1	Structure and function of nematode communities across the Indian
2	western continental margin and its oxygen minimum zone
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4	Ravail Singh ¹ and Baban S. Ingole ²
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6	¹ Senckenberg am Meer, DZMB, Südstrand 44, D-26382 Wilhelmshaven, Germany
7	² National Institute of Oceanography, Goa, India-403004
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10	Corresponding author email: rubail2010@gmail.com
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Abstract. We studied patterns of nematode distribution along the western Indian continental 12 margin to determine the influence of habitat heterogeneity and low oxygen levels on the 13 community's taxonomic and functional structure. A single transect, perpendicular to the coast at 14 14° N latitude was sampled from 34 to 2546 m depth for biological and environmental variables 15 during August 2007. The oxygen minimum zone extended from 102 m to 1001 m. Nematodes 16 were (described and undescribed) identified to species and classified according to biological and 17 functional traits. A total of 110 nematode species belonging to 24 families were found along the 18 transect. Three depth zones were identified, the shelf (depth range 34-102 m; highest nematode 19 mean density: 176.6 ± 37 ind/10 cm²), the slope (525–1524 m; 124.3 ± 16 ind/10 cm²), and the 20 basin (2001–2546 m; 62.9 \pm 2 ind/10 cm²). Across the entire study area, the dominant species 21 22 were Terschellingia longicaudata, Desmodora sp 1, Sphaerolaimus gracilis, and Theristus ensifer; their maximum density was at shelf stations. Nematode communities in different zones 23 24 differed in species composition. Chromadorita sp 2 (2.78%) and Sphaerolaimus gracilis (2.21%), were dominant on the shelf, whereas *Terschellingia longicaudata* (4.73%) and *Desmodora* sp 1 25 26 (4.42%) were dominant on the slope, but in the basin, *Halalaimus* sp 1(1.11\%) and Acantholaimus elegans (1.11%) were dominant. The information in a particular functional group 27 28 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 29 30 differed notably from information contained in other taxonomic groups. The functional composition of nematodes was strongly linked to the organic carbon and dissolved oxygen 31 concentration. Seven species were found exclusively in the oxygen minimum zone: Pselionema 32 sp 1, Choanolaimus sp 2, Halichoanolaimus sp 1, Cobbia dentata, Daptonema sp 1, 33 Trissonchulus sp 1, and Minolaimus sp 1. Moreover, in our study, species diversity was higher 34 on the shelf than on the slope or in the basin. Correlation with a number of environmental 35 variables indicated that food quantity (measured as the organic carbon content and chlorophyll 36 content) and oxygen level were the major factors that influenced nematode community structure 37 and function. 38

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40 Key words: oxygen minimum zone, habitat heterogeneity, Nematoda, functional traits, deep sea,

41 Arabian Sea, Indian continental margin.

42 1. Introduction

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The continental margin exhibits great topographical heterogeneity in geomorphological features 44 (e.g., canyons and seamounts, shelf, slope, rise, marginal highs) and their related environmental 45 conditions (e.g., depth, pressure, temperature, salinity, light, dissolved oxygen, sediment 46 characteristics) (Levin et al., 2001). This heterogeneous environment is of great ecological 47 48 interest because of its wide range of gradients in living conditions and the high faunal diversity it supports on local, regional, and global scales (Vanreusel et al., 2010). The western Indian 49 50 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 51 general, oxygen minimum zones (OMZs) are defined as layers of the water column where 52 dissolved oxygen (DO) concentrations fall below 0.5 ml l⁻¹. Oxygen minima are common in the 53 world oceans (Kamykowski and Zentara, 1990) and are found at intermediate depths in the 54 Arabian Sea, off western Mexico, and off Peru and northern Chile. The Arabian Sea OMZ is one 55 56 of the strongest and most intense in the world, with oxygen concentrations $< 2 \mu M$ in its core (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009; Zettler et al., 2009). The OMZ in the 57 Arabian Sea is spread over 285,000 km^2 of the benthic area. The OMZ occupies approximately 58 the 150–1000 m depth range and is the thickest of the three major OMZs of the open ocean 59 60 (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). 61

The entire western Indian continental margin (shelf to slope) supports a high benthic 62 biodiversity (Ingole et al., 2010). Free-living nematodes are prominent members of the 63 meiobenthos along the ocean continental margin, often constituting >90% of all metazoa (Vincx 64 65 et al., 1994). Moreover, they are more tolerant than macro- and other meiofauna to anoxic conditions (Giere, 1993; Moodley et al., 1997). Studies like those of Jensen (1987) and Murrell 66 and Fleeger (1989) reported effects of low-oxygen conditions on nematofauna in sandy sediments 67 at shallow depths and from the Gulf of Mexico, respectively, and showed that nematode 68 69 abundance was unaffected by oxygen concentration. Cook et al. (2000) studied nematodes from the Arabian Sea OMZ and concluded that nutrient input is more important than oxygen 70 71 concentration, but in another experimental study in the tidal flats, hypoxia caused a dramatic 72 change in the nematode community composition, including reduction in diversity and abundance 73 of all dominant nematodes except for genus *Odontophora* (Van Colen et al., 2008). Neira et al. (2013) found that nematode generic and trophic diversity was lowest at the most oxygen-depleted site along a central Chile margin. De Troch et al. (2013), in a short incubation experiment, found that nematodes were not affected by anoxic conditions. They further concluded that responses to stress depend on the species and the frequency of the hypoxic periods. In contrast to several studies on the effects of anoxia on Nematoda at higher taxonomic levels, little is known about their response at the species level.

80 Several transitional settings in the western Indian continental margin, including the shelf, slope (long stretch of OMZ), and basin, provide multiple oxygen and other environmental 81 82 gradients. These settings allowed us to investigate how oxygen and environmental factors affect and modulate the structure and function of nematode communities at the species level. An 83 84 exclusive study from the Indian western continental margin with reference to nematode tolerance in the OMZ is therefore important. Furthermore, nematode community structure from the western 85 86 Indian continental margin (including the OMZ) of the Arabian Sea remains unstudied. In general 87 information on nematode species data is missing from the Arabian Sea and the present study can 88 provide important basic information on nematode community structure.

