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Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazaré Canyon, Western Iberian Margin

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ABSTRACT

Samples collected in the deep Nazaré Canyon and at the adjacent slope, during the HERMES RRS Discovery D297 cruise (2005), were analysed for metazoan meiofauna, nematode structure and diversity and its relation to quality and quantity of sedimentary organic material. The amount and quality of organic matter available for direct consumption was much higher in the canyon compared to the slope and positively correlated with high nematode abundances (795–1171 ind. 10 cm⁻²) and biomass (93.2–343.5 µg dry weight 10 cm⁻²), thus leading to higher standing stocks. Canyon nematode assemblages also showed particular adaptations (e.g. higher trophic complexity, variability of nematode morphology, and presence of opportunistic genera) to canyon conditions, particularly in the deeper sediment layers. The Nazaré Canyon's nematode diversity was slightly lower than that of the adjacent slope and its assemblages were characterised by a higher dominance of certain genera. Still, the canyon contributes considerably to total Western Iberian Margin diversity due to different assemblages present compared to the slope. Furthermore, the harsh conditions in terms of hydrodynamic disturbance and the high organic matter flux are likely to have a negative impact on the establishment of species rich meiobenthic communities, especially in the canyon axis.

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1. Introduction

Submarine canyons are deep, narrow fissures that cut into the continental shelf and slope (Shepard and Dill, 1966) and represent some of the most pervasive structures that shape the present morphology of many continental margins (Mulder et al., 2004). However, these impressive features have remained one of the most difficult environments to study in the deep sea because

of their narrow sinuous structure, instability and often vigorous internal currents with a reversal of up- and down-canyon flow (Shepard et al., 1974a,b; Shepard and Dill, 1977; Quaresma et al., 2007). Submarine canyons are important, preferential conduits for the transport of sediment and organic carbon (OC) from shelf depths to the deep sea (e.g. Gardner, 1989; Durrieu de Madron, 1994; Puig and Palanques, 1998; Schmidt et al., 2001; Palanques et al., 2005a), but can also act as traps for carbon (Oliveira et al., 2007; Arzola et al., 2008). While canyon heads with steep sloped walls are known to gather inflowing organic matter (OM), the canyon axes are active zones for channelling and transporting the OM down-canyon by means of bottom nepheloid layers, gravity flows, and turbidity currents (Buscail and Germain, 1997;

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van Weering et al., 2002; Canals et al., 2006; de Stigter et al., 2007; Garcia et al., 2008). This makes submarine canyons favourable sites for the concentration and accumulation of sediments (Thorbjarnarson et al., 1986; Schmidt et al., 2001), with episodic release of these sediments to the abyssal plain, and important in budgeting carbon sinks and sources (Thomsen et al., 2002; Accornero et al., 2003).

Despite the increasing number of studies, questions as to the nature and fate of OM transported through canyons remain, i.e. its origin and utilisation by the resident fauna. Remains of macroalgae from near-shore growth are transported to canyon heads by longshore transport enriching the canyon system (Kiriakoulakis and Wolff, 2007). This OM enrichment can lead to enhanced (in)faunal density and biomass (Rowe et al., 1982; Soetaert et al., 1991; Vetter and Dayton, 1998, 1999; Palanques et al., 2005b) and increased sediment community oxygen consumption rates (Duineveld et al., 2001; Accornero et al., 2003). Enhanced burial of OC in canyon sediments suggests that the settled and reworked OM is no longer biologically labile. However, higher C/N ratios in canyon sediments relative to the open slope indicate that there can be an elevated contribution of terrestrial/riverine material to these sediments (Frignani et al., 2002; Schmiiedl et al., 2004; Heussner et al., 2006). Conversely, sediments in canyons that are not directly associated with a river system, can be enriched in labile phytodetrital OM, possibly as a result of transport through the canyon (Duineveld et al., 2001). Thus there is variability in the processes that control OM transport and fate in sea-floor canyon sediments, and part of the shelf/slope productivity may also be concentrated here.

In general, meiobenthos densities, biomass, and metabolic activity are positively correlated with the present levels and lability of OM reaching the deep-sea floor (e.g. Danovaro et al., 1995; Soltwedel, 1997; Pfannkuche et al., 1999; Lampadariou and Tselepidis, 2006), suggesting that meiofauna plays an important role in the transfer of OM within benthic food webs (Coull and Bell, 1979; Graf, 1989). In canyons, where a high influx of OM has been observed, meiobenthos might play an even more important role in the benthic community. Unfortunately, knowledge of the contribution of nematodes to total deep-sea sediment community activity is sparse and non-existent in the case for canyons. However, data suggest that nematodes are important contributors in the deep-sea carbon remineralisation process (Soetaert et al., 1997). There are a number of studies on canyon-associated meiobenthos (Vitiello, 1976; Vivier, 1978a, b; Soetaert et al., 1991; de Bovee and Labat, 1993; Soetaert and Heip, 1995; Soltwedel, 2000; Grémare et al., 2002; Accornero et al., 2003; Schmiiedl et al., 2004; Van Gaever et al., 2009), but few have concentrated on canyon sites deeper than 2000 m (de Bovee et al., 1990; Soltwedel et al., 2005; Garcia et al., 2007; Koho et al., 2007). Previous studies of the Nazaré Canyon have failed to include the 3400–4300 m depth; inclusion of this area will provide better insight into the structure of meiofauna communities in the deeper canyon with variable sedimentation rates and lower hydrographic activity

compared to the very active shallower canyon. This depth range features the middle part of the Nazaré Canyon (2700–4000 m; de Stigter et al., 2007), which is characterised by anomalously high sedimentation rates (Arzola et al., 2008) and a relatively active hydrographic regime compared to deeper sites. It also comprises the transition to the deeper canyon (>4000 m; de Stigter et al., 2007), which is relatively inactive in terms of sediment transport and functions as a sediment deposition centre compared to the upper canyon, where vigorous internal tides result in sediment resuspension and transport on a semi-diurnal time scale (de Stigter et al., 2007; Arzola et al., 2008).

