individual parameter, i.e., 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 (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). The DistLM analysis indicated that DO concentration and organic content were the only parameters that were significantly correlated with nematode species and functional data respectively.

5. Conclusions

Free-living nematodes are an abundant and diverse component of the meiofauna on the western continental margin of the 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 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. Locations and depths 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. Results of pair-wise comparison (samples from different zones) PERMANOVA analyses (based on Bray–Curtis similarity measure). Data was fourth-root transformed; resemblance was calculated according to Bray-Curtis. The values indicate differences significant at $p < 0.05$.

	Groups	t	P(perm)	Unique perms	P(MC)
Taxonomic	Shelf vs slope	1.7529	0.317	3	0.264
	Shelf vs Deep basin	3.3538	0.332	3	0.046
	Slope vs Deep basin	6.0733	0.352	3	0.067
Functional traits					
	Shelf vs slope	2.2523	0.346	3	0.181
	Shelf vs Deep basin	5.0419	0.354	3	0.013
	Slope vs Deep basin	18.508	0.342	3	0.028

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

Species	Shelf (%)	Species	Slope (%)	Species	Basin (%)
Chromadorita sp 2	2.78	*Terschellingia longicaudata*	4.73	*Halalaimus* sp 1	1.11
Sphaerolaimus gracilis	2.21	*Desmodora* sp 1	4.42	*Acantholaimus elegans*	1.11
Setosabatieria sp 1	2.06	*Theristus ensifer*	3.13	*Setosabatieria* sp 1	0.92
Theristus heterospiculum	1.98	*Sphaerolaimus gracilis*	2.36	*Anoplostoma* sp 1	0.72
Synonchiella sp 1	1.68	*Halichoanolaimus* sp 1	2.10	*Daptonema circulum*	0.53

Table 4. 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 5. 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		
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 6. 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 7. 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 habits				Tail shapes			
Depth	1A	1B	2A	2B	Clavate	Conical	Long	Round
34	12	46	15	27	62	32	5	1
48	14	39	20	27	45	41	13	1
102	17	28	19	36	40	44	15	1
525	20	17	5	58	44	41	14	0
1001	40	28	8	24	28	51	20	0
1524	30	19	8	42	31	51	17	1
2001	18	34	13	35	49	30	21	0
2456	24	33	14	29	40	29	31	0

Table 8. 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).

Depth	<1 mm	1–2 mm	2–4 mm	>4 mm	Slender	Stout	Long/thin	1	2	3	4	5
34	10	35	51	4	82	3	6	0	49	46	5	0
48	29	28	24	19	76	2	14	0	34	53	13	0
102	15	46	31	8	82	13	4	0	33	64	3	0
525	21	36	40	3	89	3	7	0	15	84	1	0
1001	25	37	35	3	83	4	12	0	24	71	5	0
1524	28	39	30	3	80	9	11	0	17	76	7	0
2001	25	35	27	13	83	0	17	0	27	52	21	0
2546	19	36	29	16	76	0	24	0	26	49	26	0

Table 9. Biological trait matrix along with contribution (%) of species at each zone

	Zones			Buccal morphology				Tail shape				Adult Length (mm)				Adult shape			Life history (c-p score)		
Species	Shelf (%)	Slope (%)	Basin (%)	1A	1B	2A	2B	R	E/F	CO	CA	>1	1-2	2-4	>4	ST	SL	L/T	2	3	4
Acantholaimus calathus	0.11	0.00	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Acantholaimus elegans	0.19	0.23	1.11	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Acantholaimus filicaudatus	0.15	0.15	0.19	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Acantholaimus mirabilis	0.31	0.00	0.00	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
Actarjania sp 1	0.15	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Actinonema sp 1	0.31	0.00	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Actinonema sp 2	0.15	0.00	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Actinonema sp 3	0.31	0.00	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Aegioloalaimus sp 1	0.38	0.00	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1
Anoplostoma blanchardi	0.69	0.69	0.50	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Anoplostoma sp 1	0.50	0.19	0.72	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Anoplostoma sp 2	0.38	0.38	0.00	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Araeolaimus sp 1	0.19	0.04	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Araeolaimus sp 2	0.23	0.00	0.27	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0

Axonolaimus sp 1	1.03	0.00	0.00	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Axonolaimus sp 2	0.15	0.04	0.00	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0
Axonolaimus sp 3	1.45	0.00	0.00	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Bathyeurstomina sp 1	0.11	0.00	0.38	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1
Campylaimus sp 1	0.19	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Ceramonema yunfengi	0.46	0.00	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Cermonema attenuatum	0.23	0.04	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Cheironchus sp 1	0.23	0.00	0.00	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0
Choanolaimus sp 2	0.04	0.38	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Chromadora sp 1	0.23	0.34	0.00	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0
Chromadorita sp 1	0.19	0.65	0.00	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0
Chromadorita sp 2	2.78	0.19	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Cobbia dentata	0.72	0.38	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 1	0.34	0.00	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 3	0.72	0.04	0.04	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 2	0.23	0.11	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Dagda sp 1	0.31	0.00	0.27	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Daptonema circulum	0.84	0.31	0.53	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Daptonema sp 1	0.72	1.14	0.00	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Daptonema sp 2	1.56	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Desmodora sp 1	0.88	4.42	0.38	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0