89 Traditional taxonomy-based methods of nematode community analyses may not,
90 however, fully account for nematodes' diverse roles in ecosystem function (Schratzberger et al.,
91 2007), so the inclusion of functional analysis has been recommended (de Jonge et al., 2006).

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

97 Nematode species in functional groups share several morphological traits (Chalcraft and Resetarits, 2003), and use of these traits may provide additional information on changes in 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 100 101 had applications in a variety of marine habitats. Thistle and Sherman (1985) found that nematode tail shape formed an important biological trait especially in locomotion and reproduction. 102 103 Furthermore, body size is known to influence many traits of an animal, such as its life history, physiology, and energy requirements, whereas species morphotype represents adaptations to life 104 105 in oxygen-poor and sulphide-rich sediments (Jensen, 1987). Bongers (1990) and Bongers et al. (1991, 1995) classified the genera (along a scale of 1 to 5) from r-selected 'colonisers' to Kselected 'persisters', according to their life history, to assess the condition of terrestrial and
freshwater habitats but also of marine environments from the shelf.

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

112 Does a heterogeneous gradient like the shelf, slope, and deep basin of the western Indian 113 continental margin affect the marine nematode community structurally and functionally?

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

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118 **2. Materials and Methods**

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120 **2.1. Study area**

121 The bottom topography of the Arabian Sea includes the Carlsberg Ridge is in the southern part, 122 the Murray Ridge in the northern part, and an unsloped region in between (from 14° N to 21° N). 123 The continental shelf is 120 km wide off the southern part, narrows to about 60 km off 11° N, 124 and widens to about 350 km off the Gulf of Cambay (Shetye and Shenoi, 1988).

Surface circulation is controlled by the seasonal variation in various types of winds. 125 During the SW monsoon, biological productivity in the Arabian Sea lies mainly around the 126 centers of seasonal upwelling off the Arabian Peninsula, Somalia, and southwest India (Qasim, 127 1977). The Arabian Sea is characterised by a very pronounced midwater oxygen minimum zone 128 (OMZ) between 150 and 1250 m; it is over 1000 m thick and extends vertically from the bottom 129 of the euphotic layer (~ 100 m) to ~ 1000 m (Wishner et al., 1990). The variations in the intensity 130 of the OMZ are related to upwelling intensity and thermocline ventilation by Indian Ocean water 131 (Reichart et al., 1998). It is located directly beneath the productive upwelling region (de Sousa et 132 133 al., 1996; Morrison et al., 1998).

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138 **2.2. Sampling**

A single transect was selected perpendicular to the coast of the Arabian Sea at 14° N latitude 139 (Fig. 1). A detailed benthic sampling was performed on board ORV Sagar Kanya during August 140 2007 (cruise no. SK 237). Eight stations were sampled, at water depths of 34, 48, 102, 525, 1001, 141 1524, 2001, and 2546 m, by means of a spade box corer ($50 \times 50 \times 50$ cm size). According to 142 Rao and Veerayya (2000) the transect can be divided into five regions—shelf (34, 48, and 102 143 144 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 145 146 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. 147 148 For nematode assemblages, a PVC core (5.7 cm diameter) was used for sub-sampling. At each station, two sub-samples were sliced per centimetre down to 5 cm sediment depth and fixed in 149 buffered 4% formalin. Separate sub-cores was collected for organic carbon (Corg) and sediment 150 chlorophyll-a (Chl-a), and they were frozen at -20° C. Bottom-water dissolved oxygen (DO) 151 152 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. 153

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155 **2.3. Laboratory analysis**

156 Dissolved oxygen was analyzed by Winkler's method (Strickland and Parsons, 1968). Sample bottles are stored upright in an ice chest in a dark location and were analyzed after a period of 8– 157 9 hours. Chl-a was estimated by means of an acetone extraction method using a fluorometer 158 (Holm-Hansen and Riemann, 1978). Total-carbon analyses were carried out in freeze-dried 159 sediments with an NCS 2500 (Model-EA / NA1110) CNS analyzer. Inorganic carbon was 160 analyzed with a CO₂ Culometer analyzer, and the percentage of CaCO₃ was calculated. 161 Percentage of Corg was calculated by subtraction of inorganic from total carbon. Sediment 162 granulometry was determined by a Malvern Laser Analyzer (Model-Hydro 2000MU). 163

Meiofauna samples were washed over a 500-µm mesh and then sieved on a 32-µm mesh, which retained the meiofauna fraction. This retained fraction was then elutriated by the centrifugation-flotation technique with LUDOX (Vincx, 1996; Heip et al., 1985). Nematodes were counted through a stereo-microscope and were picked and mounted on permanent glass slides for taxonomic identification. In all, 1798 nematodes were examined. They were identified up to described and morphotype species level from the pictorial keys of Platt and Warwick (1983) and the NeMys database (Vanaverbeke et al., 2015). For identification to species level,
each morphotype was sketched and measured by means of a camera lucida so that all specimens
of the same genus could be compared.

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174 **2.4. Nematode functional trait analysis**

175 Nematode species were classified according to their buccal morphology, tail shape, adult length,176 adult shape, and life history.