The present work aims to characterise nematode community structure, function and diversity within the metazoan meiobenthic community at the deeper end of the Nazaré Canyon, in comparison with the adjacent slope. Also the potential effect of the quantity and 'freshness' of sedimentary OM on meiobenthos, and particularly nematode diversity, is assessed and nematode community adaptations to the canyon's harsh and variable environmental conditions are investigated.

2. Material and methods

2.1. Sampling and sampling area

The Western Iberian Margin is characterised by a narrow shelf adjacent to a steep irregular slope and is cut by various canyons. The shelf hydrodynamics in this area exhibit a seasonal pattern modulated by intense winds: strong northerly winds induce summer upwelling at the shelf edge and south-westerly winds in winter establish a downwelling regime over the shelf (Vitorino et al., 2002; Quaresma et al., 2007). The largest of the Western Iberian Margin Canyons, the Nazaré Canyon, intersects the entire continental shelf (the canyon head opens 500 m from Nazaré beach, Vanney and Mougnot, 1981) and its entrenched bedding on the shelf acts as a temporary catchment area and sediment trap for material, which is transported over the shelf, until it is flushed to the deep sea (de Stigter et al., 2007; Oliveira et al., 2007).

During the HERMES RRS *Discovery* D297 cruise (Weaver, 2005) to the Portuguese canyons, meiofauna samples were taken using a multicorer (MUC; Barnett et al., 1984) and a megacorer (MGC, Ocean Scientific International Ltd), yielding virtually undisturbed sediment samples. The MUC was equipped with 12 core tubes with an internal diameter of 57 mm, equivalent to a 25.5 cm² cross-sectional area. The MGC was fitted with 60-mm-diameter cores, cross-sectional area 28.3 cm². Two stations in the Nazaré Canyon were sampled at ca. 3400 and 4300 m depth (station CM and CD, respectively) as well as two open continental slope reference sites at similar depths (station SM and SD, respectively), lying north of the Nazaré Canyon (Table 1, Fig. 1). Station CM in the Nazaré canyon was situated in the middle part of the canyon on a sediment-draped, terraced slope next to the V-shaped axial channel (*thalweg*). It is characterised by extremely

Table 1

Detailed information per sediment slice for every station analysed in this study.

Station & sampling	Latitude (°N)	Longitude (°W)	Depth (m)	Sediment depth (cm)	Clay (vol%)	Silt (vol%)	Sand (vol%)	TC (%)	TOC (%)	TN (%)	CPE (µg/g)	Chl <i>a</i> (µg/g)	C:N	Chl <i>a</i> :phaeopigment
Canyon deep (CD)	39° 34.80'	10° 18.60'	4335–4340	0–1	10.63	68.42	20.95	3.03	1.68	0.15	1.14	0.11	12.7	0.10
				1–2	11.00	63.07	25.93	2.64	1.37	0.13	0.94	0.09	12.3	0.11
				2–3	10.93	64.90	24.17	2.37	1.12	0.10	0.73	0.06	13.4	0.08
				3–4	11.17	55.17	33.67	2.76	1.66	0.16	0.49	0.03	12.3	0.06
				4–5	8.67	50.27	41.07	2.90	1.34	0.14	0.58	0.04	11.0	0.08
Canyon middle (CM)	39° 30.00'	09° 56.22'	3425–3453	0–1	12.17	78.62	9.22	3.70	1.64	0.23	1.70	0.13	8.4	0.08
				1–2	12.63	77.43	9.94	3.58	1.69	0.20	1.76	0.13	9.7	0.08
				2–3	13.53	76.16	10.31	3.58	1.70	0.22	1.79	0.12	9.0	0.07
				3–4	12.70	76.95	10.35	3.54	1.57	0.22	2.08	0.16	8.5	0.08
				4–5	11.93	76.89	11.18	3.58	1.59	0.21	1.80	0.12	8.9	0.07
Slope deep (SD)	40° 04.38'	10° 21.90'	4275–4277	0–1	22.35	71.24	6.41	5.62	0.67	0.11	0.25	0.02	6.9	0.10
				1–2	23.20	71.55	5.25	5.54	0.61	0.11	0.04	0.00	6.6	0.00
				2–3	22.93	70.86	6.20	5.42	0.64	0.12	0.03	0.00	6.5	0.00
				3–4	22.00	69.80	8.20	5.49	0.65	0.11	0.02	0.00	6.8	0.00
				4–5	23.33	70.91	5.76	5.55	0.66	0.12	0.03	0.00	6.6	0.00
Slope middle (SM)	40° 35.70'	10° 22.08'	3400–3403	0–1	21.85	69.98	8.17	6.86	0.76	0.11	0.46	0.02	8.1	0.05
				1–2	20.83	69.70	9.46	6.68	0.61	0.10	0.05	0.00	6.9	0.02
				2–3	21.37	66.78	11.85	6.69	0.62	0.12	0.04	0.00	6.3	0.02
				3–4	21.97	69.60	8.43	6.86	0.63	0.11	0.07	0.00	6.6	0.01
				4–5	24.47	64.75	10.79	6.70	0.58	0.10	0.04	0.00	6.6	0.00

MUC: Multicorer; MGC: Megacorer; sediment fractions (0.4–800 µm) classified according to [Wentworth \(1922\)](#); total carbon (TC), total organic carbon (TOC), total nitrogen (TN), chloroplastic pigment equivalents (CPE), chlorophyll *a* (Chl *a*), molar carbon:nitrogen (C:N) ratio based on TOC and TN (C:N), chlorophyll *a*: phaeopigment ratio (chl *a*:phaeopigment).