Desmoscolex sp 1	1.30	0.00	0.00	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
Diplolaimella sp 1	0.11	0.00	0.00	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0
Diplolaimelloides sp 1	0.04	0.04	0.00	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dolicholaimus sp 1	0.50	0.00	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Doliolaimus sp 1	0.00	0.00	0.11	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Dorylaimopsis sp 1	0.15	0.00	0.00	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Dorylaimopsis sp 2	0.15	0.46	0.00	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Epacanthion sp 1	0.00	0.00	0.31	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0
Gammanema sp 1	0.08	0.00	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Halalaimus gracilis	0.38	0.00	0.08	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Halalaimus sp 1	0.00	0.50	1.11	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Halalaimus sp 2	0.00	0.23	0.53	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Halalaimus sp 2	0.00	0.19	0.42	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1
Halanonchus sp 1	0.23	0.00	0.00	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Halichoanolaimus chordiurus	0.00	0.00	0.11	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0
Halichoanolaimus robustus	0.95	1.60	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Halichoanolaimus sp 1	0.08	2.10	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Halichoanolaimus sp 2	0.11	0.00	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Hopperia sp 1	0.95	0.00	0.00	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0

Longicytholaimus sp 1	0.00	0.00	0.50	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0
Marylynnia sp 1	0.23	0.00	0.00	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0
Mesacanthion sp 1	0.19	0.00	0.00	0	0	0	1	0		0	1	0	0		1	0	1	0	0	1	0
Metalinhomoeus longiseta	0.08	0.00	0.50	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0
Metalinhomoeus sp 1	0.19	0.00	0.00	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0
Metasphaerolaimus sp 1	0.00	0.00	0.38	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Metasphaerolaimus sp 2	1.33	0.04	0.27	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Meyersia minor	0.08	0.00	0.00	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Meyersia sp 1	0.23	0.15	0.23	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Meyersiaa sp 2	0.46	0.00	0.00	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Microlaimus sp 1	0.15	0.00	0.08	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Minolaimus sp 1	0.04	0.00	0.00	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Oncholaimus attenuatus	0.00	0.00	0.34	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
Oncholaimus mediterraneus	0.11	0.00	0.00	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1
Oxystomina affinis	0.42	0.00	0.00	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1
Oxystomina sp 1	0.61	0.08	0.00	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1
Paralinhomoeus filiformis	0.11	0.08	0.00	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0

Paralinhomoeus lepturus	0.34	0.84	0.00	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0
Paralinhomoeus sp 1	0.57	0.76	0.00	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Paralinhomoeus sp 2	0.42	0.00	0.08	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0
Parasphaerolaimus sp 1	1.45	0.92	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Pierickia sp 1	0.23	0.00	0.00	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Pierrickia sp 2	0.00	0.00	0.11	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Prooncholaimus sp 1	0.69	0.00	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Pselionema hexalatum	0.46	1.26	0.00	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Pselionema sp 1	0.11	1.11	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Pterygonema platti	0.19	0.00	0.00	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
Pterygonema sp 1	0.34	1.83	0.00	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
Richtersia sp 1	0.23	0.00	0.00	0	1	0	0	0	0	1	0	1	0	0	0	1		0	0	1	0
Sabatieria ornata	0.65	0.00	0.11	0	1	0	0	0	0	0	1	0	0	1	0		1	0	1	0	0
Sabatieria praedatrix	0.00	0.00	0.11	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Sabatieria pulchra	0.50	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Sabatieria punctata	0.42	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Sabatieria sp 1	0.88	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
Sabatieria sp 2	0.42	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Sabatieria sp 3	1.41	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Setosabatieria sp 1	2.06	0.00	0.92	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0

Siphnolaimus ewensis	1.11	0.88	0.38	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0
Southerniella sp 1	1.14	0.38	0.00	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Sphaerolaimus balticus	0.15	0.00	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Sphaerolaimus gracilis	2.21	2.36	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Sphaerolaimus sp 1	0.00	0.00	0.42	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Subsphaerolaimus sp 1	0.00	0.00	0.08	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Synonchiella sp 1	1.68	0.34	0.19	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Terschellingia longicaudata	1.18	4.73	0.04	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Theristus ensifer	0.42	3.13	0.04	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Theristus heterospiculum	1.98	0.00	0.08	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Theristus interstitialis	0.92	0.00	0.00	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
Tricoma sp 1	0.19	0.00	0.00	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
Trissonchulus sp 1	0.46	1.18	0.00	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0
Viscosia sp 1	0.04	0.00	0.34	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Viscosia sp 2	0.42	0.53	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0
Viscosia viscosia	0.50	0.00	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
Voscosia sp 3	0.15	0.00	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0

Vasostoma sp 1	0.57	0.57	0.00	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Wieseria sp 1	0.23	0.31	0.00	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1

1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A =epigrowth feeders, 2B = predators (Wieser, 1953). R = round. E/F = elongated/filiform, CO = conical, CA = clavate. ST = stout, L/T = long/thin, C-P = coloniser-persister score (Bongers et al., 1991, 1995; Pape et al., 2013), 1 = species exhibiting trait, 0 = species not exhibiting trait.