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

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

184 Total length and body shape: Total length and the maximum body width for adult nematodes were measured, and from the results we calculated the length-width ratio. Soetaert et 185 186 al. (2002) suggested three body-shape morphologies: stout, slender, and long/thin. Length-width ratio is a measure of a nematode's body shape; long/thin animals have high ratios, and stout 187 188 animals low ratios. From measured length, each species was therefore assigned to one of four length groups (< 1 mm, 1–2 mm, 2–4 mm, >4 mm) and three shape categories (stout, with a 189 190 length-width ratio < 18; slender, with a length-width ratio of 18–72; and long/thin, with a length–width ratio > 72). 191

Life history (C-P score): Nematodes were allocated to life-history groups according to 192 Bongers (1990) and Bongers et al. (1991); genera are classified on a scale from 1 to 5 from 193 194 colonisers (1, short life cycle, high reproduction rates, high colonisation ability, tolerance of 195 various types of disturbance) to persisters (5, long life cycles, low colonisation ability, few offspring, sensitivity to disturbance). The species belonging to the monhysterid family were 196 assigned to the C–P 2 class ("general opportunists") as advised by Bongers et al. (1995) and later 197 mentioned by Pape et al. (2013); no nematodes belonged to C-P class 1 ("enrichment 198 opportunists"). 199

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

202 **2.5. Statistical analysis**

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

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

Diversity was expressed in terms of the expected number of species in a sample, EG (51). The other diversity indices were calculated by means of Margalef's index (Margalef, 1968) for species richness (d), Pielou's index (Pielou, 1966) for species evenness (J'), and the Shannon– Wiener index (Shannon and Weaver, 1963) for species diversity (H' by using loge).

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

Analysis of collinearity was tested by means of draftsman plot and the associated standard 222 product moment correlation coefficients between all pairs of variables, and those with 223 correlations $r^2 > 0.9$ were omitted from the model. If distribution of residuals was skewed, natural 224 logarithm transformation was applied to the response variable until assumptions were met by the 225 best model. The relationships of taxonomic and functional traits with environmental variables 226 227 were examined by means of the BIOENV procedure (Clarke and Ainsworth, 1993), which calculates rank correlations between a similarity matrix derived from biological data and matrices 228 229 derived from the environmental variables, thereby defining a set of variables that 'best explain' the biotic structure. We performed RELATE and a stepwise distance-based linear model 230 231 permutation test (DistLM, McArdle and Anderson, 2001) to identify which set of environmental variables predicted the multivariate variation in nematode species assemblages. The adjusted R^2 232 233 was used as a selection criterion to permit the fitting of the best explanatory environmental variables in the model. Euclidean distance was used as the resemblance measure in all DISTLM
procedures. Results were visualised with a distance-based redundancy analysis (dbRDA)
(Anderson et al., 2008).

To identify the species that would characterise the three zones compared (shelf, slope, and 237 basin) we performed the Indicator Species Analysis or IndVal (Dufrêne and Legendre, 1997) 238 using multi-level pattern analysis (De Cáceres et al., 2010) in the R environment (R Development 239 Core Team, 2010) with the 'indicspecies' function. The statistical significance of the relationship 240 between the species and site was tested by means of Monte Carlo randomisations with 1000 241 242 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, 243 244 2010; Dimitriadou et al., 2011) and the PERMANOVA+ module of the PRIMER v6 software (Clarke and Gorley, 2006; Anderson et al., 2008). A schematic diagram was prepared from the 245 246 taxonomic and functional dataset that represented the pattern in the benthic zones of western Indian continental margin. 247

- 248
- 249 **3. Results**
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3.1. Environmental parameters

252 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 253 254 slope (1524 m), and basin were characterised by clayish silts. The salinity of the bottom water varied little, but temperature decreased with increasing depth. The bottom-water DO ranged from 255 0.08 to 2.3 ml 1^{-1} . The lowest near-bottom oxygen levels were recorded on the upper slope and 256 mid slope (0.08 and 0.28 ml 1⁻¹, respectively), defined as the OMZ. Oxygen values began to 257 increase at the lower slope. Higher values of DO were observed in the basin (Table 1). The core 258 of the OMZ was located at 525 m, where the lowest DO $(0.08 \text{ ml } l^{-1})$ value was recorded. 259

The OMZ was also characterised by higher values of sediment Chl-*a* and organic carbon (Table 1) than were the shelf and basin. A PCA ordination constructed from the eight environmental factors (DO, sediment chlorophyll, C_{org} , CaCO₃, C:N ratio, clay, silt, and sand; Fig. 2) showed that the first two components accounted for about 81% of the variability of the data (PC1 explained 43.5%, PC2 33.3%). Two shelf stations were characterised by high coarse sand and CaCO₃ content, whereas one (at depth 102 m) clustered mainly with the slope stations, largely because of higher organic-matter content, and was clearly separated from the others onthe basis of its higher silt content. Basin samples were characterised by higher DO level (Fig. 2).

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269 **3.2.** Nematode density and community structure

A total of 110 nematode species belonging to 24 families were found along the transect. Nematode density was higher at the shelf stations than on the slope or in the basin. The lowest average density was observed in the basin: 62.9 ± 2 ind/10 cm². The mean nematode density in the slope region was 124.3 ± 16 ind/10 cm², and the lowest density was observed on the lower slope (98.1 ind/10 cm²), whereas the upper slope station near the shelf was represented by a density of 155.2 ind/10 cm², but the mid slope density was 120.0 ind/10 cm². The highest average nematode density 176.6 \pm 37 ind/10 cm² was observed at shelf depth.

nMDS based on nematode species abundance (Bray-Curtis) and presence/absence data 277 illustrates clearly the extent to which the three zones differ (Fig. 3 and 4). The nMDS plot based 278 on the Bray-Curtis similarity measure indicated three groups of samples (Fig. 3). The largest 279 280 group included the slope stations and the deepest shelf station-those stations that form the OMZ. The PERMANOVA community results indicated significant differences between the three 281 282 zones (p = 0.03), but the nMDS based on presence/absence separated only the slope and basin. The stations on the shelf were distributed randomly (Fig. 4), and the PERMANOVA community 283 results confirmed nonsignificant differences between the zones (p = 0.12). In pair-wise 284 PERMANOVA, comparisons between shelf and deep basin nematode assemblages differ 285 286 significantly, p = 0.046, whereas the pairwise comparisons between slope and shelf and between 287 slope and basin were not significant (Table 2).