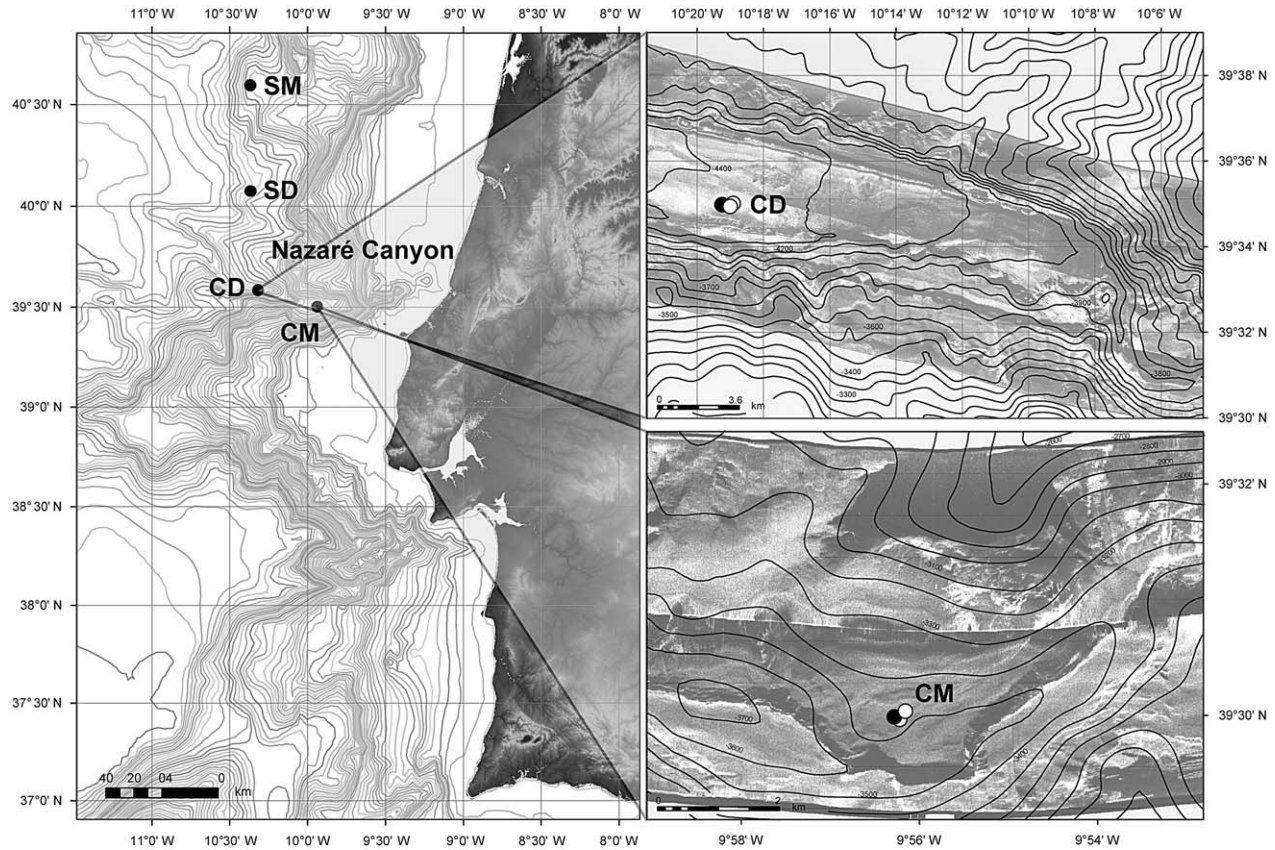


Fig. 1. Left: Overview of the Western Iberian Margin with sampling stations (SM: 3400 m slope station, SD: 4300 m slope station, CM: 3400 m canyon station, CD: 4300 m canyon station). Right: Two detailed maps presenting the local geomorphological setting of the Nazaré Canyon sample stations CM and CD, adapted from Weaver (2005) (Bathymetry data compiled from a variety of sources, courtesy NOCS and Instituto Hydrografico, Lisbon; 30 kHz TOBI sidescan sonar data, courtesy NOCS; both data sets published by Lastras et al. (2009); ○: MUC deployments; ●: MGC deployments).

high sediment accumulation rates (Arzola et al., 2008) and an active hydrographic regime (de Stigter et al., 2007). The CD site was situated in the flat-floored lower canyon valley which descends gently from 4000 to 5000 m depth and widens gradually into the Iberia Abyssal Plain. The lower end of the canyon is presently relatively inactive in terms of sediment transport, but intermittent mass sedimentation events occur on a yearly or longer time-scale (de Stigter et al., 2007).

2.2. Environmental variables

Three replicate cores per sampling site were taken for granulometry and geochemical analyses and analysed every cm down to 5 cm sediment depth. Grain-size distribution of the 4- to 800- μm sediment fraction was measured using a Coulter Counter LS 100TM Particle Size Analyzer and classified according to Wentworth (1922). Replicate sediment samples (3 and 2 replicates for station CD and CM, respectively, and 3 replicates for all slope stations) from the same deployments were used to determine total organic carbon (TOC) and total nitrogen (TN). Samples for TOC analyses were acidified according to the acid vapour method of Yamamuro and Kayanne (1995); TN in these samples was determined without acidification. These analyses were carried out using a CE Instruments NC 2500 CHN analyser in duplicate (mean value quoted here; all values were within 10% of the mean). Chloroplast Pigment Equivalents (CPE, which is the sum of chlorophyll *a* (chl *a*) and its degradation products (phaeopigments); Thiel, 1978) were analysed to estimate the amount of OM in the sediment that is derived from primary production. After freeze-drying and homogenization of the sediment samples the pigments were extracted in 90% acetone, separated using reverse phase HPLC, and measured with a Gilson fluorescence detector according to Wright and Jeffrey (1997). The ratio chl *a*:phaeopigments was used as a measure of 'freshness' of the photosynthetically derived OM in the sediments.