Table 10. 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

Table 11. Result of distance-based linear model (DistLM) analyses showing the influence of environmental parameters on nematode species abundance data and (Bray-Curtis similarity of square-root-transformed abundance).

Marginal tests							
Variable	SS(trace)	Pseudo-F	P	Prop.			
DO, mll-1	321.67	23.209	0.068	0.27892			
Chl aµg-1	179.35	11.049	0.362	0.15552			
Corg (%)	399.65	31.819	0.008	0.34654			
Clay (%)	168.03	10.233	0.391	0.14571			
Silt (%)	121.46	0.70635	0.606	0.10532			
Sand (%)	164.27	0.99661	0.426	0.14244			
Sequential tests							
Variable	R^2	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
DO, mll-1	0.4647	6420.3	52.087	0.007	0.4647	0.4647	6
Chl aµg-1	0.50376	539.58	0.39351	0.81	3.91E-02	0.50376	5
Corg (%)	0.73435	3185.9	34.722	0.048	0.23059	0.73435	4
Clay (%)	0.827	1280	16.065	0.22	9.26E-02	0.827	3
Silt (%)	0.89849	987.83	14.088	0.34	7.15E-02	0.89849	2
Sand (%)	0.97481	1054.4	30.302	0.254	7.63E-02	0.97481	1

Table 12. Result of distance-based linear model (DistLM) analyses showing the influence of environmental parameters on nematode species functional biological traits (Bray-Curtis similarity of square-root-transformed abundance.

Marginal tests

Variable	SS(trace)	Pseudo-F	P	Prop.
DO, mll-1	6420.3	5.2087	0.013	0.4647
Chl aµg-1	1424	0.68948	0.668	0.10307
Corg (%)	4771.6	3.1655	0.048	0.34537
Clay (%)	3635.9	2.1429	0.13	0.26316
Silt (%)	1741.9	0.86558	0.426	0.12608
Sand (%)	2235.4	1.1582	0.313	0.1618

Sequential tests

Variable	R^2	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
DO, mll-1	0.4647	6420.3	5.2087	0.007	0.4647	0.4647	6
Chl aµg-1	0.50376	539.58	0.39351	0.81	3.91E-02	0.50376	5
Corg (%)	0.73435	3185.9	3.4722	0.048	0.23059	0.73435	4
Clay (%)	0.827	1280	1.6065	0.22	9.26E-02	0.827	3
Silt (%)	0.89849	987.83	1.4088	0.34	7.15E-02	0.89849	2
Sand (%)	0.97481	1054.4	3.0302	0.254	7.63E-02	0.97481	1