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

Only seven species were found exclusively in the OMZ: *Pselionema* sp 1, *Choanolaimus* sp 2, *Halichoanolaimus* sp 1, *Cobbia dentata*, *Daptonema* sp 1, *Trissonchulus* sp 1, and *Minolaimus* sp 1. Only nine species were found exclusively in the basin: *Acantholaimus* *calathus, Acantholaimus mirabilis, Sphaerolaimus* sp 1, *Subsphaerolaimus* sp 1, *Pierrickia* sp 2, *Sabatieria praedatrix, Epacanthion* sp 1, *Longicyatholaimus* sp 1, and *Oncholaimus attenuateus*.
The top 10 dominant species from OMZ and from the remaining areas are given in Table 4.

The IndVal index produced a list of indicator species for each group of sites: four genera 301 were indicative of the shelf area and five genera of the slope (Table 5). Viscosia viscosia (p =302 0.005; stat value = 0.751) was a good indicator of the shelf, whereas *Choanolaimus* sp 2 was 303 strongly and significantly (p = 0.005; stat value = 0.950) associated with the slope. 304 Acantholaimus mirabilis (p = 0.005; stat value = 1.000) was significantly associated with the 305 306 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 307 308 conditional probability or positive predictive value of the species and the conditional probability 309 of finding the species at sites belonging to any of the zones are shown in Table 5 for the relevant 310 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, 311 312 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 313 314 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.

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320 **3.3. Functional Traits**

321 Functional attributes of nematode communities in the Arabian Sea are listed in Tables 7 and 8. 322 The geographic separation was less pronounced in the ordinations derived from functional 323 characteristics of nematode communities, although the basin and slope samples were clumped into groups but shelf stations were randomly distributed (Fig. 5). As shown by the results of pair-324 325 wise PERMANOVA, three zones containing nematode assemblages (shelf vs deep basin; slope vs deep basin) differed significantly. Assemblages were dominated by deposit feeders (1B, 1A) 326 followed by predators (2B), whereas proportions of epigrowth feeders (2A) were comparatively 327 low (Table 7). The shelf area was dominated by non-selective deposit feeders (1B) and predators 328 329 (2B), whereas the slope stations showed the highest proportions (29–48%) of predators/omnivores (group 2B). Similarly the dominance of predators (2B) was seen in OMZ
stations, from 102 to 1001 m. The shelf and basin areas were dominated by deposit feeders
(mainly the non-selective 1B group).

Clavate and conical were the most prevalent tail shapes at the majority of stations (Table 333 334 7); the average proportion of conical tails was higher on the slope and at the OMZ stations (33– 49%). Clavate tails dominated at all stations, but slightly less on the slope and inside the OMZ 335 336 (1001 m) than on the shelf and in the basin area. Average adult lengths of nematodes ranged from 1 to 4 mm, and the majority of all recorded individuals occurred in the two intermediate length 337 338 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 339 340 was also dominated by these two length categories.

The majority of the nematodes were slender, although their proportion decreased with depth (from 82% in the shelf to 76% in the basin), whereas stout animals accounted for between 2 and 13%. Long/thin animals continuously decreased with increasing depth until the lower slope (at the core of OMZ), but they were more abundant (17–24%) in the basin than were those of slender or stout shape. Over 76% of all identified individuals attained a C-P score of 2 to 3. The shelf, slope, basin regions harbored mostly colonisers in the range of 2–3. Extreme persisters (C-P score of 5) and colonisers were completely absent (Table 8).

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

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

The schematic model represents the exact trend of each functional trait at each benthic zone. The relative abundance of each trait was plotted as an area graph, and a schematic figure was prepared to show the pattern according to the zones. For example, the shelf region favors the dominance of clavate tail shape, epigrowth feeding, slender body shape, and coloniser life style with length in the range of 1–2 mm. Similarly the OMZ shows a higher abundance of some traits, like round tail shape, stout body shape, 2–4 mm length, and greater prevalence of omnivores and deposit feeders. Coloniser life style (C-P 2–3) was more frequent, whereas persisters (C-P 4) decreased to lower numbers in the OMZ. In the basin, however, the sediment characteristics changed from silty sand to clay. Feeding habit and tail shape also differed in the basin (Fig. 6).

368 3.4. Influence of abiotic parameters on structure and function of the nematode community

The RELATE analyses indicated that patterns based on environmental variables were 369 370 significantly related to the patterns inherent in nematode community structure both taxonomically (r = 0.37, p = 0.01) and functionally (r = 0.41, p = 0.01). Results of BIOENV analyses revealed 371 372 several notable relationships of species abundance data and biological traits with environmental parameters. For example feeding types have the best correlation with Corg, sediment Chl-a, and 373 silt. Body size was well correlated with DO, clay, and Corg, whereas tail shape was correlated 374 with clay, DO, and silt, and body length with sand, clay, and C:N ratio. C-P score, however, was 375 376 significantly correlated with clay and DO (Table 10). Moreover in the case of species abundance data, bottom water DO, clay, and C_{org} were proved to be the best correlated (r = 0.712, p =0.02). 377 378 Of the 10 environmental parameters, 6 were retained for further analysis on the basis of collinearity analysis (Draftsman plot). Only 4 variables—salinity, temperature, water Chl-a, and 379 C:N ratio) with correlation r^2 values 0.9 (considered redundant) were omitted for the DISTLM 380 381 procedures; the remaining variables and their pair-wise spearman correlations are shown in Table 382 11.

Analyses with distance-based linear models (DistLM) indicated that the six abiotic 383 variables related to the variation in nematode community structure explained 97% of its total 384 385 variation, although not all variables were significant. Similarly for the functional traits of the eight variables, six were used by the DISTLM procedure to construct the best-fitting model, 386 together explaining 96% of total variation. The DistLM analysis allowed the identification of 387 those abiotic variables that were best correlated with the observed distribution patterns of 388 389 taxonomic and functional traits of nematode species (Table 11, 12). Results based on the abundance and presence/absence data were virtually identical; therefore, only the results based on 390 the abundance data and functional traits are reported. Variables such as the C_{org} and near-bottom 391 oxygen content showed the highest correlations (p < 0.05) with the nematode assemblages, 392 393 whereas the functional traits were mainly explained by total organic carbon input (p < 0.05). Figs 7, 8 show the DISTLM results by means of a dbRDA plot, with the species abundance and
biological traits superimposed. The vectors of the environmental variables retained by the
DISTLM procedure as fitting the best explanatory model indicate the important role of OC in the
slope area and Chl-*a* and sand in the shelf, whereas DO and clay were important in the basin.