2.3. Meiofauna and nematode analysis

At all stations, three replicate sediment samples were sliced every cm down to 5 cm sediment depth and fixed in buffered 4% formalin. In the laboratory, samples were passed through a 1000- μm mesh and then sieved on a 32- μm mesh to retrieve the meiofauna, which were separated from any surrounding sediment by the standard centrifugation-flotation technique using the colloidal silica polymer LUDOX TM 40 (Heip et al., 1985; Vincx, 1996). After staining with Rose Bengal, all metazoan meiobenthic organisms were classified at higher taxon level (following Higgins and Thiel, 1988) and counted under a stereomicroscope; 100–150 nematodes were picked out randomly from each slice of each replicate sample, then transferred using the formalin-ethanol-glycerol technique of Seinhorst (1959) and Vincx (1996) and mounted on Cobb slides (Cobb, 1917). Nematodes (3 replicates for the 0–1 cm slice, 1 replicate for all deeper slices) were

identified to genus level using the pictorial key to nematode genera of Platt and Warwick (1983), relevant taxonomic literature from the nematode library of Ghent University, and the NeMys database (Deprez et al., 2005, www.nemys.ugent.be), a generic biological information system that provides online nematode identification keys. All identified individuals were grouped into four feeding type groups (selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A), and predators/scavengers (2B)) following Wieser (1953). Length (excluding filiform tail tips) and maximal width were measured using a Leitz dialux 20 compound microscope and Quantimet 500 image analysis software. Nematode dimensions were used to estimate biomass using Andrassy's formula (Andrassy, 1956), a dry-to-wet ratio of 0.25 was assumed (Heip et al., 1985) to calculate nematode dry weight (dwt), and Jensen's (1984) conversion factor of 12.4% was used to translate nematode wet weight (wwt) into carbon weight to compare with literature values.

2.4. Data analysis

As measures for nematode diversity and evenness at generic level we calculated Hill (1973) numbers (H_0 , H_1 , H_2 and H_∞) because they are variably dependent on sample size (i.e. with increasing order they become less sensitive to the rare, more sensitive to the more abundant genera) and reflect both evenness as well as genus richness (Heip et al., 1998). We used the notation H for Hill's indices as suggested by Heip et al. (1998). In addition, Pielou (1969) evenness measure was calculated as well as the Shannon-Wiener diversity index H' (Krebs, 1989) and the expected number of genera for 51 individuals (EG(51); Hurlbert, 1971) to enable comparison with other studies. To investigate trophic diversity of the nematode assemblages, the trophic diversity index was calculated according to Heip et al. (1988).

All analyses, apart from correlations, were performed using PRIMER v6 software (Clarke and Gorley, 2006). A multi-variate Principal Component (PCA) analysis was used to display the variability of our samples based on environmental parameters. Environmental data were checked for normality and uniformity and consequently $\log(0.1+X)$ transformed and normalised (subtracting the mean and dividing by the standard deviation, for each variable) before analysis. All nematode assemblage data were standardised and $\log(1+X)$ transformed prior to analysis except for the calculation of diversity and evenness indices. The non-metric multi-dimensional scaling (MDS) technique served to visualise the samples based on Bray-Curtis similarity values for generic assemblages. The ANOSIM function (Analysis of Similarities using Bray-Curtis similarity measures) was explored to test differences between slices, stations, habitat and depth. Firstly, three one-way ANOSIMs were performed, using only the 0–1 cm replicates, to test for station, habitat, and depth differences. Secondly, an ANOSIM test for a non-replicated two-way layout was calculated to infer whether there were among-station slice differences

and station differences across all slice groups. This double across-group analysis is useful in testing if the differences between the non-replicated slice samples for each station are responsible for the differences observed between stations. A one-way SIMPER analysis (Similarity Percentages – species contributions) was performed on station data to indicate which genera are mainly responsible for similarity in the canyon and slope and for dissimilarity between both habitats. The SIMPER analysis incorporated abundance differences between slices before summation of the slices per station and the data were consequently standardised and $\log(X+1)$ transformed. To investigate whether the environmental patterns correspond with those inferred from the nematode genera assemblages and to define which variables correspond best, RELATE and BEST (Bio-Env) routines were used. The RELATE technique calculates a Spearman's ρ rank correlation coefficient between all elements of the nematode assemblage and environmental variable resemblance matrices, followed by a permutation test. The BEST routine then searches for an environmental variable set that maximises ρ , which is obtained by computing the among-sample distances of each subset of variables and correlated with the nematode assemblage similarities.

Non-parametric Kendall tau statistics were used to investigate correlations between the geochemical variables and nematode abundance and biomass using Statistica 5.5.

3. Results

3.1. Sediment characteristics

Sediment characteristics are summarised in Table 1 and shown in Figs. 2 and 3. The canyon sediments were predominantly muddy with high silt content (50–79%). At station CD we found increased levels of sand (21–41%) and reduced silt content especially towards the deeper layers (3–5 cm depth) compared to the (sub-)surface layers (0–3 cm, Table 1). At station CM the granulometric distribution was consistent throughout the vertical profile with very high silt-clay content (89–91%) and low sand content (9–11%). At the slope stations, grain size was slightly finer (more clay). A slightly lower sand fraction was also noticeable at station SD (5–8%) compared to station SM (8–12%).

The canyon sediments were enriched in TOC, TN, and CPE compared to the open slope equivalents (Figs. 2 and 3). Also the 'freshness' (chl *a*:phaeopigment) of the phytodetrital OM was highest in the canyon (Fig. 3). Highest TOC, TN, and CPE values were measured at station CM whilst highest chl *a*:phaeopigment ratios were measured in the upper surface layers at station CD (0–3 cm). Contrary to the open slope, the deeper sediment layers in the canyon showed a clear CPE enrichment. A similar trend was found for the 'freshness' of the phytodetritus: below one cm sediment depth a steep