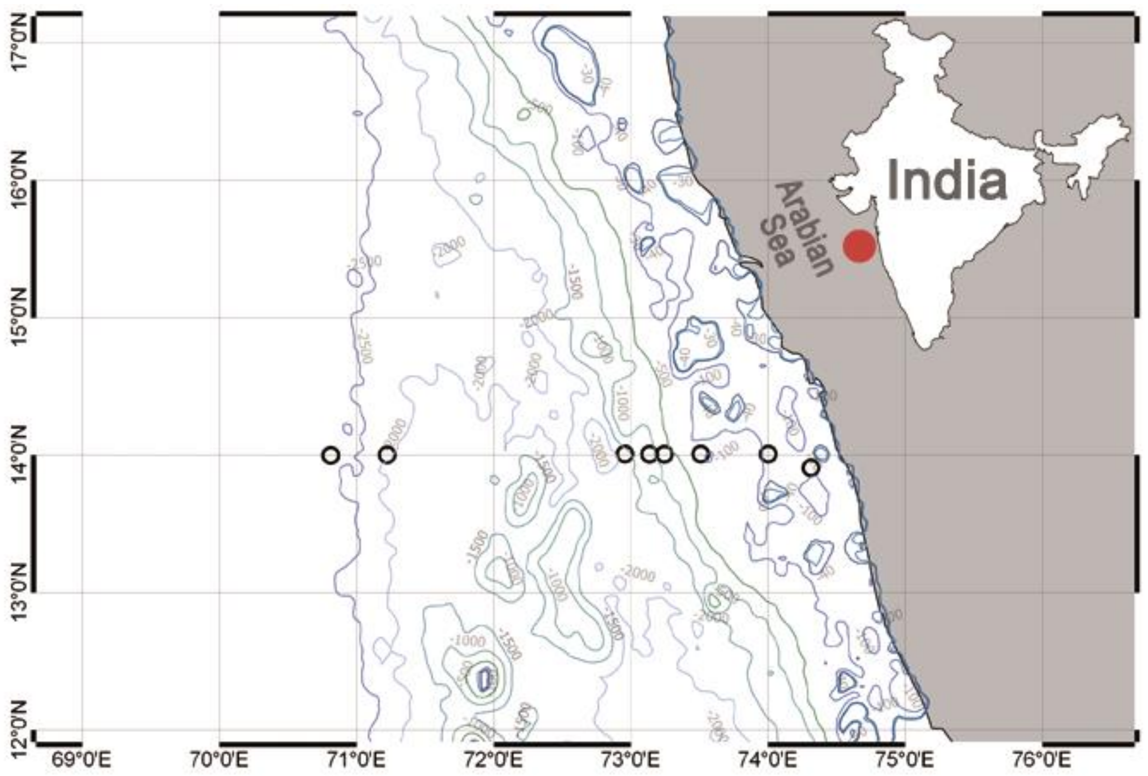

Figure 1. Map showing locations of the 8 sampling stations (circles) on the coast of the Arabian Sea (marked as red circle) along with depth contours and the positions of the sampling stations.

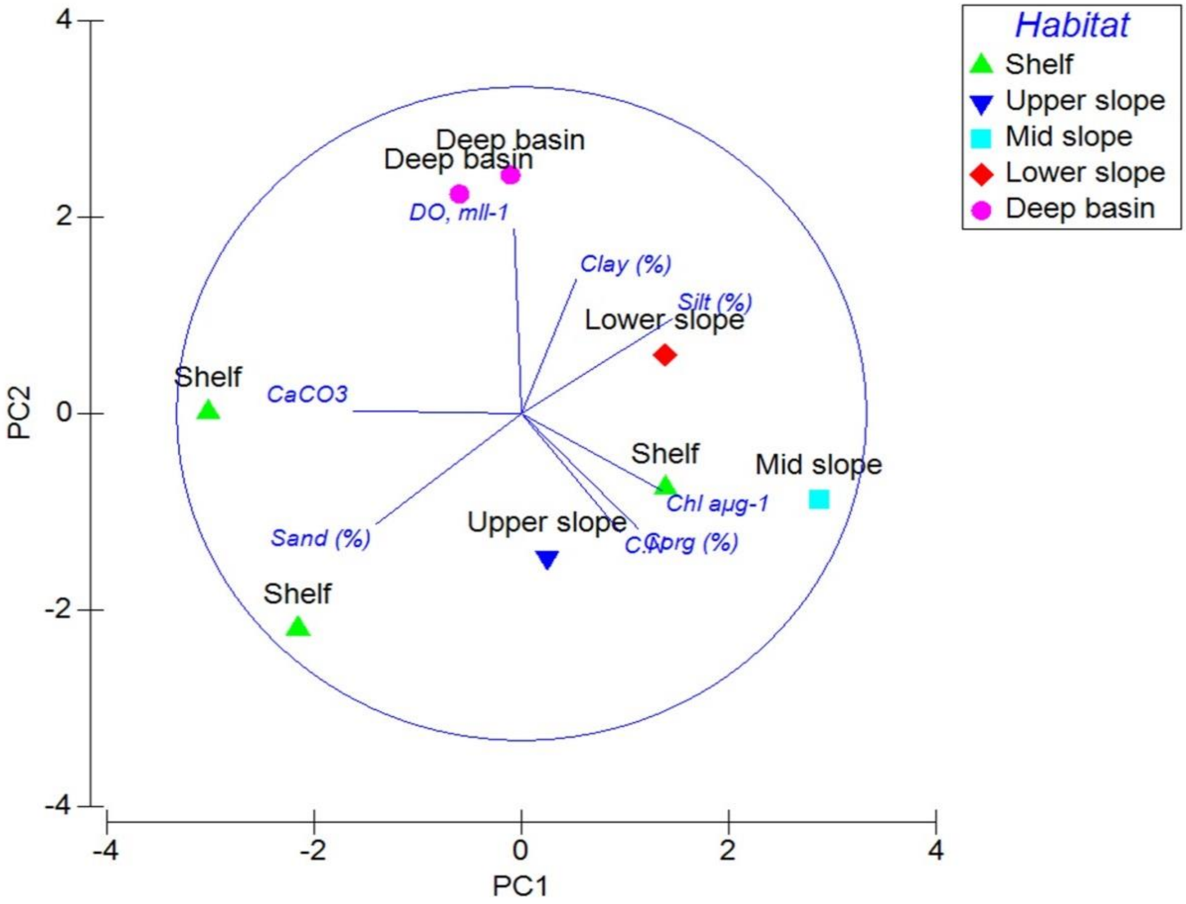

Figure 2. Principal-components analysis derived from the contribution of parameters in each benthic zone. PC 1 and 2 accounted for 81% of the total variation present.