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399 **4. Discussion**

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401 **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 1^{-1} . Nematode abundance was highest in the center of the OMZ (525 m) and decreased to its lowest value in the lower part of the OMZ (1001 m). Total metazoan meiofauna, and more specifically nematode densities, often reach maximum values at the lowest oxygen concentrations within OMZs (reviewed in Levin, 2003).

In our results, nematode densities were lower than those reported by Cook et al. (2000) 413 for the bathyal Oman margin (range: 494–2495 ind/10 cm²). Moreover they found the highest 414 abundances inside the OMZ (700 m) not in its center (400 m), but Levin et al. (1991) found the 415 highest densities of nematodes (190 ind/10 cm^2) in the center of the OMZ (at 745 m), where high 416 concentrations of organic carbon and pigments were found. In our study the combined OMZ 417 stations showed higher density than non-OMZ stations, perhaps as a result of the ability of some 418 species to tolerate low-oxygen conditions to take advantage of abundant food (Levin et al., 1991, 419 Cook et al., 2000). Although data do not exist to identify which, if any, of the factors shapes the 420 nematode community assemblages, we note that C_{org} ($r^2 = 0.734$, p < 0.05) and near-bottom 421 oxygen content showed the highest correlations $(r^2 = 0.464, p < 0.05)$. Similarly many previous 422 OMZ investigations have noted a correlation between food quality and meiofaunal abundance 423 and the absence of oxygen. For example, Cook et al. (2000) reported a strong positive correlation 424 425 between nematode density and food quality, measured as the hydrogen index, along a transect through the Oman margin OMZ. Meiofaunal densities were correlated only with sediment Chl-*a*,
and not with oxygen or other sediment parameters along a similar OMZ transect on a seamount
off Mexico (Levin et al., 1991).

Moreover, in general, nematode abundance did not follow any particular gradient though 429 it was lowest at the deep basin stations. Generally, depth can have a major influence on nematode 430 density (Soltwedel, 2000; Udalov et al., 2005). The pattern of quantitative distribution of 431 nematode abundance has been described for intertidal and upper subtidal (<50 m) zones. The 432 average world-wide nematode density is 1530 ind/10 cm^2 ; for continental slope (1000–2500 m) it 433 drops to 430 ind/10 cm², for lower slope (2500–3500 m) to 360 ind/10 cm², and for abyssal and 434 hadal depths (>5000 m) it is still lower (140 ind/10 cm²) (Soltwedel, et al., 2003; Mokievsky et 435 436 al., 2004). Large-scale comparisons of nematode community structure in other ocean basins indicate that continental-shelf nematode communities differ significantly from slope communities 437 (Vanreusel et al., 2010). 438

439 The nMDS based on nematode species abundance and presence-absence separated the 440 three zones, and the difference was confirmed by PERMANOVA (p = 0.03). Group 1 comprised the stations of the shelf region, with the exception of the deepest shelf station, which was grouped 441 442 with the slope area to form the OMZ stations, where opportunistic species such as *Pselionema* sp 1, Choanolaimus sp 2, Halichoanolaimus sp 1, Cobbia dentata, Daptonema sp 1, Trissonchulus 443 444 sp 1, and *Minolaimus* sp 1 were found. The exculsive presence of these species in the OMZ may be the result of OMZ sediments that favor the success of nematode species that are tolerant 445 446 (colonists) or adapted (endemics). In addition to the seven species found exclusively in the OMZ a number of species were found exclusively outside it. One might speculate that OMZs have 447 isolated hypoxia-tolerant nematode species as a result of their different life strategies, small size, 448 lower mobility, and lack of pelagic larval stage. Some species might therefore be able to tolerate 449 the oxygen minima while others cannot. The exact mechanisms of adaptation to or preferences of 450 species for the anoxic environment remains unclear, however. Several authors have pointed out 451 that nematode species can successfully cope with anoxic conditions by developing appropriate 452 453 physiological and behavioural mechanisms (e.g., symbiosis with bacteria, which we also observed, and migration to "oxygen islands," sensu Reise and Ax (1979) and Wetzel et al. 454 (1995). Mouthless and gutless nematodes carrying endosymbionts have been observed previously 455 456 in deep-sea environments (Ingels et al., 2011).

Our study did not reveal that nematode species have developed any obvious adaptations, 457 but they must have a certain tolerance for anoxic conditions. The dominant species in the OMZ, 458 like Terschellingia longicaudata, Desmodora sp 1, and Sphaerolaimus gracilis, have been 459 recognised extensively as tolerant (Schratzberger et al., 2006). Adaptations in *Terschellingia* sp 460 and *Sphaerolaimus* sp—the presence of dark, often multilayered intracellular globules in the 461 intestinal cells-are often pointed out as typical for sulphidic muds, but their significance is 462 463 ambiguous, and their adaptive value for the thiobiotic life rather disputed. Moreover, the deposition of insoluble metal sulphides in intracellular inclusions in Terschellingia longicaudata 464 465 has been suggested to be a mechanism of detoxification of sulfide (Nicholas et al., 1987). Further, some specimens belonging to the OMZ showed some morphological differences, 466 467 whereas others were observed to have epibionts, like the majority of specimens of *Desmodora* sp. Some species were observed to have unidentified blackish gut content. A small nematode was 468 469 found in the gut of *Metalinhomoeus* sp 1, which has a very small buccal cavity.

Even though the majority of the species identified in our study were common and 470 471 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 472 473 ecosystem monitoring and assessments because it expresses a value for species or genera that can characterise the particular environment (Dufrêne and Legendre, 1997). The genus Acantholaimus 474 475 (Acantholaimus mirabilis significantly associated with basin, p = 0.005) is quite typical of the 476 deep sea and is rarely found in shallow water; only one species has been described from intertidal 477 sediments (Platt and Zhang, 1982). The genus Acantholaimus increased in relative abundance 478 with increasing depth in many deep-sea areas (Soetaert and Heip, 1995). Moreover, Viscosia 479 viscosia was a good indicator of the shelf because it often inhabits the surface layers of sediment 480 and is apparently capable of floating (Fonsêca-Genevois et al., 2006).

