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 was extending from 102 m to 1001 m. Nematodes were identified to species (described and undescribed) and classified according to biological/functional traits. A total of 110 nematode species belonging to 24 families 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 (525-1524m; 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 differed in species composition according to the zones, *Chromadorita* sp 2 (2.78%) *Sphaerolaimus gracilis* (2.21%) were dominant in shelf whereas *Terschellingia Longicaudata* (4.73%) and *Desmodora* sp 1 (4.42%) were dominant in the slope. However, in the deep basin *Halalaimus* sp 1(1.11%) *Acantholaimus elegans* (1.11%) were seen 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. The OMZ harboured seven exclusively species: *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. 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 the 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 terms of 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 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 entire 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 Jensen (1987) and Murrell and Fleeger (1989) reported on effects of low-oxygen condition on nematofauna in sandy sediments at shallow depths and from the Gulf of Mexico, respectively 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. However in another experimental study in the tidal flats, hypoxia caused a dramatic change in the nematode community composition with reduction in diversity and abundance of all dominant nematodes

73   except for genus Odontophora (Van Colen et al., 2009). Niera et al. (2013) found that nematode

74   generic and trophic diversity was lowest, at the most oxygen-depleted site along a central Chile

75   margin. De Torch et al. (2013) in a short incubation experiment found that nematodes were not

76   affected by anoxic conditions. He further concluded that responses to stress depend on the species

77   and the frequency of the hypoxic periods. In contrast to several studies on the effects of anoxia

78   on Nematoda at higher taxonomic levels little is known about their response at species level.

79   Several transitional settings in the western Indian continental margin, including the shelf, slope

80   (long stretch of OMZ) and basin, provide multiple oxygen and other environmental gradients.

81   These settings allowed us to investigate how oxygen and environmental factors affect and

82   modulate the structure and function of nematodes community at species level. An exclusive study

83   from the Indian western continental margin with reference to nematode tolerance in the OMZ is

84   therefore important. Furthermore, nematode community structure from the western Indian

85   continental margin (including the OMZ) of the Arabian Sea remains unstudied. In general

86   information on nematode species data is missing from the Arabian Sea and the present study can

87   provide important basic information on nematode community structure.

88   However, traditional taxonomic based methods of nematode community analyses may not fully

89   account for their diverse roles in ecosystem function (Schratzberger et al., 2007) therefore the

90   inclusion of functional analysis has been recommended (de Jonge et al., 2006).

91   Many previous studies (e.g. Bremner et al., 2003; Bostrom et al., 2006) on macrobenthic

92   invertebrates have shown that linking the taxonomic and functional aspects can reveal different

93   relationships between assemblages and in order to explore the relationship between biodiversity

94   and ecosystem function nematode could be considered the ideal model organism (Danovaro et al.,

95   2008).

96   Nematode species in functional groups share several morphological traits (Chalcraft and

97   Resetarits, 2003), and use of these traits may provide additional information on changes in

98   biodiversity and also facilitate better comparison with other geographical regions (Bremner,

99   2008). Giere (1993) showed that a classification based on buccal structures of marine nematodes

100   had applications in a variety of marine habitats. Thistle and Sherman (1985) found that nematode

101   tail shape formed an important biological trait especially in locomotion and reproduction.

102   Furthermore, body size is known to influence many traits of an animal, such as its life history,

103   physiology, and energy requirements, whereas species morphotype represents adaptations to life

104   in oxygen-poor and sulphide-rich sediments (Jensen, 1987a). Bongers et al., (1990) 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 this study 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 the heterogeneous gradient like shelf, slope and deep basin of western Indian continental margin affect 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

A single transect was selected perpendicular to the coast of the Arabian Sea at 14° N latitude (Fig. 1). The bottom topography in the Arabian Sea has following characteristics i.e. the Carlsberg Ridge is in the southern part of Arabian Sea and Murray Ridge is in the north part, however in the mid-Arabian Sea (from 14° N to 21° N) there is a topographic slope. The continental shelf is 120 km wide off the southern, 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 in the Arabian Sea 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 Arabian Peninsula, Somalia and southwest India (Qasim, 1977). The Arabian Sea, is characterized by a very pronounced midwater oxygen minimum zone (OMZ) between 150 to 1250 m and is over 1000m thick 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, 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 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 ($50 \times 50 \times 50$ 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 cm down to 5 cm sediment depth and fixed in buffered 4% formalin. Separate one sub-core was collected for organic carbon (C_{org}), 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 ice chest, dark location and were analyzed after a period of 8-9 hours. Chl-*a* was estimated by means of an acetone extraction method using 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 to retain the meiofauna fraction. The retained fraction on 32-µm mesh was then elutriated by the centrifugation-flotation technique using LUDOX (Vincx 1996; Heip et al., 1985). Nematodes

168 were counted through a stereo-microscope, and were picked and mounted on permanent glass

169 slides for taxonomic identification. In all, 1798 nematodes were examined from the whole area.

170 They were identified up to described and morphotype species level from the pictorial keys of

171 Platt and Warwick (1983) and the NeMys database (Vanaverbeke et al., 2015). For identification

172 to species level, each morphotype was sketched and measured by means of a camera lucida so

173 that all specimens of the same genus could be compared.

174

175 **2.4 Nematode functional trait analysis**

176 Nematode species were classified according to their buccal morphology, tail shape, adult length,

177 adult shape, and life history.

178

179 Feeding types: Individual nematode species were assigned to four feeding categories according to

180 Wieser (1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth

181 feeders (2A), and predators/omnivores (2B).

182

183 Tail shape: Thistle and Sherman (1985) developed a functional-trait scheme based on tail shape.

184 Tail types are diverse and variable and suggested as an effective method of characterizing

185 nematode communities. Nematodes were assigned to four tail-shape groups, which are common

186 in free-living marine nematodes: short/round, elongated/filiform, conical, and clavate.

187

188 Total length and body shape: Total length and the maximum body width for adult nematodes

189 were measured, and from the results we calculated the length-width ratio. Soetaert et al. (2002)

190 suggested three body-shape morphologies: stout, slender, and long/thin. Length-width ratio is a

191 measure of a nematode's body shape; long/thin animals have high ratios, and stout animals low

192 ratios. From measured length, each species was therefore assigned to one of four length groups (<

193 1 mm, 1–2 mm, 2–4 mm, >4 mm) and three shape categories (stout, with a length–width ratio <

194 18; slender, with a length–width ratio of 18–72; and long/thin, with a length–width ratio > 72).

195

196 Life history (C-P score) : Nematodes were allocated to life-history groups according to Bongers

197 (1990) and Bongers et al. (1991); genera are classified on a scale from 1 to 5 from colonisers (1,

198 short life cycle, high reproduction rates, high colonisation ability, tolerance of various types of

199 disturbance) to persisters (5, long life cycles, low colonisation ability, few offspring, sensitivity to

200 disturbance). The species belonging to Monhysterid family were assigned to the c–p 2 class
201 ("general opportunists") as advised by Bongers et al. (1995) and latter mentioned by Pape et al.
202 (2013) and as such there were no nematodes belonging to c–p class 1 ("enrichment
203 opportunists").
204 A biological traits matrix was constructed by assigning to each nematode species its affinity to
205 each trait category and the percent (%) contribution of each species.
206

2.5 Statistical analysis

208 The similarity analysis at the species level was based on two types of similarity measures: the
209 Bray-Curtis dissimilarity (standardised, square-root transformed) (Bray and Curtis, 1957), based
210 on the relative abundances of nematode genera, and ordination using the Jaccard similarity index
211 based on presence-absence (Clarke, 1993). Differences between the samples were visualized by
212 means of non-metric multidimensional scaling (nMDS) plots.
213 PERMANOVA designed with two factors: "station" (combined all the station in the zone) nested
214 in "zones" (shelf, slope and deep basin) was applied to detect the statistical significance of
215 differences in pair-wise comparison of nematode communities from different zones
216 (PERMANOVA Anderson, 2005; Anderson et al., 2008).
217 Diversity was expressed in terms of the expected number of species in a sample, EG (51). The
218 other diversity indices were calculated by means of Margalef's index (Margalef, 1968) for
219 species richness (d), Pielou's index (Pielou, 1966) for species evenness (J'), and the Shannon–
220 Wiener index (Shannon and Weaver, 1963) for species diversity (H' by using loge).
221 Environmental variables were then subjected to principal-components analysis (PCA) to identify
222 the spatial patterns based on environmental data. A lower triangular Euclidean distance matrix
223 relating to the ordination was constructed (Clarke and Green, 1988). Prior to the calculation of
224 the Euclidean distance resemblance matrix, the data were checked for uniform distribution
225 followed by normalisation (subtracting the mean and dividing by the standard deviation, for each
226 variable) before analysis.
227 Analysis of collinearity was tested using draftsman plot and the associated standard product
228 moment correlation coefficient between all pairs of variables and those with correlations (r2) >
229 0.9 were omitted from the model. If distribution of residuals was skewed, natural logarithm
230 transformation was applied to the response variable until assumptions were met by the best
231 model. 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. RELATE and stepwise distance-based linear model permutation test (DistLM, McArdle and Anderson, 2001) was performed to identify which set of environmental variables predict the multivariate variation to nematode species assemblages. The adjusted R^2 was used as a selection criterion to enable the fitting of the best explanatory environmental variables in the model. Euclidean distance was used as resemblance measure in all DISTLM procedures. Results were visualized with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008).