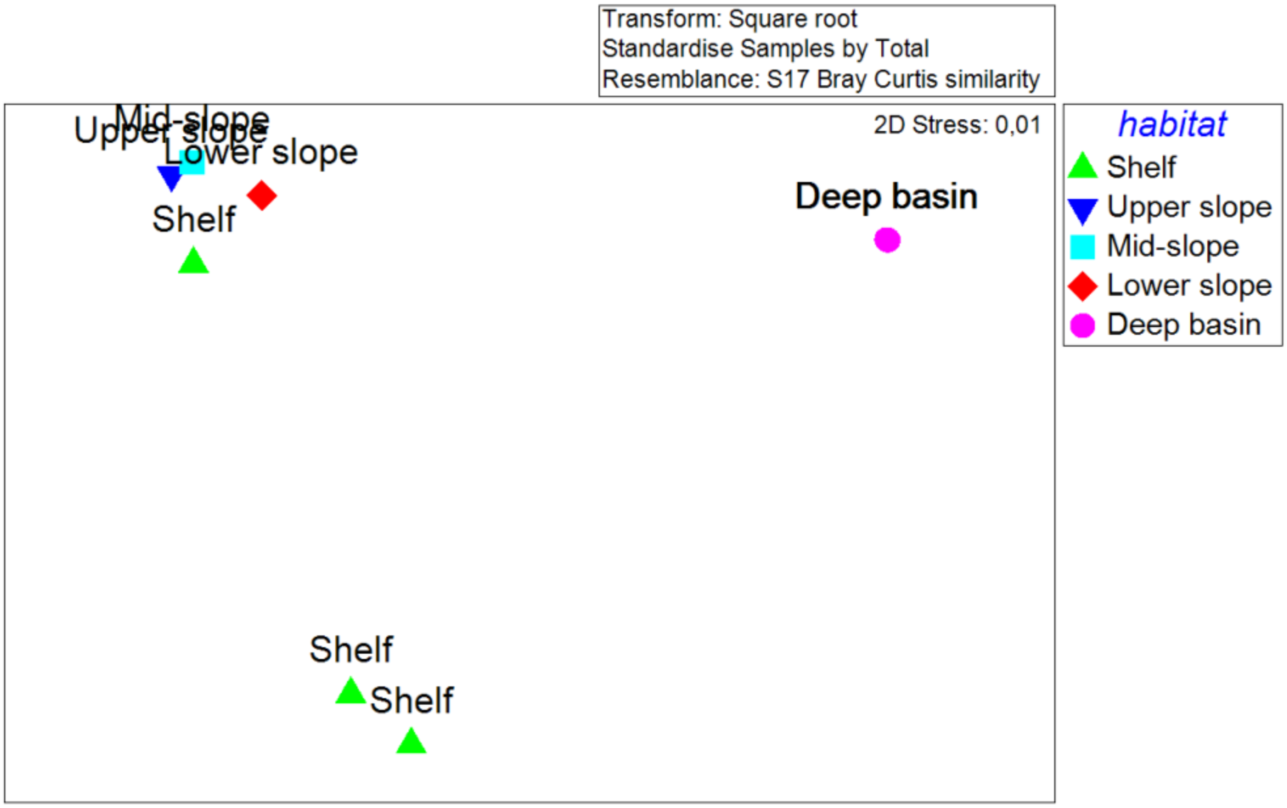

Figure 3. nMDS ordination based on nematode species abundance according to the Bray–Curtis similarity index.