The IndVal index reaches its maximum (100%) when individuals of the target species are observed at all the sites of one group and at no sites of any other (Dufrêne and Legendre, 1997). For those species that were found in equal proportions in each of the three zones, the association with the set of all the sites cannot be statistically tested, because no external group is available for comparison, so these species cannot be treated as indicators of a particular habitat but can be considered cosmopolitan.

487 Species diversity was higher on the shelf than on the slope or in the basin. This difference 488 appears to be partly due to the bottom-water DO gradient, which includes values that are below 489 the oxygen tolerance of many nematode species. Therefore very few species were present on the 490 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 491 influence on the species composition and diversity than do other oceanographic conditions 492 (Ingole et al., 2010). The species number and diversity were positively correlated to DO and 493 negatively correlated with Chl-a and Corg. Species diversity is not always correlated with the 494 495 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 496 497 organic loading. The lower species diversity of the nematode community under hypoxic conditions is accompanied by high dominance by a very few highly abundant species. Nematode 498 499 species especially from OMZs seem able to develop some functional adaptations, as they must 500 have a certain tolerance for sulphidic and/or anoxic conditions.

501

502 **4.2. Functional Traits**

503 Marine organisms are often challenged by fluctuations in the aquatic environment, which they 504 must survive, regulate, tolerate, or resist (Odiete, 1999). The different gradients of biological, 505 chemical, and physical properties in the aquatic environment complicate the situation. One major 506 challenge is the depletion of DO, but some organisms are able to cope by means of extreme 507 changes in their body morphology and physiology (Schneider and Bush-Brown, 2003). In our 508 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 slopearea (OMZ) stations, where predators/omnivores were most abundant. Epigrowth feeders were more abundant at lower shelf stations and at some stations of the OMZ region, probably because of the higher organic content of the sediment. OMZs often support mats of large sulfur-oxidising bacteria, including *Thioploca, Beggiatoa,* and *Thiomargarita*, which are often conspicuous features of the sediment surface there (Levin, 2003). These bacterial mats have been observed previously at the Oman margin (Levin et al., 1997).

Several previous workers have speculated that *Thioploca* mats represent a significant source of food for the OMZ faunas of the Peru–Chile margin (Gallardo, 1977, Arntz et al., 1991; Levin et al., 2000). Epigrowth feeders have been found to feed on microbiota by scraping them off solid surfaces or mucus threads with their teeth. Higher amounts of organic matter enriched the growth of diatoms and ciliates in the OMZ, which can contribute significantly to food for epigrowth feeders, but in general the proportion of predators/omnivores and epigrowth feeders was low in the our study. Gambi et al. (2003) suggested that the low prevalence of predatory and omnivorous nematodes can be attributed to the absence of freshly dead organisms provided they acquire large teeth and are capable of ingesting other animals.

The dominance of the deposit feeders in silty sediments of the basin is in agreement with 525 results from most previous deep-sea studies (Tietjen, 1984; Jensen, 1988; Netto et al., 2005). 526 527 Jensen (1988) found that the deep sea fauna in the Norwegian Sea was dominated by deposit feeders and included few predators and scavengers. Deposit feeders were also the dominant 528 529 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-530 531 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 532 533 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 534 feeding types were well correlated with Corg, sediment chlorophyll, and silt, which represent the 535 substratum condition and feeding content. 536

537 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 538 539 significantly correlated with sediment texture and Corg. Nematodes with clavate tail shape 540 dominated at each depth, although to a greater degree in the shelf and basin regions (Table 3). 541 Riemann (1974) considered this type of tail morphology to be typical of the inhabitants of the 542 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 543 544 fine sand and muddy sediments, where only an incomplete interstitial system exists. The 545 proportion of long-tail shape and round shape was much lower than that of the above-mentioned categories, but the scant availability of data on this aspect prevents comparison and any 546 generalised conclusion. 547

548 Vanhove et al. (1995) and Soetaert et al. (2002) noted that length and width are important 549 functional attributes for describing chemical stress, metabolic rate, the ability to move or migrate, 550 and vulnerability to predation. In fact, size of animals is an integrative feature strongly correlated 551 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.

554 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, 555 as was the case in earlier studies (Jensen, 1987). Pronounced body elongation in nematodes and 556 557 greater surface-volume ratio in thiobiotic species are adaptive characters related to low oxygen 558 partial pressure and epidermal uptake of dissolved organic matter (Jensen, 1987). Further, increased length under suboxic or anoxic conditions reflects increased mobility. The increasing 559 560 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 561 562 nematodes were even more abundant, suggesting the relationship with fine clay and silt 563 sediments where only an incomplete interstitial system exists. In general comparison, however, 564 the organisms inhabiting the oxygenated environments are found to be of a size and shape different from those of organisms from the OMZs (Schneider and Bush-Brown, 2003). 565

566 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). 567 568 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 569 570 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 571 572 feeders, which often score 3–4 on the C-P scale (Bongers et al., 1991). Bongers and Ferris (1999) 573 also distinguished two types of opportunists: enrichment and general opportunists. The genus 574 Monhystera (family Monhysteridae), which was represented by only two species (Diplolaimella 575 sp 1, Diplolaimelloides sp 1) in the present study were classified as C-P class 2 (general opportunist) (Bongers, 1990). 576

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 584 traits seems to be a more reliable approach for assessing the functional structure of nematode 585 586 communities than was relying on single functional groups (Schratzberger et al., 2007). Our schematic model presents the trait responses in different zones (Fig. 4). The outcome confirmed 587 that functional-trait analysis is of additional ecological importance, and the information captured 588 by the biological-trait matrix was not a simple reflection of the information contained in 589 590 taxonomy. Nematodes with different functional characteristics differ in their abilities to respond to environmental stresses and disturbance, thereby providing resilience to the community. 591 592 Environmental conditions thus influence the importance of functional complementarity in structuring communities (Hooper et al., 2005). 593

594

595 **4.3. Environmental parameters and their impact on the nematode community**

The Arabian-Sea OMZ spreads over 285,000 km² 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.