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 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., 2011) and the PERMANOVA+ module of the PRIMER v6 software (Anderson et al., 2008; Clarke and Gorley, 2006). A schematic diagram was prepared using the taxonomic and functional dataset in order to represent 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 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), 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 OMZ extended

264 from 102 to 1001 m in the study area; its core was located at 525 m, where the lowest DO (0.08
265 ml l^{-1}) value was recorded.

266 The OMZ was also characterised by higher values of sediment Chl-*a* and organic carbon
267 (Table 1) than were the shelf and basin. A PCA ordination constructed from the eight
268 environmental factors (DO, sediment chlorophyll, C_{org}, $CaCO_3$, C:N ratio, clay, silt, and sand
269 (Fig. 2) showed that the first two components accounted for about 81% of the variability of the
270 data (PC1 explained 43.5 %, PC2 33.3 %). Two shelf stations were characterised by high coarse
271 sand and $CaCO_3$ content, whereas one (at depth 102 m) clustered mainly with the slope stations,
272 largely because of higher organic-matter content and was clearly separated from the others on the
273 basis of its higher silt content. Basin samples were characterised by higher DO level (Fig. 2).

274

275 **3.2 Nematode density and community structure**
276 A total of 110 nematode species belonging to 24 families were found along the transect.
277 Nematode density was higher at the shelf stations than on the slope or in the basin. The lowest
278 average density was observed in the basin with 62.9±2 ind/10 cm^2. The mean nematode density
279 in the slope region was 124.3±16 ind/10 cm^2 and the lowest density was observed on the lower
280 slope (98.1 ind/10 cm^2) while upper slope station near to the shelf was represented with the
281 density of 155.2 ind/10 cm^2 however the mid slope has density of 120.0 ind/10 cm^2 the highest
282 average nematode density 176.6±37 ind/10 cm^2 was observed at shelf depth.
283 nMDS (non-metric multidimensional scaling) based on nematode species abundance (Bray-
284 Curtis) and presence/absence data illustrates clearly the extent to which the three zones differ
285 (Fig. 3 and 4). The nMDS plot based on the Bray-Curtis similarity measure indicated three
286 groups of samples (Fig. 3). The larger group included the slope stations and the deepest shelf
287 station—those stations that form the OMZ. The PERMANOVA community results indicated
288 significant differences between the three zones (p=0.03) but the nMDS based on
289 presence/absence separated only the slope and basin. The stations on the shelf were distributed
290 randomly (Fig. 4), and the PERMANOVA community results confirmed insignificant differences
291 between the different zone (p=0.12). Pair-wise PERMANOVA, comparison between shelf and
292 deep basin nematode assemblages differ significantly as p=0.046 whereas the pairwise
293 comparison between slope and shelf, slope and deep basin was not significant (Table 2).

294

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) (3.13%), 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 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, although the basin and slope samples were clumped into groups but shelf stations were seen randomly distributed (Fig.5). As shown by the results of pair-wise PERMANOVA, three zones containing nematode assemblages significantly different (shelf vs deep basin; slope vs deep basin) differ 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 area stations showed the highest proportions (29–48%) of the predators/omnivores (group 2B). Similarly the dominance of predators (2B) was also seen in OMZ stations covered from the depth of 102 to 1001m. 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 at the slope and OMZ stations (33–49%). Clavate tails dominated at all stations, but slightly less in the slope and so in the inside the OMZ (1001m) 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, and the 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 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) 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 didn't reveal any particular notable relationships between traits. However certain trends has been observed for example, 1-2 and 2-4mm length size was generally correlated with slender and colonisers (2-3 C-P score) whereas > 4mm length size nematodes had higher C-P scores with long/thin body shape. 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 (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 area graphs and then a schematic figure is prepared in order to see 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 an increasing abundance of some traits like round tail shape, stout body shape, 2-4mm and greater prevalence of omnivores and deposit feeders. Coloniser life style (2-3) were increased while persister (4) were droped down to lower numbers in OMZ however, in the basin, 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 nematode community

The RELATE analyses indicated that the pattern based on the environmental variables is significantly related to the patterns inherent to the nematode community structure both taxonomic ($r = 0.37$, $p = 0.01$) 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, silt, and body length with sand, clay, and C:N ratio. However, C-P score was significantly correlated with clay and DO (Table 10). Moreover in case of species abundance data bottom water DO, clay, and C_{org} were proved to be the best three parameters which correlated significantly ($r = 0.712$, $p=0.02$). Of the 10 set of environmental parameters, 6 were retained for further analysis based on collinearity analysis (Draftsman plot). Only 4 variables salinity, temperature, water chl-a and C:N ratio with correlation r2 values .0.9 (considered redundant)

391   were omitted for the DISTLM procedures; the remaining variables and their pair-wise spearman

392   correlations are shown in Table 11.

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394   Analyses with distance-based linear models (DistLM) indicated that the 6 abiotic variables

395   related to the variation in nematode community structure explained 97 % of its total variation,

396   although not all variables were significant. Similarly for the functional traits of the 8 variables, 6

397   were used by the DISTLM procedure to construct the best-fitting model, together explaining 96

398   % of total variation. The DistLM analysis allowed the identification of those abiotic variables that

399   were best correlated with the observed distribution patterns of taxonomic and functional traits of

400   nematode species (Table 11, 12). Results based on the abundance and presence/absence data were

401   virtually identical; therefore, only the results based on the abundance data and functional traits

402   are reported. Variables such as the C_{org} and near-bottom oxygen content showed the highest

403   correlations (P < 0.05) with the nematode assemblages, whereas the functional traits were mainly

404   explained by with total organic carbon input (P < 0.05). Figs 7, 8 shows the DISTLM results by

405   means of a dbRDA plot, with the species abundance and biological traits superimposed. The

406   vectors of the environmental variables retained by the DISTLM procedure as fitting the best

407   explanatory model indicate the important role of OC in the slope area and chl a and sand in the

408   shelf whereas DO and clay showed their importance to basin.

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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 OMZ (525 m) and decreased to its lowest value in the lower part of the OMZ (1001 m). Metazoan meiofauna in total and more specific nematode densities often reach maximum values at lowest oxygen concentrations within OMZs (reviewed in Levin, 2003).

In the present paper, nematode densities were lower to 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 the center of the OMZ (400 m), however, 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$_{org}$ and near-bottom oxygen content showed the highest correlations (P < 0.05). Similarly many previous OMZ investigations have noted a correlation between food quality and meiofaunal abundance and the absence of oxygen. Like Cook et al. (2000) reported a strong positive correlation between nematode density and food quality, measured as the hydrogen index, along the transect through the Oman margin OMZ. Meiofaunal densities correlated only with sediment chlorophyll a concentration, and not with oxygen or other sediment parameters along a similar OMZ transect on a seamount off Mexico (Levin et al., 1991).

454 Moreover, in general nematode abundance did not follow any particular gradient tough it was

455 lowest in the deep basin stations. Generally, depth can have a major influence on nematode

456 density (Udalov et al., 2005; Soltwedel, 2000). The pattern of quantitative distribution of

457 nematode abundance is described for intertidal and upper subtidal (<50 m) zones, the average

458 world-wide nematode density is 1530 ind/10 cm^2, for continental slope (1000–2500 m) it drops to

459 430 ind/10 cm^2, for lower slope (2500–3500 m) – 360 ind/10 cm^2, for abyssal and hadal depths

460 (>5000 m) this value is still lower (140 ind/10 cm^2) (Mokievsky et al., 2004; Soltwedel, et al.,

461 2003). Large-scale comparisons of nematode community structure in other ocean basins indicate

462 that continental-shelf nematode communities differ significantly from slope communities

463 (Vanreusel et al., 2010).