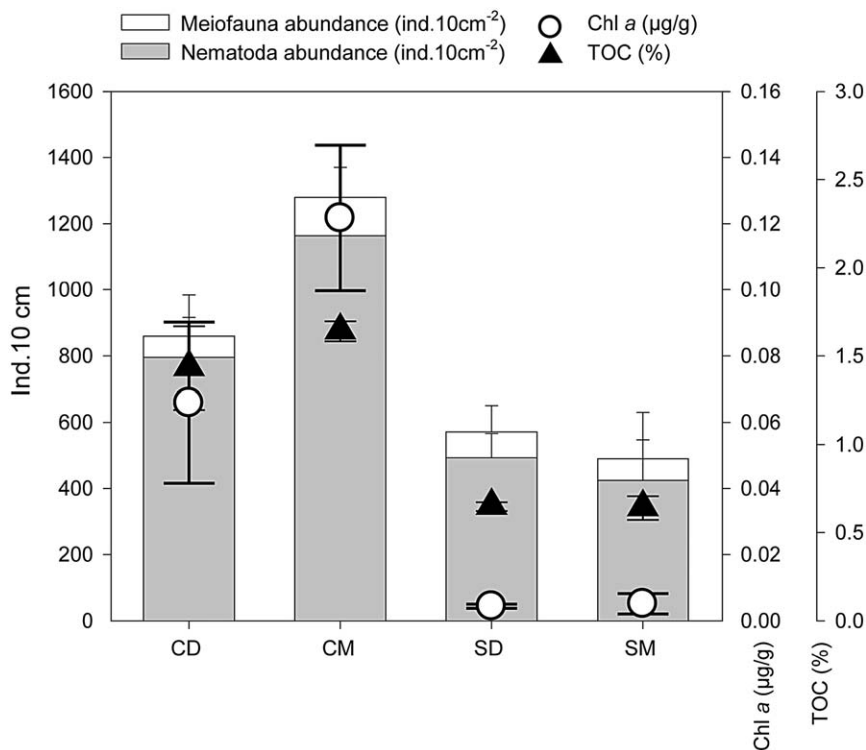


Fig. 2. Meiofauna and nematode abundances for all stations, including chl *a* and TOC content of the sediments (0–5 cm sediment depth, average over replicates, error bars show standard deviation). CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle, chl *a*: sedimentary chlorophyll *a*, TOC: sedimentary total organic carbon, ind.: individuals.

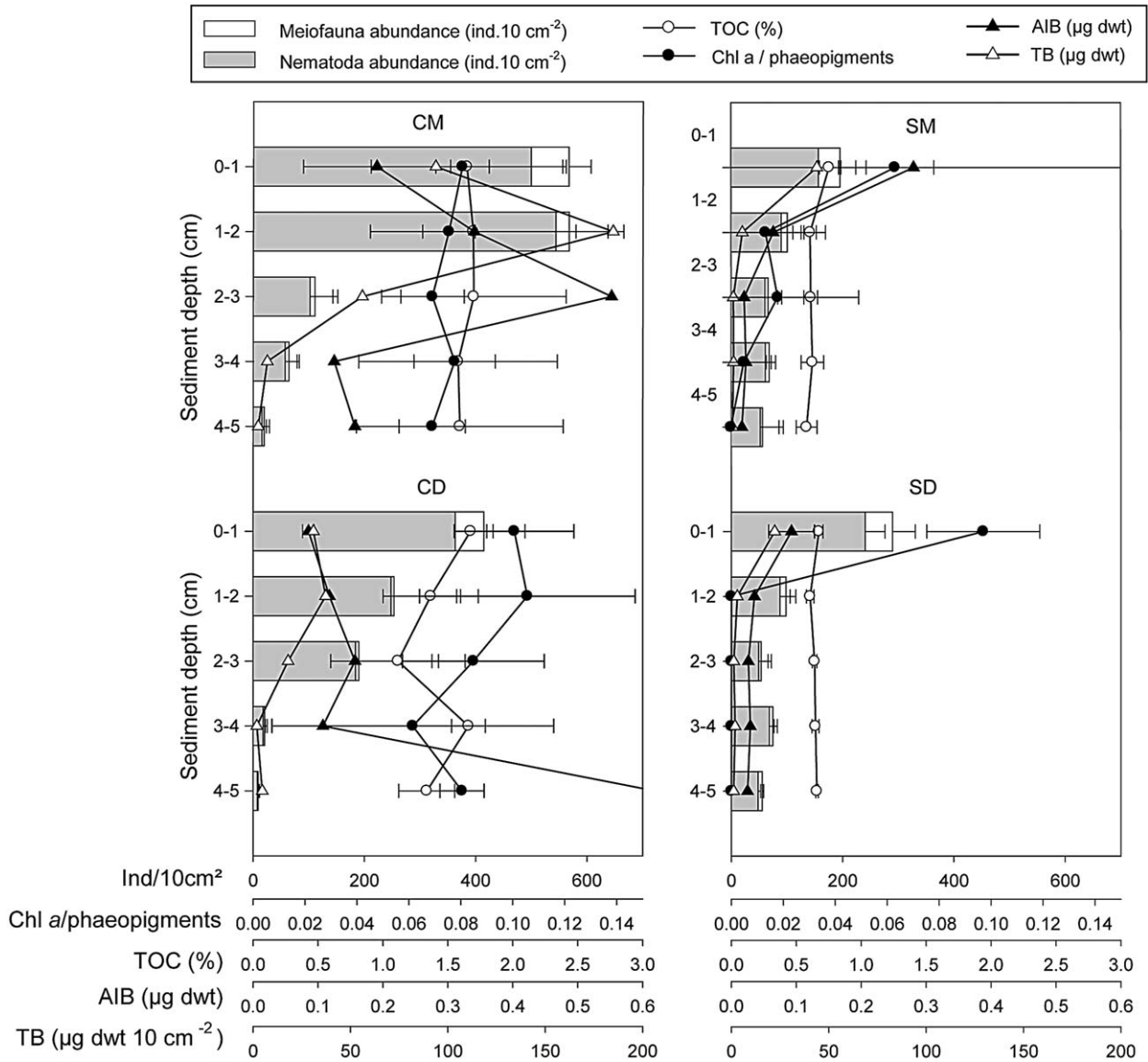


Fig. 3. Meiofauna and nematode abundances along the vertical profile. Superimposed are values for total organic carbon (TOC, %), chl *a*/phaeopigments, nematode average individual dryweight biomass (AIB, µg dryweight (dwt)), and nematode biomass 10 cm⁻² (TB, µg dryweight (dwt)). Scales were made uniform for better comparison. CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle, ind.: individuals.

decline of ‘freshness’ was observed at the slope while at the canyon ‘fresher’ material was present along the complete vertical profile (Fig. 3). Molar C:N ratio values were higher in the Nazaré Canyon compared to the open slope samples, with highest values recorded at station CD.