600 Results of BIOENV analysis revealed the best correlation between the functional trait and individual parameter, i.e., the importance of Corg, sediment chlorophyll, and silt content for 601 602 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 603 regime, and low DO (Snelgrove and Butman, 1994). Nematode assemblages were dominated by 604 605 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 606 607 spatial patterns of distribution of free-living nematodes in some habitats (Olafsson and Elmgren, 1997; Schratzberger et al., 2006). Body size was well correlated with DO, clay, and C_{org}, whereas 608 609 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 610 morphological characteristics of species. The highest values of sediment Corg on the slope are 611 probably due to the diverse topographic features there, and the associated hydrodynamic 612 processes play an important role in the enrichment of Corg (Rao and Veerayya, 2000). The 613 DistLM analysis indicated that DO concentration and organic content were the only parameters 614 615 that were significantly correlated with nematode species and functional data respectively.

617 **5.** Conclusions

618

Free-living nematodes are an abundant and diverse component of the meiofauna on the western 619 continental margin of the Arabian Sea. They follow the general trends of decreasing nematode 620 abundance and diversity with increasing depth observed among other benthic taxa along the 621 continental shelf and in the deep sea. We aimed to determine the nematode community structure 622 and functional traits in the Indian western continental margin, including the OMZ. The effects of 623 624 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 625 626 communities, the presence of the OMZ seems to be paramount. Along with organic content, DO 627 plays a vital role in structuring nematode communities and certain functional adaptations among 628 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 629 630 zones. Our results support the previous finding that nematodes are the taxon most tolerant of environmental variation but that within the nematode community only a few species can tolerate 631 632 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 633 634 whether this pattern is broadly applicable.

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- 967 off northern Namibia, Mar. Biol., 156, 1949–1961, 2009.

969 Table 1. Locations and depths of sampling stations and sediment texture.

Depth	34	48	102	525	1001	1524	2001	2546
Lat(°N)	13°54.26'	13°59.88'	14°00.29'	14°00.24'	14°00.25'	14°00.30'	14°00.09'	13°59.55'
Long(°E)	74°18.97'	74°00.03'	73°29.94'	73°13.97'	73°08.11'	72°57.22'	71°13.21'	70°48.40'
Temperature, °C	23.2	20.84	18	10.7	7.85	5	_	_
Salinity (psu)	35.8	35.5	35.1	35.3	35.2	35	_	_
DO, ml l ⁻¹	0.69	0.56	0.38	0.08	0.28	1.35	2.3	2.3
Sediment Chl-– µg-1	1.4	0.2	0.6	0.7	2.1	0.6	0.6	0.2
C _{org} (%)	1.9	0.8	1.5	3.8	4.4	2.2	0.3	0.9
C:N	11.0	-	10.3	10.8	8.9	8.2	4.6	4.9
Clay (%)	8.3	9.8	3.0	12.9	13.2	8.7	15.1	15.6
Silt (%)	75.6	39.7	38.5	53.6	84.5	89.4	79.2	71.7
Sand (%)	16.0	50.5	58.5	33.5	2.3	1.9	5.7	12.7
Texture	Clayey silt	Silty sand	Silty sand	Sandy silt	Clayey silt	Clayey silt	Clayey silt	Clayey silt
CaCO ₃	26.8	69.2	65.1	44.5	28.3	24.5	49.3	53.7
970								

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

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

975 resemblance was calculated according to Bray-Curtis. The values indicate differences significant

976 at p < 0.05.

	Groups	t	P(perm)	Unique	P(MC)
	Ĩ		ú /	perms	978
Taxonomic	Shelf vs slope	1.7529	0.317	3	0.264
	Shelf vs Deep	3.3538	0.332	3	0 . 04 6 79
	basin				
	Slope vs Deep	6.0733	0.352	3	0.06980
	basin				
Functional trai	its				981
	Shelf vs slope	2.2523	0.346	3	0.181
	Shelf vs Deep	5.0419	0.354	3	0.013^{982}
	basin				092
	Slope vs Deep	18.508	0.342	3	0.028
	basin				984

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989

Table 3. Average relative abundances (%) of the most abundant species belonging to each of

three benthic zones. Only the top five dominant species from each zone are presented.

992

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

993

Table 4. The 10 most abundant species recorded from the oxygen minimum zone (OMZ) andfrom 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	8.3			
		heterospiculum				
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			

1002 Table 5. List of indicator species calculated by IndVal index, number of genera associated with

1003 the shelf group = 4, number of genera associated to slope groups = 5, number of genera

1004 associated with the basin = 7.

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

1005

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

				1011
Zone	d	J'	ES(51)	H'(loge)
				1012
Shelf	13.53 ± 1.53	0.98 ± 0.01	40.54 ± 2.57	4.04 ± 01003
				1014
Slope	7.89 ± 0.51	0.98 ± 0.01	31.69 ± 1.24	3.56 ± 0.06
				1015
Basin	7.49 ± 0.11	0.97 ± 0.0	28.16 ± 0.22	3.48 ± 0.01

Table 7. Functional trait matrix showing the percentages of all individuals belonging to four
nematode feeding categories (1A, no buccal cavity or a fine tubular one, selective deposit
(bacterial) feeders; 1B, large but unarmed buccal cavity, non-selective deposit feeders; 2A,
buccal cavity with scraping tooth or teeth, epigrowth (diatom) feeders; 2B, buccal cavity with
large jaws, predators/omnivores) and four tail-shape categories.

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

Table 8. Functional trait matrix showing the percentages of all individuals belonging to four
body-length categories, three body-shape categories, and five life-history strategies (coloniser-

1026 persister score).