464 The nMDS based on nematode species abundance and presence-absence separated the

465 three zones, and the difference was confirmed with PERMANOVA (p=0.03). Group 1 comprised

466 the stations of the shelf region, with the exception of the deepest shelf station, which was

467 clumped with the slope area to form the OMZ stations, where opportunistic species such as

468 *Pselionema* sp 1*, Choanolaimus* sp 2*, Halichoanolaimus* sp 1*, Cobbia dentata, Daptonema* sp 1*,

469 *Trissonchulus* sp 1 and *Minolaimus* sp 1 were found. The exculsive presence of these species in

470 OMZ may be the result of OMZ sediments that favor the success of nematode species that are

471 tolerant (colonists) or adapted (endemics). In addition to the seven species found exclusively in

472 the OMZ a number of species were found exclusively outside it. It is reasonable to speculate that

473 OMZs have isolated hypoxia-tolerant nematode species due to their different life strategies, small

474 size, less mobile with no pelagic larval stage. Therefore there could be some species which can

475 tolerate the oxygen minima while others cannot. However the exact mechanisms of adaptation or

476 preferences of species to the anoxic environment remains unclear. Several authors have pointed

477 out that nematode species can successfully cope with anoxic conditions by developing

478 appropriate physiological and behavioural mechanisms (e.g., symbiosis with bacteria, which we

479 also observed, and migration to "oxygen islands," sensu Reise and Ax (1979) and Wetzel et al.

480 (1995). Mouthless and gutless nematodes carrying endosymbionts have been observed previously

481 in deep-sea environments (Ingels et al., 2011).

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In present study nematode species have not developed any obvious adaptations, but they must have certain tolerance for anoxic conditions. The dominant species in OMZ 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 typical for sulphidic muds. However, 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 OMZ showed some morphological differences while some were observed with epibionts like the greatest numbers of specimens of *Desmodora* sp. Some species were observed to have unidentified blackish gut content. A small nematode was found in the gut of the *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 characterize the particular environment (Dufrene and Legendre, 1997). The genus *Acantholaimus* (*Acantholaimus mirabilis* significantly p = 0.005 associated with basin) 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 (Fonseca-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 in diversity 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 of 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 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 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. OMZ often support mats of large sulfur-oxidising bacteria, including Thioploca, Beggiatoa, 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 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 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 capable of ingesting other animals.

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., 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 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}. 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 very less as compared to 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 inhabited in the oxygenated environments are found to be of size and shape a 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 with only two species (*Diplolaimella* sp 1, *Diplolaimelloides* sp 1) in 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 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. 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 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, nematodes are the most tolerant taxon 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.

References

676 **References**

678 Anderson, M.: PERMANOVA: Permutational multivariate analysis of variance. Auckland:
679 Department of Statistics. (2005)

681 Anderson, M.J., Gorley, R.N., and Clarke, K.R.: PERMANOVA+ for PRIMER: guide to
682 software and statistical methods, PRIMER-E Ltd., Plymouth, UK, p. 214, 2008.

683 Arntz, W., Tarazona, J., Gallardo, V.A., Flores, L.A., and Salzwedel, H.: Benthos communities in
684 oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and
685 changes caused by El Nino, In: Modern and ancient continental shelf anoxia, edited by: Tyson,
686 R.V., Pearson, T.H., Geological Society Special, 58, 131–154, 1991.

688 Banse, K., Naqvi, S. W. A., Narvekar, P. V., Postel, J. R., and Jayakumar, D. A.: Oxygen
689 minimum zone of the open Arabian Sea: variability of oxygen and nitrite from daily to decadal
690 time scales, Biogeosciences 11, 2237–2261, 2014.

692 Bongers, T.: The maturity index: an ecological measure of environmental disturbance based on
693 nematode species composition, Oecologia, 83, 14–19, 1990.

695 Bongers, T., Alkemade, R., and Yeates, G.W.: Interpretation of disturbance-induced maturity
696 decrease in marine nematode assemblages by means of the Maturity Index, Mar. Ecol. Prog. Ser.,
697 76, 135–142, 1991.

699 Bongers, T., de Goede, R. G. N., Korthals, G. W., and Yeates, G.W.: Proposed changes of c–p
700 classification for nematodes, Russ.J. Nematol., 3, 61–62, 1995.

702 Bongers, T., Ferris, H., Nematode community structure as a bioindicator in environmental
703 monitoring, Trends Ecol. Evol., 14, 224–228, 1999.

707 Boström, C., Lastuniemi, M., Bonsdorff, E.: Infaunal responses to habitat structure: a study of
708 life-history traits and population dynamics of Corophium volutator (Pallas), Mar Biol Res.,
709 2:398– 410,2006.

711 Bray, J.R. and Curtis, J.T.: An ordination of the upland forest communities of southern
712 Wisconsin, Ecol. Monogr., 27, 325–349, 1957.

714 Bremner, J., Rogers, S.I., Frid, C.L.J.: Assessing functional diversity in marine benthic
715 ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser., 254, 11–25, 2003.

717 Bremner, J., Rogers, S.I., Frid, C.L.J.: Matching biological traits to environmental conditions in
718 marine benthic ecosystems. J Mar. Syst., 60, 302–316, 2006a.

721 Bremner, J.: Species' traits and ecological functioning in marine conservation and management, J.
722 Exp. Mar. Biol. Ecol., 366, 37-47, 2008.

724 Chalcraft, D.R. and Resetarits, W.J., Jr.: Predator identity and ecological impacts: functional
725 redundancy or functional diversity, Ecology, 84, 2407–2418, 2003.

727 Clarke, K.R.: Non-parametric multivariate analysis of changes in community structure. Aust. J.
728 Ecol., 18,117–43, 1993.

730 Clarke, K.R. and Ainsworth, M.: A method of linking multivariate community structure to
731 environmental variables, Mar. Ecol. Prog. Ser., 92, 205–219, 1993.

733 Clarke, K.R. and Gorley, R.N.: PRIMER v6*: User Manual/ Tutorial. Version 6. PRIMER-E
734 Ltd., Plymouth, UK, p. 192, 2006

736 Clarke, K.R. and Green, R.H.: Statistical design and analysis for a 'biological effects' study. Mar.
737 Ecol. Prog. Ser., 46, 213–226, 1988.

739 Cook, A.A., Lambshead, P.J.D., Hawkins, L.E., Mitchell, N., and , L.A.: Nematode abundance at
740 the oxygen minimum zone in the Arabian Sea, Deep-Sea Res. II, 47, 75–85, 2000.
741
742
743 De Cáceres, M., Legendre, M.P., and Moretti, M.: Improving indicator species analysis by
744 combining groups of sites, Oikos, 119, 1674–1684, 2010.
745
746
747 de Jonge, V.N., Elliott, M., Brauer, V.S., 2006. Marine monitoring: its shortcomings and
748 mismatch with the EU Water Framework Directive's objectives. Mar Poll Bull 53, 5–19
749
750 De Troch, M., Roelofs, M., Riedel, B., and Grego, M.: Structural and functional responses of
751 harpacticoid copepods to anoxia in the Northern Adriatic: an experimental approach, Biogeo-
752 sciences, 10, 4259–4272, 2013.
753
754 Dimitriadou, E., Hornik, K., Leisch, F., Meyer, D., and Weingessel, A.: Misc functions of the
755 Department of Statistics (e1071), TU Wien. R package version, 1.6. http: //CRAN.R
756 project.org/package=e1071, 2011.
757
758 Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx,
759 M., Gooday, A.: Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic
760 Biodiversity Loss, Current Biology 18, 1–8, 2008.
761
762
763 Dufrêne, M. and Legendre, P.: Species assemblages and indicator species: the need for a flexible
764 asymmetrical approach, Ecol. Monogr., 67, 345–366, 1997.
765
766 Fonsêca-Genevois V., Somerfield, P.J., Baeta Neves, M.H., Coutinho R., and Moens T.:
767 Colonization and early succession on artificial hard substrata by meiofauna, Mar Biol., 148,
768 1039-1050, 2006.
769

770 Gallardo, V.A.: Large benthic microbial communities in sulphide biota under Peru-Chile
771 Subsurface Countercurrent, Nature, 268, 331–332, 1977.

772

773 Gambi, C., Vanreusel, A., and Danovaro, R.: Biodiversity of nematode assemblages from deep-
774 sea sediments of the Atacama Slope and Trench (South Pacific Ocean), Deep-Sea Res. I, 50,
775 103–17, 2003.