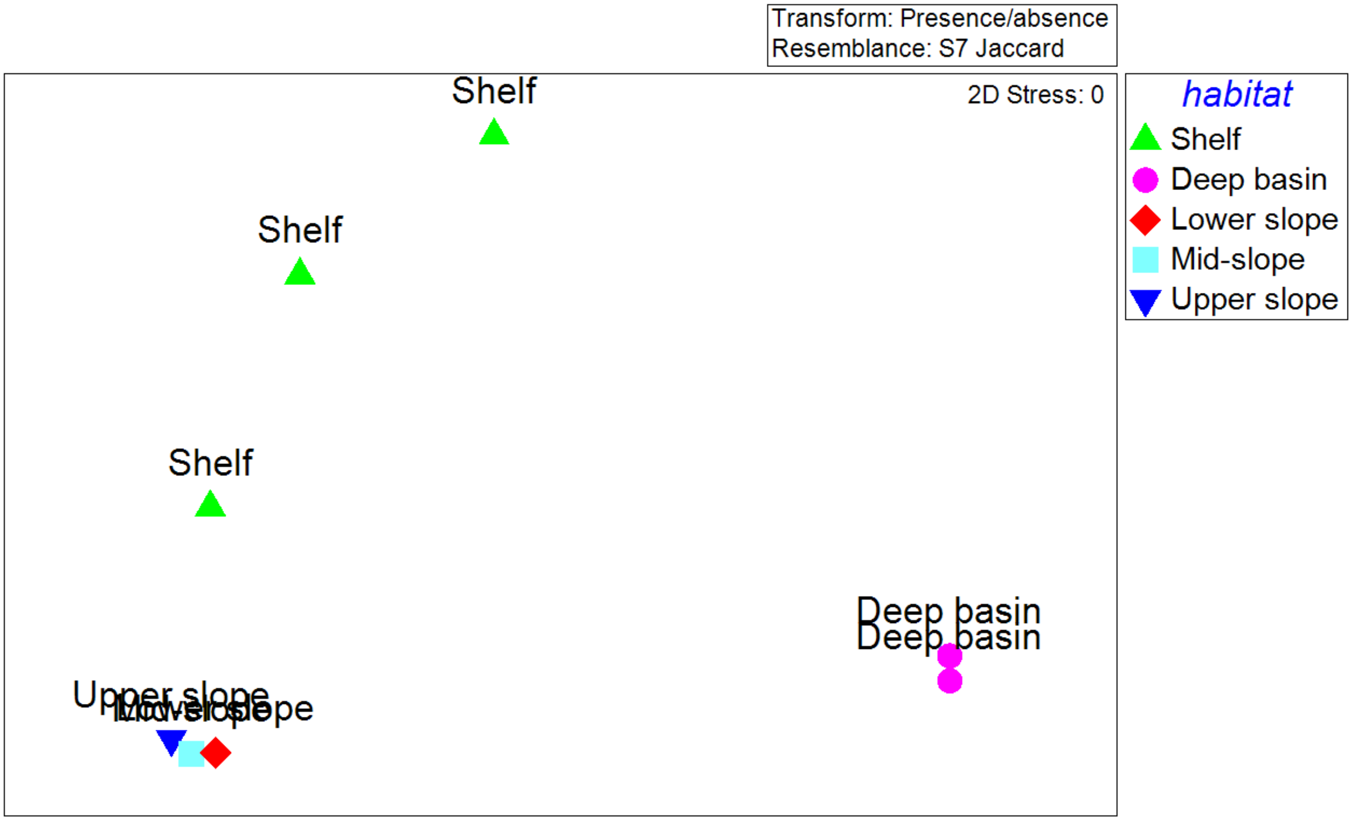

Figure 4. nMDS ordination based on nematode species presence/absence according to the Jaccard similarity index

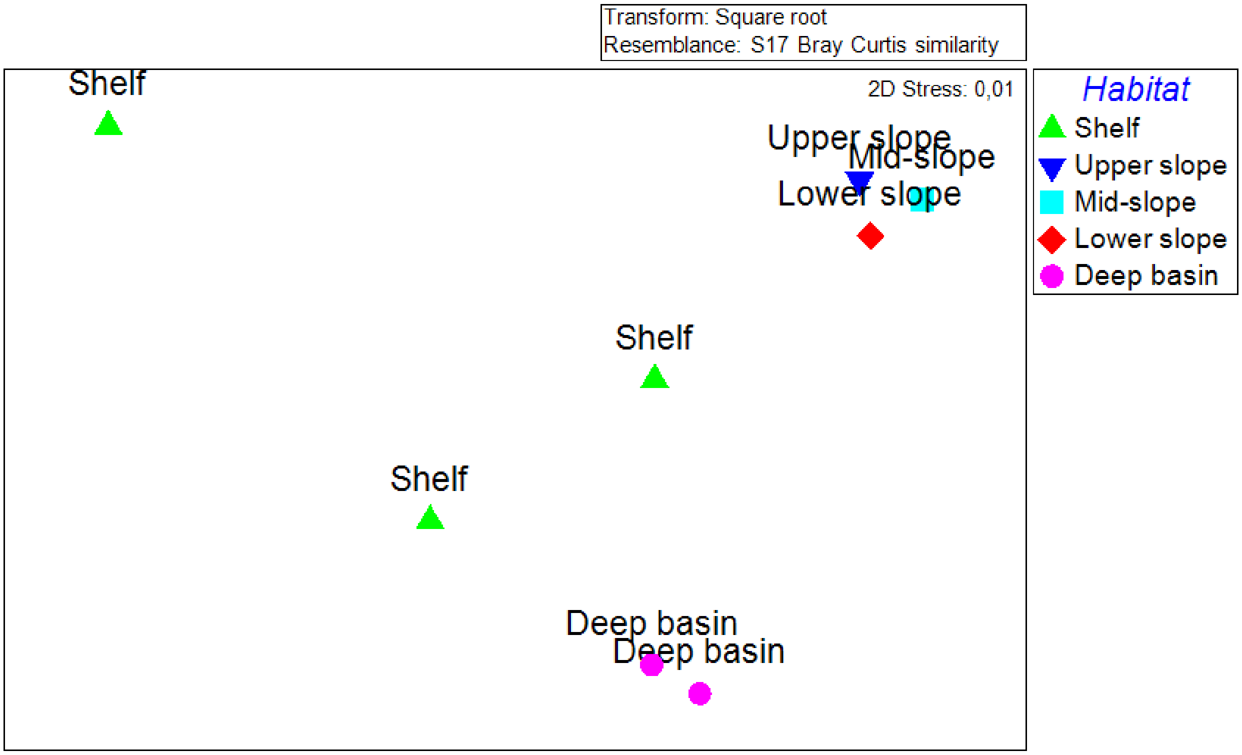

Figure 5. nMDS ordination based on nematode species biological traits according to the Bray–Curtis similarity index.