Depth	<1	1–2	2–4	>4	Slender	Stout	Long/thin	1	2	3	4	5
	mm	mm	mm	mm								
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

	Zones			Buccal morphologyTail shapeA					Adult Length			Adult shape		Life history							
											(mm)						(c-p	(c-p score)			
Species	Shelf	Slope	Basin	1A	1B	2A	2B	R	E/F	CO	CA	>1	1-2	2-4	>4	ST	SL	L/T	2	3	4
	(%)	(%)	(%)																		
Acantholaimus	0.11	0.00	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
calathus																					
Acantholaimus	0.19	0.23	1.11	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
elegans																					
Acantholaimus	0.15	0.15	0.19	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
filicaudatus																					
Acantholaimus	0.31	0.00	0.00	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
mirabilis																					
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	0.69	0.69	0.50	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
blanchardi																					
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	0.11	0.00	0.38	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1
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	0.46	0.00	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
yunfengi																					
Cermonema	0.23	0.04	0.00	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
attenuatum																					
Cheironchus sp 1	0.23	0.00	0.00	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0
Choanolaimus sp 2	0.04	0.38	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Chromadora sp 1	0.23	0.34	0.00	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0
Chromadorita sp 1	0.19	0.65	0.00	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0
Chromadorita sp 2	2.78	0.19	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Cobbia dentata	0.72	0.38	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 1	0.34	0.00	0.00	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 3	0.72	0.04	0.04	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Cobbia sp 2	0.23	0.11	0.00	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Dagda sp 1	0.31	0.00	0.27	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Daptonema circulum	0.84	0.31	0.53	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Daptonema sp 1	0.72	1.14	0.00	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Daptonema sp 2	1.56	0.00	0.00	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Desmodora sp 1	0.88	4.42	0.38	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0

Desmoscolex sp 1	1.30	0.00	0.00	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
<i>Diplolaimella</i> 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	0.04	0.04	0.00	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
1																					
Dolicholaimus sp 1	0.50	0.00	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0
Doliolaimus sp 1	0.00	0.00	0.11	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Dorylaimopsis sp 1	0.15	0.00	0.00	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Dorylaimopsis sp 2	0.15	0.46	0.00	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Epacanthion sp 1	0.00	0.00	0.31	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0
Gammanema sp 1	0.08	0.00	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Halalaimus gracilis	0.38	0.00	0.08	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Halalaimus sp 1	0.00	0.50	1.11	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Halalaimus sp 2	0.00	0.23	0.53	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Halalaimus sp 2	0.00	0.19	0.42	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1
Halanonchus sp 1	0.23	0.00	0.00	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Halichoanolaimus	0.00	0.00	0.11	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0
chordiurus																					
Halichoanolaimus	0.95	1.60	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
robustus																					
Halichoanolaimus sp	0.08	2.10	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
1																					
Halichoanolaimus sp	0.11	0.00	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
2																					
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	0.00	0.00	0.50	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0
1																					
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	0.08	0.00	0.50	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0
longiseta																					
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	0.00	0.00	0.38	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
sp 1																					
Metasphaerolaimus	1.33	0.04	0.27	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
sp 2																					
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	0.00	0.00	0.34	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
attenuatus																					
Oncholaimus	0.11	0.00	0.00	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1
mediterraneus																					
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
filiformis																					

Paralinhomoeus	0.34	0.84	0.00	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0
lepturus																					
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	1.45	0.92	0.00	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
sp 1																					
Pierickia sp 1	0.23	0.00	0.00	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Pierrickia sp 2	0.00	0.00	0.11	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Prooncholaimus sp 1	0.69	0.00	0.00	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Pselionema	0.46	1.26	0.00	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
hexalatum																					
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	0.00	0.00	0.11	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0
praedatrix																					
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	1.11	0.88	0.38	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0
ewensis																					
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	0.15	0.00	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
balticus																					
Sphaerolaimus	2.21	2.36	0.00	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
gracilis																					
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	0.00	0.00	0.08	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
1																					
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	1.18	4.73	0.04	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
longicaudata																					
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	1.98	0.00	0.08	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
heterospiculum																					
Theristus	0.92	0.00	0.00	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0
interstitialis																					
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

1032 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epigrowth feeders, 2B = predators (Wieser, 1953). R = round. E/F

1033 = elongated/filiform, CO = conical, CA = clavate. ST = stout, L/T = long/thin, C-P = coloniser-persister score (Bongers et al., 1991,

1034 1995; Pape et al., 2013), 1 = species exhibiting trait, 0 = species not exhibiting trait.

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

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

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

Marginal tests							
Variable	SS(trace)	Pseudo-F	Р	Prop.			
DO, mll-1	321.67	23.209	0.068	0.27892			
Chl aµg-1	179.35	11.049	0.362	0.15552			
Corg (%)	399.65	31.819	0.008	0.34654			
Clay (%)	168.03	10.233	0.391	0.14571			
Silt (%)	121.46	0.70635	0.606	0.10532			
Sand (%)	164.27	0.99661	0.426	0.14244			
Sequential tests							
Variable	R^2	SS(trace)	Pseudo-F	Р	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

1060 Table 12. Result of distance-based linear model (DistLM) analyses showing the influence of

- 1061 environmental parameters on nematode species functional biological traits (Bray-Curtis similarity
- 1062 of square-root-transformed abundance.

Marginal tests							
Variable	SS(trace)	Pseudo-F	Р	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	Р	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





1074 Figure 1. Map showing locations of the 8 sampling stations (circles) on the coast of the Arabian

1075 Sea along with depth contours and the positions of the sampling stations.





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





1092 Figure 3. nMDS ordination based on nematode species abundance according to the Bray–Curtis

- 1093 similarity index.
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- 1121 Figure 5. nMDS ordination based on nematode species biological traits according to the Bray-
- 1122 Curtis similarity index.



- 1136 Figure 6. Schematic model of the functional traits in each benthic zone.





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





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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 vectors (strength and direction of effect of the variable on the ordination plot). Axis legends include percentage of variation explained by the fitted model and percentage of total variation explained by the axis.

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