776

777 Giere, O.: Meiobenthology, Springer-Verlag, Berlin Heidelberg, pp 328, 1993.

778

779 Helly, J.J. and Levin, L.A.: Global distribution of naturally occurring marine hypoxia on
780 continental margins, Deep-Sea Res. I, 51, 1159–1168, 2004.

781

782 Heip C, Vincx M, Vranken G. The ecology of marine nematodes, Oceanogr. Mar. Biol. Ann.
783 Rev. 1985; 23: 399–489.

784

785 Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P., and Thompson, K.: Allocating C-S-R plant
786 functional types: a soft approach to a hard problem, Oikos, 85, 282–294, 1999.

787

788 Holm-Hansen, 0., Riemann, B.: Chlorophyll a determination: improvements in methodology,
789 Oikos, 30,438–447, 1978.

790

791 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,
792 Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setalä, H., Symstad, A.J., Vandermeer, J., and
793 Wardle, D.A.: Effects of biodiversity on ecosystem functioning: a consensus of current
794 knowledge, Ecol. Monogr., 75, 3–35, 2005.

795

796 Ingels, J., Billett, D.S.M., Van Gaever, S., and Vanreusel, A.: An insight into the feeding ecology
797 of deep-sea canyon nematodes—results from field observations and the first *in-situ* [13]C feeding
798 experiment in the Nazaré Canyon, J. Exp. Mar. Biol. Ecol., 396, 185–193, 2011.

799

800

Ingole, B.S., Sautya, S., Sivadas, S., Singh, R., and Nanajkar, M.: Macrofaunal community structure in the Western Indian continental margin including the oxygen minimum zone, Mar. Ecol., 31, 148–166, 2010.

Jensen, P.: Feeding ecology of free-living aquatic nematodes, Mar. Ecol. Prog. Ser., 35, 187–196, 1987.

Jensen, P.: Nematode assemblages in the deep-sea benthos of Norwegian Sea, Deep-Sea Res., 35, 1173–1184, 1988.

Kamykowski, D. and Zentara, S.J.: Hypoxia in the world ocean as recorded in the historical dataset, Deep-Sea Res., 37, 1861–1874, 1990.

Kelly, J.R. and Nixon, S.W.: Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community, Mar. Ecol. Prog. Ser., 17, 157–169, 1984.

Levin, LA.: Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr. Mar, Biol. , 41, 1–45, 2003.

Levin, L., Gage, J., Lamont, P., Cammidge, L., Martin, C., Patience, A. and Crooks, J.: Infaunal community structure in a low-oxygen, organic-rich habitat on the Oman continental slope, NW Arabian Sea,in: The responses of marine organisms to their environments: Proceedings of the 30th European Marine Biology Symposium, University of Southampton, Southampton, UK, 223-230, 1997.

Levin, L.A. and Gage, J.D., Relationships between oxygen, organic matter and the diversity of bathyal macrofauna, Deep-Sea Res., 45, 129–163, 1998.

Levin, L.A., Huggett, C.L., and Wishner, K.F.: Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean, J. Mar. Res., 49, 763–800, 1991.

Levin, L.A., Gage, J.D., Martin, C., and Lamont, P.A.: Macro-benthic community structure within and beneath the oxygen-minimum zone, NW Arabian Sea, Deep-Sea Res. II, 47,189–226, 2000.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., and Pawson, D.: Environmental influences on regional deep sea species diversity, Annu. Rev. Ecol. Syst., 32, 51–93, 2001.

Margalef, R.: Perspectives in Ecological Theory. University of Chicago Press, Chicago, 111, 1968.

McArdle, B., and Anderson, M.: Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecol Lett 82: 290–297, 2001.

Mokievsky, V. O., Udalov, A. A., Azovsky, A. I. (2004). On the quantitative distribution of meiobenthos on the shelf of the World Ocean. Oceanology, 44, 110–120.

Moodley, L., van der Zwaan, G.J., Herman, P.M.J., Kempers, L., and van Breugel, P.: Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina), Mar. Ecol. Prog. Ser., 158, 151–163, 1997.

Morrison, M., Codispoti, L.A., Gaurin, S., Jones, B., Manghnani, V., and Zheng Z.: Seasonal variation of hydrographic and nutrient fields during the US JGOFS Arabian Sea Process Study Deep Sea Res. II, 45, 2053–2101, 1998.

Murrell, M.C. and Fleeger, J.W.: Meiofaunal abundance on the Gulf of Mexico continental shelf affected by hypoxia, Cont. Shelf Res., 9, 1049–1062, 1989.

Nicholas, W.L., Goodchild, D.J., and Steward, A.: The mineral composition of intracellular inclusions in nematodes from thiobiotic mangrove mud-flats, Nematologica, 33, 167-179, 1987.

865

866   Neira, C., Sellanes, J., Levin, L.A., and Arntz, W.A.: Meiofaunal distributions on the Peru
867   Margin: relationship to oxygen and organic matter availability, Deep-Sea Res., 48, 2453–72,
868   2001.

869

870   Neira, C., King, I., Mendoza, G., Sellanes, J., De Ley, P., and Levin, L.A.: Nematode community
871   structure along a central Chile margin transect influenced by the oxygen minimum zone. Deep
872   Sea Res Part I, 78:1–15, 2013.

873

874

875   Netto, S.A., Gallucci, F., and Fonseca, G.F.C.: Meiofauna communities of continental slope and
876   deep-sea sites off SE Brazil, Deep-Sea Res., 52, 845–859, 2005.

877

878   Odiete, W.O.: Environmental physiology of animals and pollution, Diversified Resources Ltd.,
879   Lagos, pp 261, 1999.

880

881   Ólafsson, E. and Elmgren, R.: Seasonal dynamics of sublittoral meiobenthos in relation to
882   phytoplankton sedimentation in the Baltic Sea, Estuar. Coast. Shelf. Sci., 45, 149–164, 1997.

883

884   Qasim, S.Z.: Biological productivity of the Indian Ocean, I. J. M. S., 6, 122–137,1977.

885

886   Pape E., Bezerra T. N., Jones, D. O. B., Vanreusel A., Unravelling the environmental drivers of
887   deep-sea nematode biodiversity and its relation with carbon mineralisation along a longitudinal
888   primary productivity gradient, Biogeosciences, 10, 3127–3143 , 2013.

889

890   Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, Prog.
891   Oceanogr., 80, 113–128, 2009.

892

893   Pielou, E.C.: Species diversity and pattern diversity in the study of ecological succession, J Theor
894   Biol, 10, 372–383, 1966.

895

Platt, H.M. and Warwick, R.M.: The significance of freeliving nematodes to the littoral ecosystem. In: The shore environment, Vol. 2. Ecosystems, edited by: Price, J.H., Irvine, D.E.G., Famham, W.F., Academic Press, London, p.729–759, 1980.

Platt, H.M. and Warwick, R.M.: Free-living marine nematodes Part I: British Enoplids. In:, Synopses of the British fauna (New Series), edited by Kermack, D.M., Barnes, R.S.K., Cambridge University Press, p. 307, 1983.

Platt, H.M. and Zhang, Z.N.: New species of marine nematodes from Loch Ewe, Scotland. Bulletin of the British Museum of Natural History (Zoology) 42, 227-246, 1982.

Rao, B.R. and Veerayya, M.: Influence of marginal highs on the accumulation of organic carbon along the continental slope off western India, Deep-Sea Res. II, 47, 303–327, 2000.

R Development Core Team R.: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/, 2010.

Reichart, G. L., Lourens, L. J., Zachariasse, W. J.: Temporal variability in the northern Arabian Sea oxygen minimum zone (OMZ) during the last 225,000 years, Paleoceanography 13, 607–621,1998.

Reise, K. and Ax, P.: A meiofaunal 'thiobios' limited to the anaerobic sulfide system of marine sand does not exist. Mar. Biol., 54, 225–237, 1979.

Riemann, F.: On hemisessile nematodes with flagelliform tails living in marine soft bottoms and micro-tubes found in deep sea sediments, Mikrofauna Meeresboden, 40, 1–15, 1974.

Ryther, J.H. and Menzel, D.W.: On the production, composition, and distribution of organic matter in the Western Arabian Sea, Deep Sea Res., 12, 199–209, 1965.

Schneider,C.C. and Bush-Brown, S.: Oxygen Minimum Zones, The Traprock, 2,19-23,2003.

928

Schratzberger, M. and Warwick, R.M.: Effects of the intensity and frequency of organic enrichment on two estuarine nematode communities, Mar. Ecol. Prog. Ser., 164, 83–94, 1998.