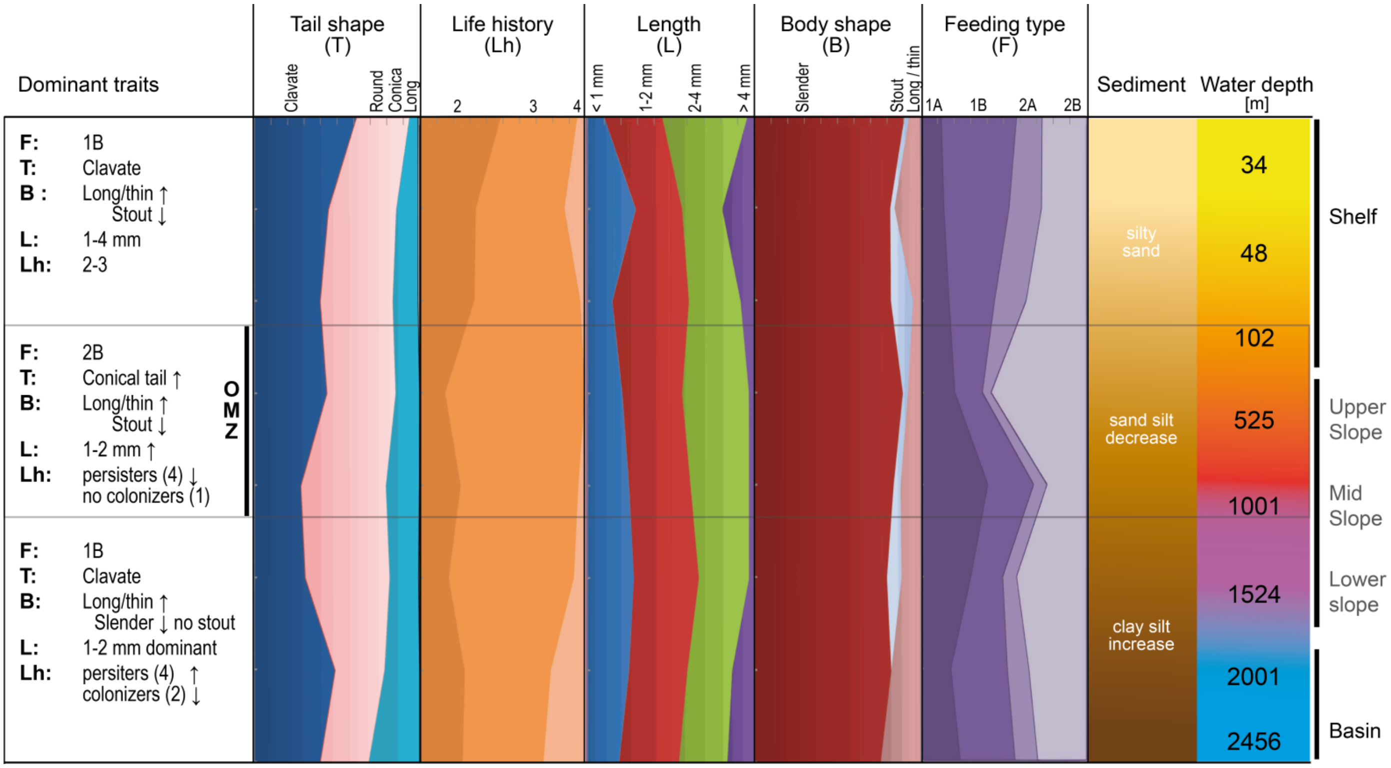

Figure 6. Schematic model of the functional traits in each benthic zone.