Results of principal component analysis on the environmental variables indicated that there is a distinct difference between canyon and slope stations and between stations CD and CM (Fig. 4). Furthermore, the 0–1 cm sediment layers at the slope stations were distinct from the deeper layers of the open slope, which grouped together. This was caused by the large differences in CPE concentrations and in chl *a*:phaeopigment ratios between the surficial and deeper sections. Differences were apparent between all sediment layers at the canyon

stations and no depth related trends were observed. The two PC axes comprising the plot shown in Fig. 4 explain 88.2% of the variation observed (75.0% and 13.2% for PC1 and PC2, respectively). The main contributors were CPE (–0.339), TOC (–0.315) for PC1 and C/N (+0.546), TN (–0.472), median grain size (+0.401), and TC (–0.389) for PC2 (numbers in parentheses represent eigenvector values).

3.2. Metazoan meiofauna

A total of 21 major taxa were identified (Table 2), of which nematodes were always the dominant group (81–98.5%), followed by harpacticoid copepods, nauplii,

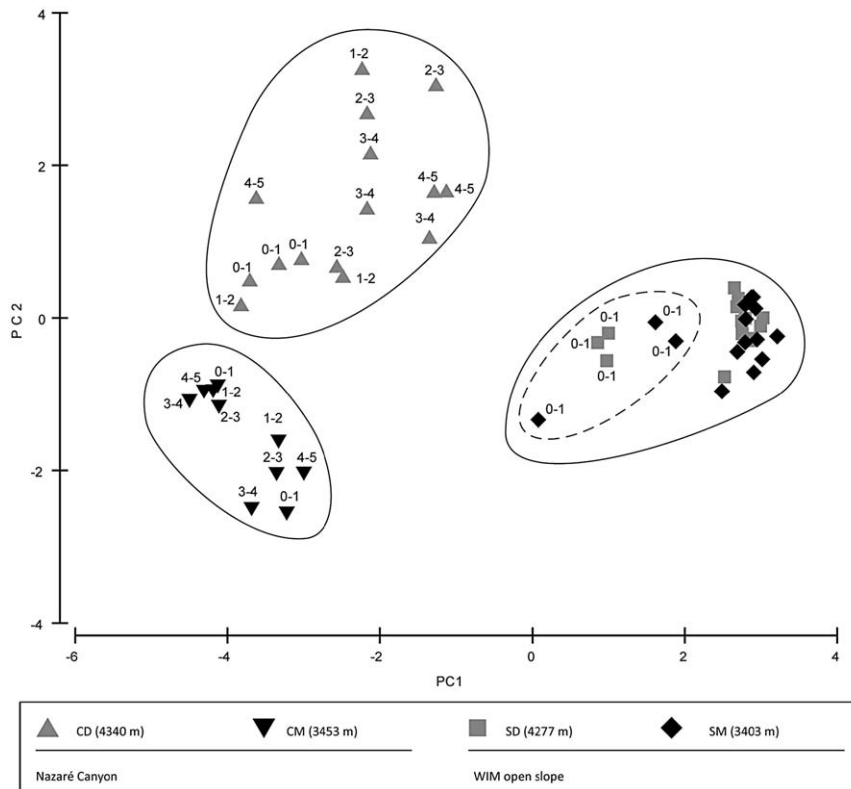


Fig. 4. PCA (based on Euclidean Distance values of $\log(0.1+X)$ transformed and normalised environmental sediment data), combining all sediment slices (including all 3 replicates, apart from station CM where only 2 replicates were available for every slice). The PC1 and PC2 axes explain a cumulative 83.5% of the variation observed. Included data parameters are: median grain size, TC, TN, TOC (2 sets of data), C/N, chl *a*, phaeopigments, chl *a*/phaeopigments, and CPE. Solid and broken lines indicate supported groups (left upper solid: station CM; left lower solid: station CD; right solid: open slope stations SD and SM; right broken: 0–1 cm slices of all open slope stations). The numbers in data labels refer to the sediment layers (0–1; 1–2; 2–3; 3–4 and 4–5 cm). For better visualisation of the plot, labels for slices deeper than 1 cm from the open slope stations were omitted. CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle, WIM: Western Iberian Margin.

and polychaetes. Other taxa were observed but in very low abundances (<1%). At the canyon stations a total of 18 taxa were present, whilst at the open slope stations only 16 were found. No large differences were observed when comparing the relative nematode abundances of open slope and canyon stations. However, slope sediments showed higher relative abundances of harpacticoid copepods and nauplii compared to the canyon stations and their distribution along the vertical profile was more uniform (Table 2).

Total core metazoan meiofauna abundances in the Nazaré Canyon at stations CD and CM were much higher (850.5 ± 125.6 and 1267.6 ± 66.7 ind. 10 cm^{-2} , respectively) than at the deep and middle slope sites (553.8 ± 79.3 and 481.1 ± 134.6 ind. 10 cm^{-2} , respectively). These high abundances were associated with higher TOC and chl *a* concentrations in the sediment (Fig. 2). When comparing the vertical profiles of slope and canyon sediments (Fig. 3) it is clear that the main difference was in the deeper sediment layers (1–3 cm): higher canyon subsurface abundances were associated with higher TOC and ‘freshness’ of OM relative to the slope. Highest total core (0–5 cm) metazoan meiofauna abundances were recorded

at station CD (1267.6 ± 66.7 ind. 10 cm^{-2}) and lowest at station SM (481.06 ± 134.6 ind. 10 cm^{-2}).