Schratzberger, M., Warr, K., and Rogers, S.I.: Patterns of nematode populations in the southwestern North Sea and their link to other components of the benthic fauna, J. Sea Res., 55, 113–127, 2006.

Schratzberger, M., Warr, K., and Rogers, S.I.: Functional diversity of nematode communities in the southwestern North Sea, Mar. Environ. Res., 63, 368–389, 2007.

Shannon, C.E. and Weaver, W.: The Mathematical Theory of Communication, University of Illinois Press, Urbana, Illinois, 144, 1963.

Shetye, S. R. and Shenoi, S. C. C.: Seasonal cycle of surface circulation in the coastal north Indian Ocean. Proceed. Ind. Acad. Sci. Earth and Planet. Sci., 97, 53–62,1988.

Snelgrove, P.V.R. and Butman, C.A.: Animal-sediment relationships revisited: cause versus effects. Oceanogr. Mar. Biol. Annu. Rev., 32, 111–177, 1994.

Soetaert, K., Heip, C.: Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea, Mar. Ecol. Prog. Ser., 125, 171–183, 1995.

Soetaert, K., Middelburg, J., Wijsman, J., Herman, P., and Heip, C.: Ocean margin early diagenetic processes and models. In: Wefer, G., Billett, D., Hebbeln, D., Jørgensen, B.B., von Weesing, T.J. (Eds.), Ocean margin systems, Springer Verlag, Berlin, 157–177, 2002.

Soltwedel, T.: Metazoan meiobenthos along continental margins: a review. Prog Oceanogr. 2000;46:59–84, 2000.

960   Soltwedel, T., M. Miljutina, V. Mokievsky, D. Thistle and K. Vopel, 2003, The meiobenthos of

961   the Molloy deep (5600 M) Fram Strait, Arctic Ocean, Vie Milieu 53 (1), pp. 1–13

962

963

964   Strickland, J.D.H. and Parsons, T.R.: A practical handbook of seawater analysis, Bull. Fish. Res.

965   Board Can., 311, 1968.

966

967   Thiel, H.: The size structure of the deep-sea benthos, Int. Rev. ges. Hydrobiol., 60, 575–606,

968   1975.

969

970   Thistle, D. and Sherman, K.M.: The nematode fauna of a deep-sea site exposed to strong near-

971   bottom currents, Deep-Sea Res., 32, 1077–1088, 1985.

972

973   Tietjen, J.H.: Distribution and species diversity of deep-sea nematodes in the Venezuela basin.

974   Deep-Sea Res., 31, 119–132, 1984.

975

976   Udalov, A.A., Azovsky, A.I., Mokievsky, V.O.: Depth-related pattern in nematode size: What

977   does the depth itself really mean? Prog Oceanogr., 67:1–23, 2005.

978

979

980   Vanhove, S., Wittoeck, J., Desmet, G., Van Den Berghe, B., Herman, R.L., Bak, R.P.M.,

981   Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., and Vincx, M.: Deep sea meiofauna

982   communities in Antarctica: structural analysis and the relation with the environment, Mar. Ecol.

983   Prog. Ser., 127, 65–76, 1995.

984

985   Van Colen C., Montserrat, F., Vincx, M., Herman, P.M.J., Ysebaert, T., and Degraer, S.:

986   Macrobenthic recovery from hypoxia in an estuarine tidal mudflat, Mar. Ecol. Prog. Ser., 372:31–

987   42, 2008.

988

989

990

991   Vanreusel, A., Fonseca, G., Danovaro, R., Silva, M. C. d., Esteves, A. M., Ferrero, T., Gad, G.,

992   Galtsova, V., Gambi, C.,Genevois, V. d. F., Ingels, J., Ingole, B., Lampadariou, N., Merckx, B.,

993   Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D., Radziejewska, T., Raes, M.,

994   Tchesunov, A.,Vanaverbeke, J., van Gaever, S., Venekey, V., Bezerra, T. N.,Flint, H., Copley, J.,

995   Pape, E., Zeppilli, D., Martinez, P. A.,and Galeron, J.: The contribution of deep-sea macrohabitat

996   heterogeneity to global nematode diversity, Mar. Ecol., 31, 6–20, 2010.

997

998   Vanaverbeke, J., Bezerra, T.N., Braeckman, U., De Groote, A., De Meester, N., Deprez, T.,

999   Derycke, S., Gilarte, P., Guilini, K., Hauquier, F., Lins, L., Maria, T., Moens, T., Pape, E., Smol,

1000   N., Taheri, M., Van Campenhout, J., Vanreusel, A., Wu X., Vincx, M.: NeMys: World Database

1001   of Free-Living Marine Nematodes. 10-30, 2015.

1002

1003

1004   Vincx, M., Bett, B.J., Dinet, A., Ferrero, T., Gooday, A.J., Lambshead, P.J.D., Pfannkuche, O.,

1005   Soltwedel, T., and Vanreusel, A.: Meiobenthos of the deep northeast Atlantic, Adv. Mar. Biol.,

1006   30, 2–88, 1994.

1007

1008   Wetzel, M.A., Jensen, P., and Giere, O.: Oxygen/sulfide regime and nematode fauna associated

1009   with *Arenicola marina* burrows: new insights in the thiobios case, Mar. Biol., 124, 301–312,

1010   1995.

1011

1012   Wieser, W.: Die Beziehung zwischen Mundhohlen gestalt, Ernahrungsweise und Vorkommen bei

1013   frelebenden mainen Nernatoden, Ark. Zool., 4, 439–484, 1953.

1014

1015   Wishner, K., Levin, L., Gowing, M., and Mullineaux, L.: Involvement of the oxygen minimum in

1016   benthic zonation on a deep seamount. Nature, 346, 57–59, 1990.

1017

1018

1019   Zettler, M.L., Bochert, R., and Pollehne, F.: Macrozoobenthos diversity in an oxygen minimum

1020   zone off northern Namibia. Mar. Biol., 156, 1949–1961, 2009.

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1025 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

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1028 Table 2. Results of pair-wise comparison (samples from different zones) PERMANOVA

1029 analyses (based on Bray–Curtis similarity measure). Data was fourth-root transformed;

1030 resemblance was calculated using Bray-Curtis. Bold values indicate significant differences at p <

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	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**

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Table 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.

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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

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1077 Table 4. The 10 most abundant species recorded from the oxygen minimum zone (OMZ) and
1078 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

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1088 Table 5. List of indicator species calculated by IndVal index, number of genera associated with
1089 the shelf group =4, number of genera associated to slope groups = 5, number of genera associated
1090 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

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1097 Table 6. Mean and standard error for diversity indices of the nematode communities at species
1098 level. d, Margalef's index for species richness; J′, Pielou's index for species evenness; ES (51),
1099 estimated total number of species; H′(loge), log2 Shannon–Wiener Index for species diversity.

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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

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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.

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	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

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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 (colonizer-
persister score).

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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

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

Species	Zones			Buccal morphology				Tail shape				Adult Length (mm)				Adult shape			Life history (c-p score)		
	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

Taxon																								
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	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	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	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	0.11	0.08	0.00	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0

Species																					
filiformis																					
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	0	1	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	0	1	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

Species																				
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

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1154 1A= selective deposit feeders, 1B= non-selective deposit feeders, 2A=epigrowth feeders, 2B= predators (Wiser, 1953). R= round. E/F=
1155 elongated/filiform, CO= conical, CA= clavate. ST= stout, L/T= long/thin, C-P= coloniser-persister score (Bongers et al., 1991, 1995.
1156 Pape et al., 2013), 1= species belonging trait, 0= species not belonging trait.

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1160 Table 10. Results from BIOENV analyses: Spearman rank correlation (rho) and significance level
1161 (P) between nematode biological traits and environmental variables. Values P < 0.05 are
1162 significant. DO, dissolved oxygen.