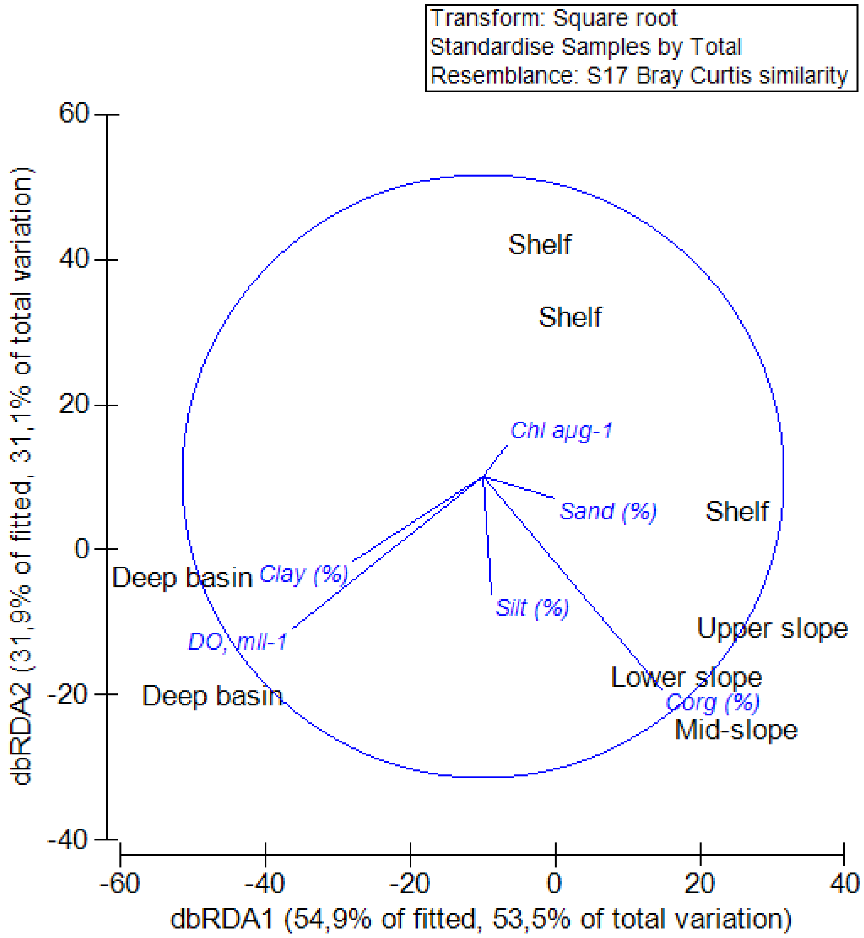

Figure 7. Distance-based redundancy (dbRDA) bubble plot illustrating the DISTLM model based on the species assemblage data and fitted environmental variables with their vectors (strength and direction of effect of the variable on the ordination plot). Axis legends include percentage of variation explained by the fitted model and percentage of total variation explained by the axis.

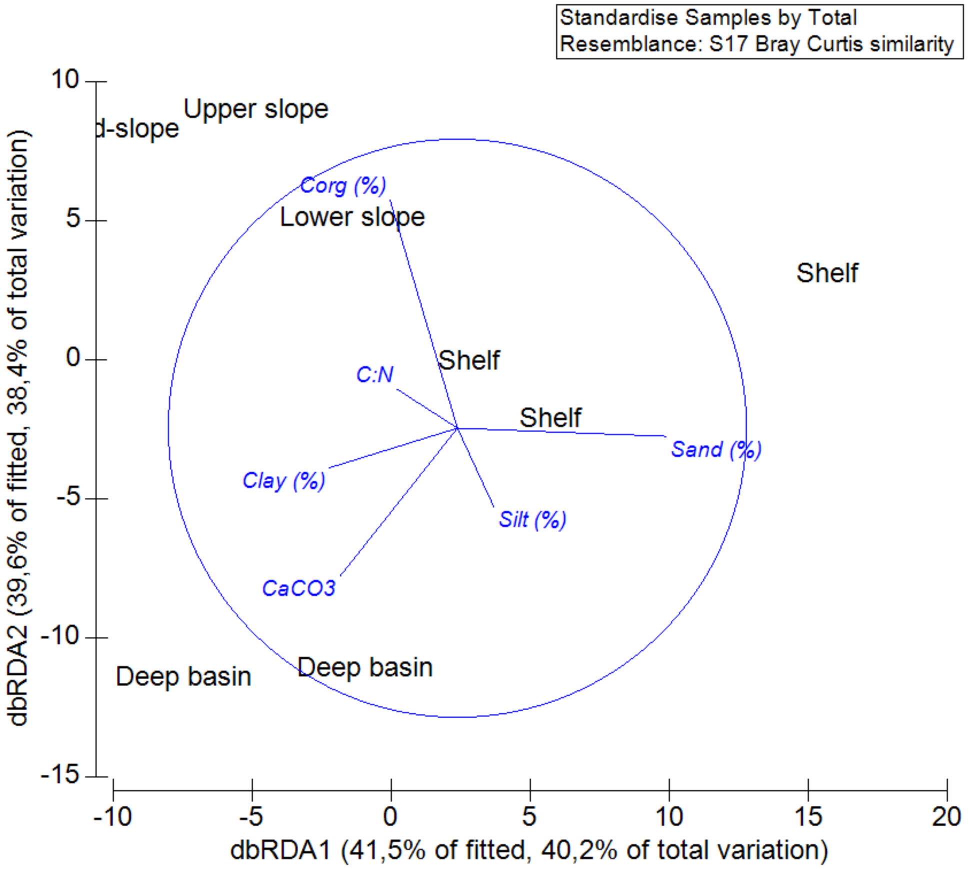

Figure 8. Distance-based redundancy (dbRDA) bubble plot illustrating the DISTLM model based on the species functional assemblage data and fitted environmental variables with their vectors (strength and direction of effect of the variable on the ordination plot). Axis legends include percentage of variation explained by the fitted model and percentage of total variation explained by the axis.