3.3. Nematodes

3.3.1. Nematode biomass and biometrics

Total core nematode biomass (TB, 0–5 cm) was highest in the canyon with 343.5 and $93.2 \mu\text{g dwt } 10 \text{ cm}^{-2}$ for stations CM and CD, respectively. The slope stations had much lower biomass (53.7 and $29.9 \mu\text{g dwt } 10 \text{ cm}^{-2}$ for stations SM and SD, respectively). In addition, average nematode individual dry weight was higher in the canyon when compared to slope stations at similar depths (0.116, 0.256, 0.093, and $0.120 \mu\text{g ind}^{-1}$ for stations CD, CM, SD, and SM, respectively). Down the vertical profile, nematode dimensions changed as nematodes were longer and slenderer deeper in the sediment, in comparison to the surface nematodes (Fig. 5). However, average individual nematode biomass (AIB) increased with sediment depth in the canyon, but AIB decreased with depth at the slope sites (Fig. 3). Consequently, total nematode biomass was higher in sub-surface canyon sediments in contrast to the

Table 2

Relative abundances of major taxa within the metazoan meiofauna per station and per sediment slice and total meiofauna abundances were averaged over replicates (ind. 10 cm⁻²).

Station	Sediment depth	Aplacophora	Bivalvia	Gastropoda	Gastrotrich	Gnathostomulidae	Halacarida	Copepoda	Isopoda	Kinorhyncha	Loricifera	Nauplii	Nematoda	Oligochaeta	Ostracoda	Polychaeta
CD	0–1	–	0.07	–	0.03	0.03	0.03	4.66	–	0.06	–	6.40	88.19	0.03	0.07	0.25
	1–2	–	–	–	0.04	–	–	0.52	–	0.08	–	0.57	98.50	0.04	0.13	0.08
	2–3	0.12	0.12	–	–	–	–	0.44	–	–	–	0.12	98.29	–	–	0.92
	3–4	–	–	–	–	–	–	–	–	–	–	0.64	96.57	–	–	2.78
	4–5	–	–	–	–	–	–	–	–	1.40	–	–	89.61	–	–	5.90
	Total	0.02	0.05	–	0.03	0.01	0.01	2.45	–	0.07	–	3.26	93.48	0.03	0.08	0.39
CM	0–1	–	–	0.05	0.02	0.02	–	4.62	0.02	2.14	–	4.21	88.24	0.02	0.07	0.35
	1–2	–	–	–	0.02	0.07	–	0.70	–	0.77	–	0.65	96.34	0.07	–	1.05
	2–3	–	–	0.13	–	–	–	0.64	–	0.50	–	1.65	93.81	0.11	0.13	2.45
	3–4	–	–	–	–	–	0.20	0.88	–	0.86	–	2.48	93.40	0.23	–	1.27
	4–5	–	–	–	–	–	–	–	–	–	–	8.74	89.74	–	–	0.72
	Total	–	–	0.03	0.02	0.04	0.01	2.39	0.01	1.34	–	2.46	92.41	0.06	0.04	0.86
SD	0–1	–	–	–	0.32	–	–	5.61	0.05	0.23	–	7.90	84.07	0.18	0.50	0.64
	1–2	–	–	–	–	–	–	4.43	–	–	–	2.21	92.53	0.14	0.14	0.41
	2–3	–	–	–	–	–	–	3.56	–	–	–	0.51	95.42	0.25	–	0.25
	3–4	–	–	–	–	–	–	1.29	–	–	–	1.11	96.49	0.74	–	0.37
	4–5	–	–	–	–	–	–	3.32	–	–	–	1.79	94.13	0.77	–	–
	Total	–	–	–	0.17	–	–	4.46	0.02	0.12	–	4.81	89.06	0.31	0.28	0.47
SM	0–1	–	0.07	–	0.13	–	–	6.60	–	0.40	–	9.70	81.00	0.07	0.67	1.01
	1–2	–	–	–	–	–	–	3.01	–	0.13	–	4.19	90.71	–	0.13	1.18
	2–3	–	–	–	–	–	–	1.59	–	–	–	3.58	93.64	0.20	0.40	0.40
	3–4	–	–	–	0.19	–	0.39	3.50	–	–	–	2.91	92.43	–	–	0.39
	4–5	–	–	–	–	–	–	1.20	–	–	0.24	0.48	97.12	–	–	0.24
	Total	–	0.03	–	0.08	–	–	0.05	4.13	–	0.19	0.03	5.73	88.16	0.05	0.35
		Priapulida	Tanaidacea	Tantulacarida	Tardigrada	Turbellaria	Hydrozoa	Total	St. dev.							
CD		0.03	0.07	–	–	–	–	0.09	–	–	–	401.14	91.88			
		–	0.04	–	–	–	–	–	–	–	–	310.45	64.51			
		–	–	–	–	–	–	–	–	–	–	112.13	17.02			
		–	–	–	–	–	–	–	–	–	–	18.32	2.83			
		–	–	–	3.10	–	–	–	–	–	–	8.43	2.77			
		0.02	0.04	0.03	–	–	0.04	–	–	–	–	850.5	125.6			

Table 2 (continued)

	Priapulida	Tanaidacea	Tantulacarida	Tardigrada	Turbellaria	Hydrozoa	Total	St. dev.
CM	0.05	0.02	–	–	0.17	–	547.65	68.48
	0.02	0.05	–	–	0.27	–	542.78	75.71
	–	–	–	–	0.59	–	102.84	31.47
	–	–	–	–	0.68	–	57.84	16.66
	–	–	–	–	0.79	–	16.43	8.17
	0.03	0.03	–	–	0.27	–	1267.6	66.7
SD	–	–	–	0.41	0.09	–	286.18	39.87
	–	–	–	0.14	–	–	94.44	16.96
	–	–	–	–	–	–	51.33	17.07
	–	–	–	–	–	–	70.66	9.19
	–	–	–	–	–	–	51.20	3.85
	–	–	–	0.24	0.05	–	553.8	79.3
SM	–	–	0.07	–	0.27	–	193.83	46.41
	–	–	0.13	–	0.39	0.13	99.79	24.55
	–	–	–	–	0.20	–	65.70	23.89
	–	–	–	–	0.19	–	67.27	10.11
	–	–	–	–	0.72	–	54.47	34.88
	–	–	0.05	–	0.33	0.03	481.1	134.6

St. dev.: standard deviation.

slope where it was concentrated in the surface layer (0–1 cm).