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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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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

MARGINAL TESTS

Variable	SS(trace)	Pseudo-F	P	Prop.
DO, mll-1	321.67	2.3209	0.068	0.27892
Chl aµg-1	179.35	1.1049	0.362	0.15552
Corg (%)	399.65	3.1819	0.008	0.34654
Clay (%)	168.03	1.0233	0.391	0.14571
Silt (%)	121.46	0.70635	0.606	0.10532
Sand (%)	164.27	0.99661	0.426	0.14244

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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

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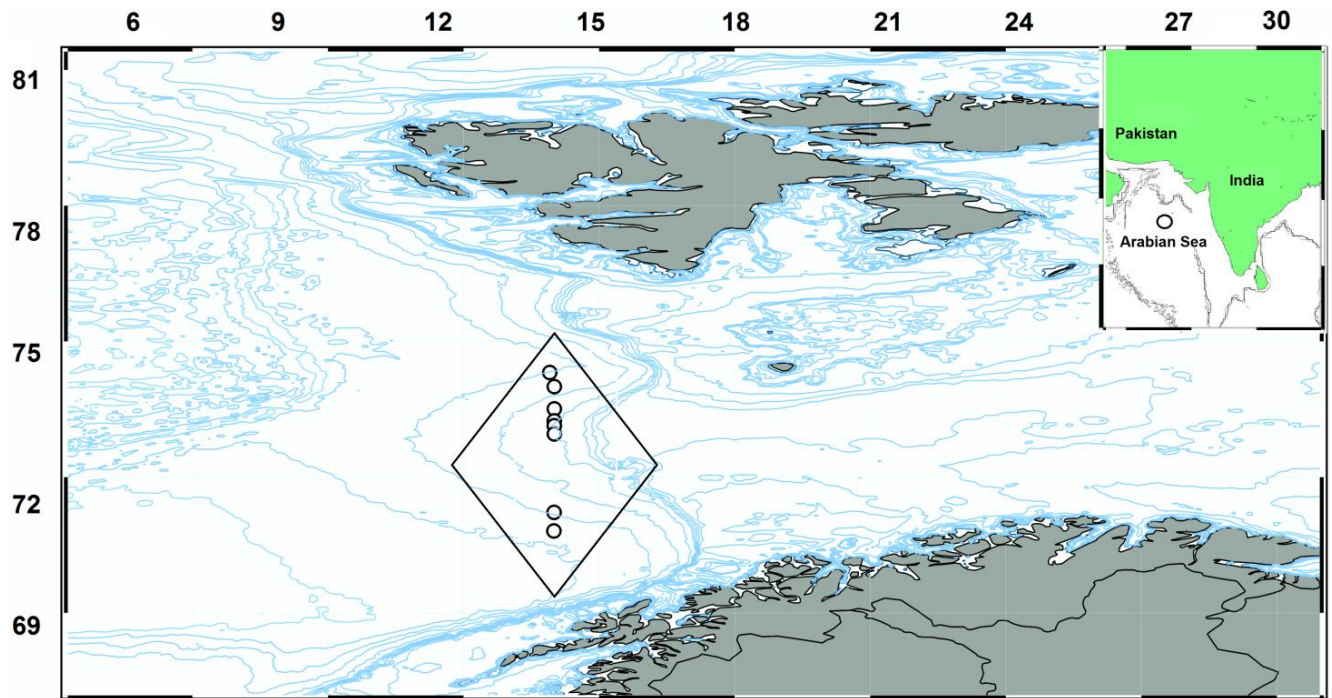
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1211   Figure 1. Map showing location of the 8 sampling stations (in circle) in the coast of Arabian
1212   Sea along with depth contours and the positions of the sampling stations.
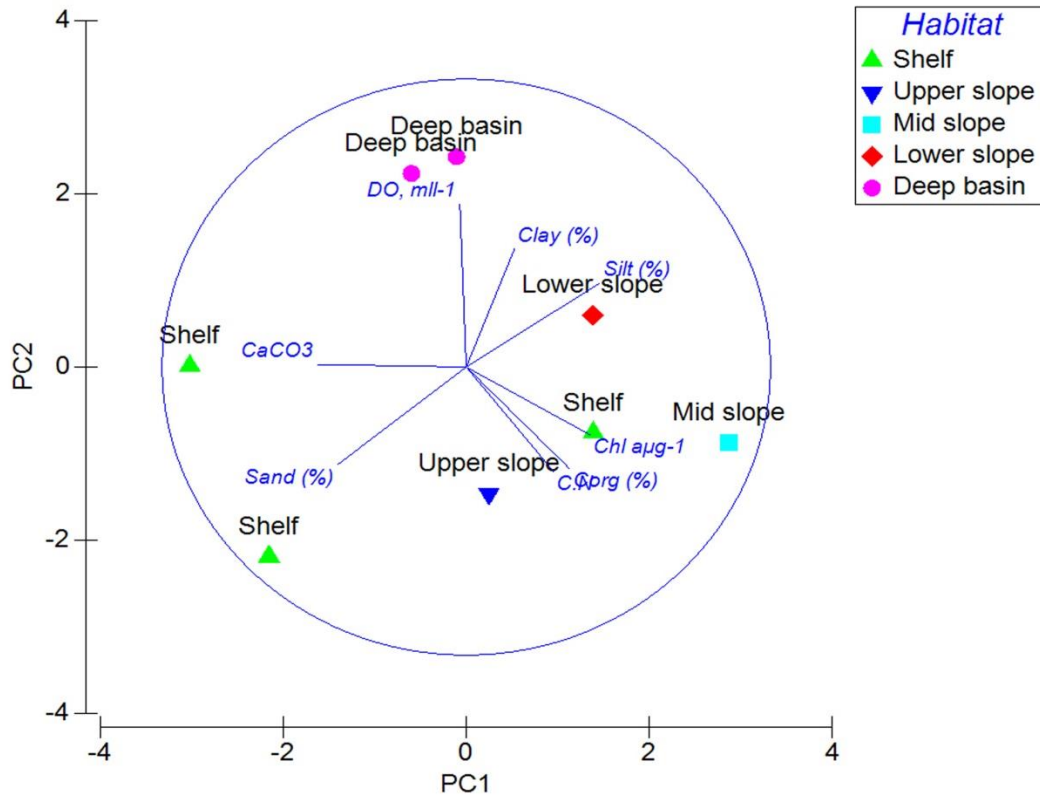
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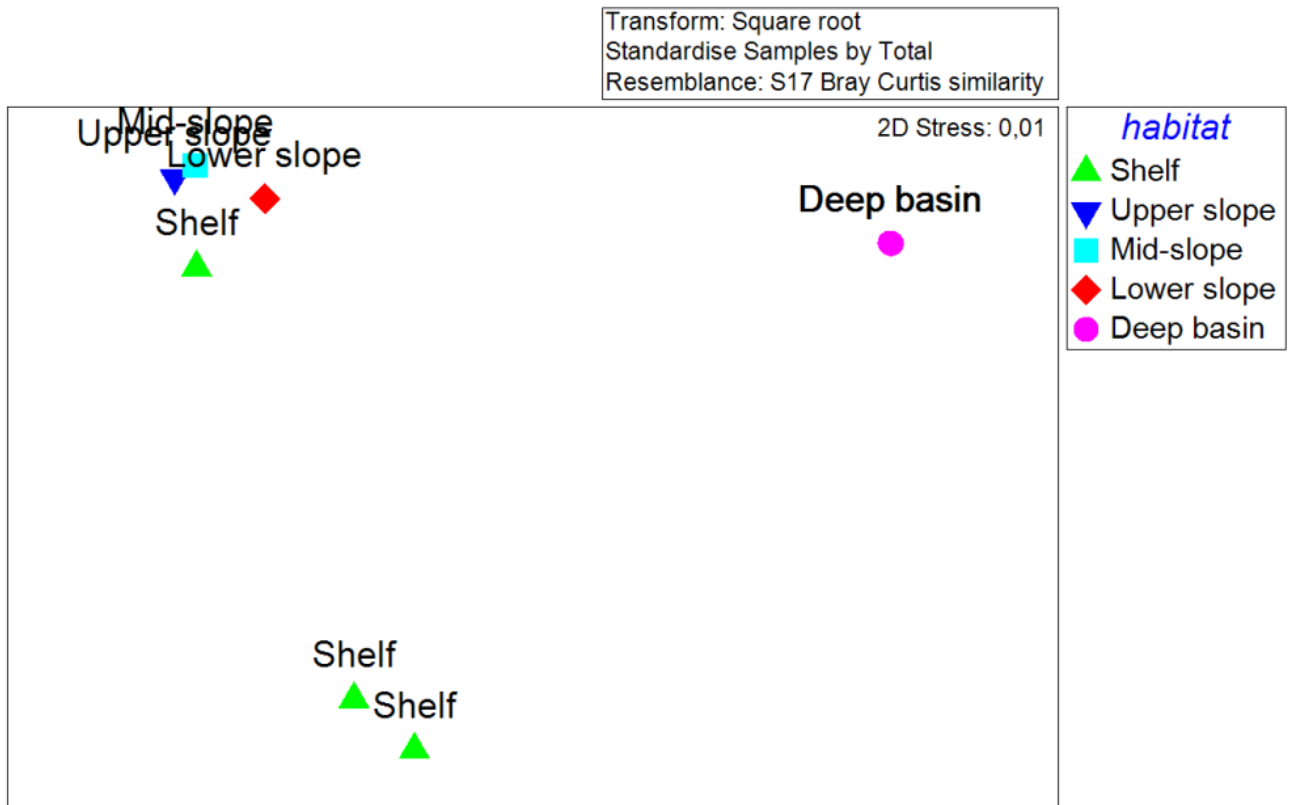
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Figure 2. Principal component analysis derived from the contribution of parameters in each benthic zone. PC 1 and 2 accounted for 81 % of the total variation present.

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

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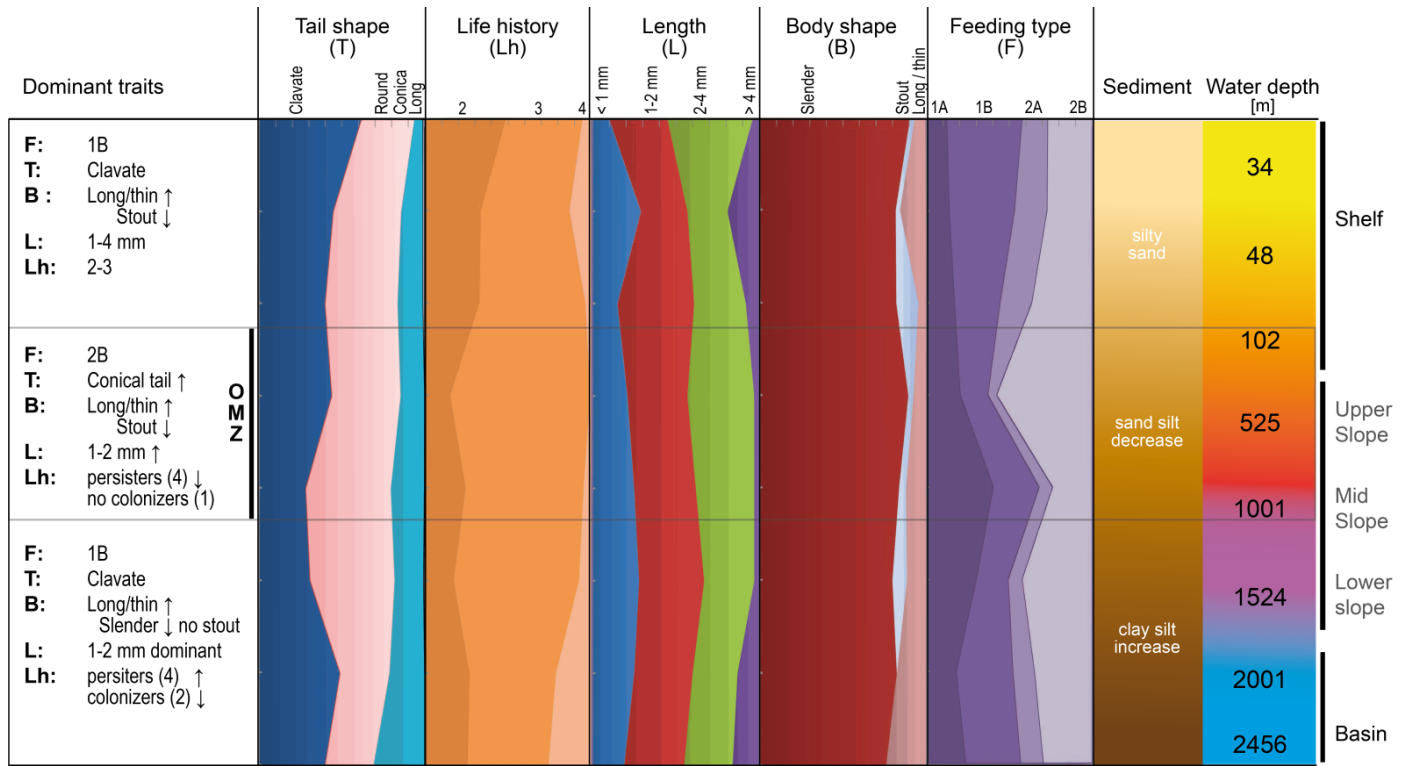Figure 4. nMDS ordination based on nematode species presence/absence.
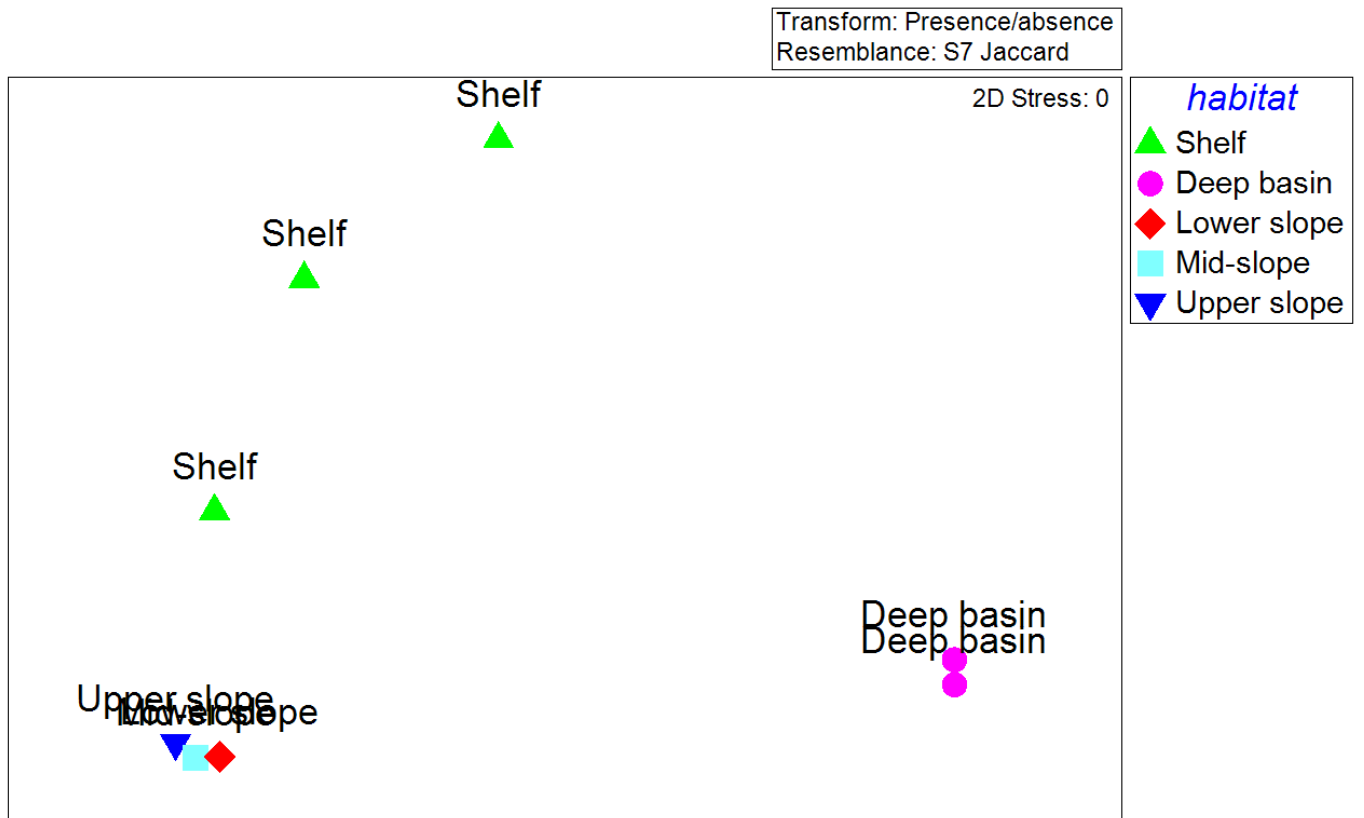
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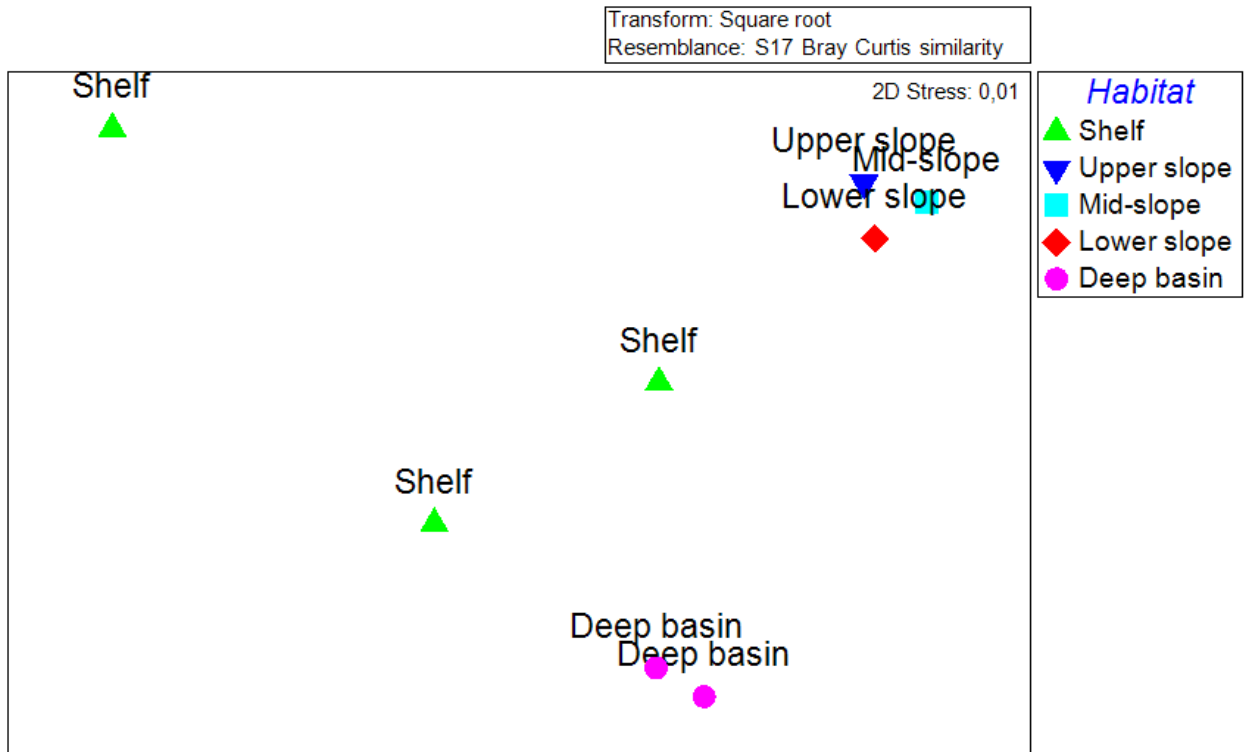
Figure 5. nMDS ordination based on nematode species biological traits using the Bray–Curtis similarity index.

Figure 6. Schematic model of the functional traits at each benthic zones
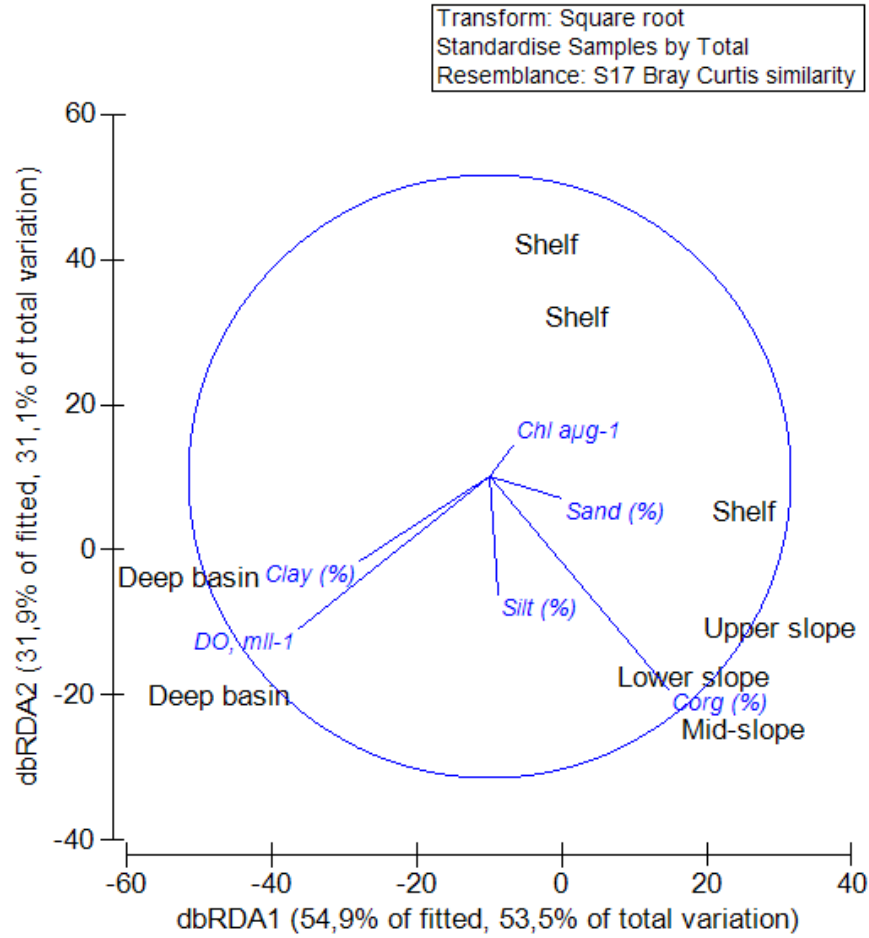
Figure 7. Distance-based redundancy (dbRDA) bubble plot illustrating the DISTLM model based on the species assemblage data and fitted environmental variables with their vector (strength and direction of effect of the variable on the ordination plot). Axis legends include % of variation explained by the fitted model and % of total variation explained by the axis.

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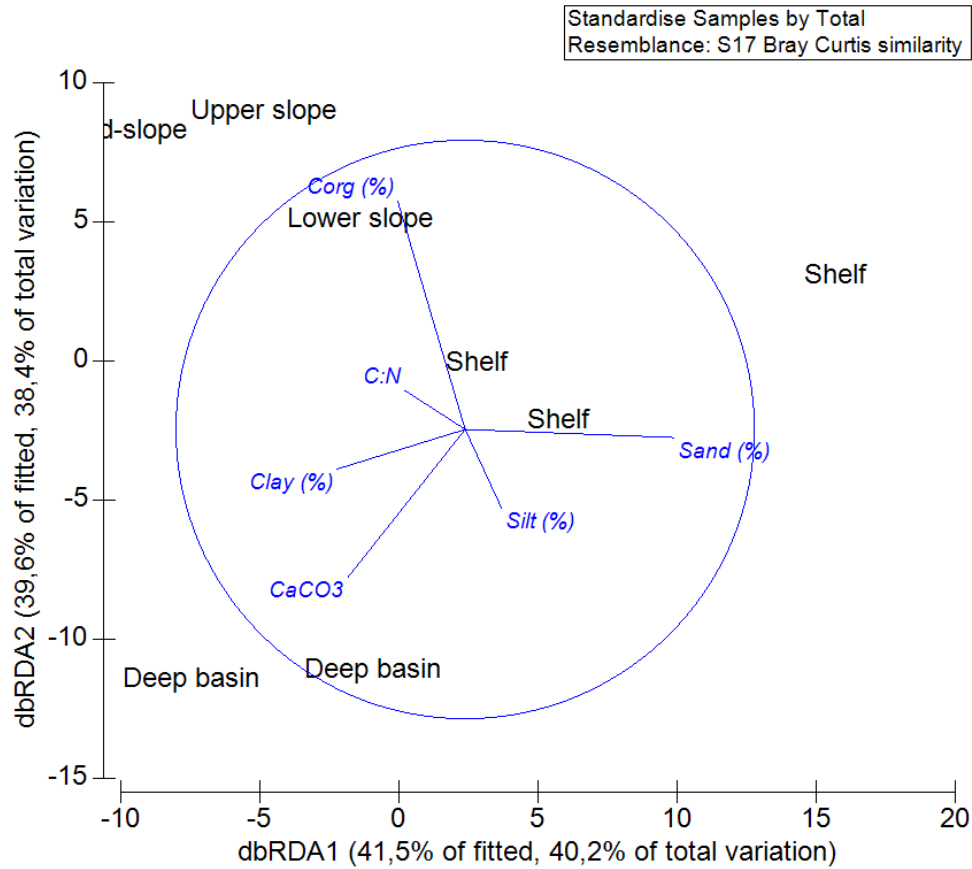Figure 8. Distance-based redundancy (dbRDA) bubble plot illustrating the DISTLM model based on the species functional assemblage data and fitted environmental variables with their vector (strength and direction of effect of the variable on the ordination plot). Axis legends include % of variation explained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

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