3.3.2. Nematode assemblages

The presence and higher abundance at station CD of *Sabatieria* (6.47%), *Sphaerolaimus* (2.47%) and the highly dominant *Acantholaimus* (31.28%) defined an aberrant

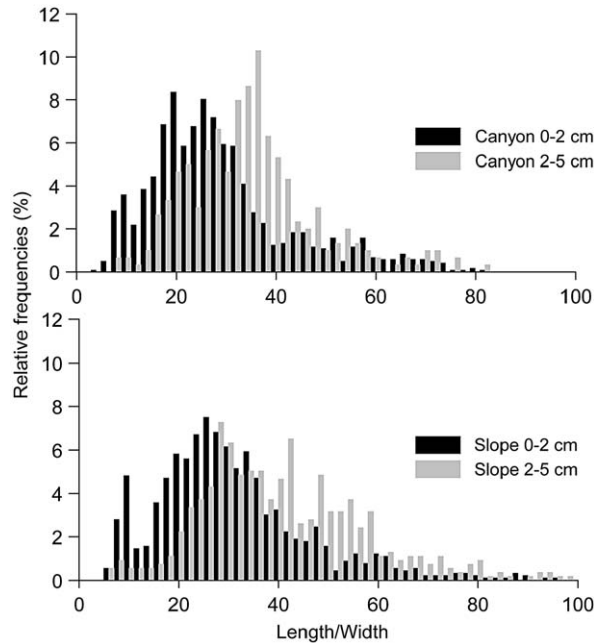


Fig. 5. Relative frequency distributions of length/width ratios of nematodes for the upper 2 cm of the sediment and the lower 2–5 cm; data combined for both canyon stations (upper histogram) and both slope stations (lower histogram); $n_{\text{canyon}} = 1499$, $n_{\text{slope}} = 1447$.

assemblage when compared to both typical open slope assemblages (Table 3). The generic composition of the station CM assemblage was also different from the corresponding open slope assemblage, with 7 of the top 10 genera not present on the slope. Within the canyon, only 4 dominant genera were common to stations CD and CM, whereas there were no apparent differences between the two slope assemblages. These differences were clearly reflected in the MDS plot (Fig. 6). There was no clear separation between the generic assemblages at stations SD and SM. All surficial sediments (0–1 cm) were grouped together, suggesting that surficial genera assemblages are more similar to each other than the deeper layers. This is a clear indication that the differences in genera assemblages were mainly in the deeper sediment layers.

One-way ANOSIMs, based on assemblage data of only three 0–1 cm replicates per station, indicate significant differences between stations and between canyon and slope, but not between the deeper and middle sites (Table 4). The two-way ANOSIM (average of three 0–1 cm replicates and one non-replicated value per deeper slice) test results show that there are significant differences between the slices across all station groups ($\rho = 0.564$, $p < 0.001$) as well as significant differences between stations when compared over all slice groups ($\rho = 0.823$, $p < 0.001$). The significant differences between the assemblages of the different sediment layers for every station comprise a large part of the total observed station differences since the sample statistic for the slice test was only slightly lower than that for the station test (0.564 vs. 0.823).

The one-way SIMPER results show that the average similarity in the canyon (47.81%) is mainly attributed (with contributions $> 5\%$) to the genera *Halalaimus*, *Sabatieria*, *Daptonema*, *Dichromadora* and *Sphaerolaimus*. The average similarity value of 67.27 in the slope group

Table 3

Relative abundance of the dominant ($\geq 1\%$) nematode genera per station (0–5 cm, all replicates included).

CD	CM	SD	SM
<i>Acantholaimus</i>	31.28	<i>Halalaimus</i>	13.06
<i>Halalaimus</i>	10.63	<i>Paralongicyatholaimus</i>	9.76
<i>Desmoscolex</i>	8.32	<i>Daptonema</i>	8.46
<i>Sabatieria</i>	6.47	<i>Molgolaimus</i>	8.32
<i>Tricoma</i>	4.16	<i>Dichromadora</i>	7.03
<i>Daptonema</i>	3.85	<i>Pomponema</i>	4.88
<i>Thalassomonhystera</i>	3.54	<i>Retrotheristus</i>	4.45
<i>Dichromadora</i>	3.39	<i>Elzalia</i>	4.30
<i>Xyalidae</i>	2.93	<i>Sabatieria</i>	4.02
<i>Sphaerolaimus</i>	2.47	<i>Actinonema</i>	3.59
<i>Greeffiella</i>	1.69	<i>Axonolaimus</i>	3.16
<i>Halichoanolaimus</i>	1.69	<i>Sphaerolaimus</i>	2.58
<i>Campylaimus</i>	1.39	<i>Xyalidae</i>	2.30
<i>Metasphaerolaimus</i>	1.39	<i>Parasphaerolaimus</i>	2.01
<i>Manganonema</i>	1.23	<i>Amphimohystrella</i>	1.72
		<i>Thalassomonhystera</i>	1.43
		<i>Nannolaimus</i>	1.43
		<i>Campylaimus</i>	1.29
		<i>Eleutherolaimus</i>	1.29
		<i>Aegialoalaimus</i>	1.15
		<i>Thalassomonhystera</i>	18.97
		<i>Acantholaimus</i>	13.55
		<i>Halalaimus</i>	9.27
		<i>Theristus</i>	7.56
		<i>Daptonema</i>	5.85
		<i>Diplopeltula</i>	2.71
		<i>Xyalidae</i>	2.14
		<i>Microlaimus</i>	2.14
		<i>Tricoma</i>	2.00
		<i>Cervonema</i>	2.59
		<i>Aegialoalaimus</i>	5.00
		<i>Tricoma</i>	4.81
		<i>Cervonema</i>	2.59
		<i>Actinonema</i>	2.41
		<i>Desmoscolex</i>	2.41
		<i>Syringolaimus</i>	1.57
		<i>Actinonema</i>	1.57
		<i>Leptolaimus</i>	1.43
		<i>Chromadoridae</i>	1.43
		<i>Thalassomonhystera</i>	1.28
		<i>Southerniella</i>	1.14
		<i>Metasphaerolaimus</i>	1.00
		<i>Cervonema</i>	1.00
		<i>Marylynnia</i>	1.30
		<i>Disconema</i>	1.11

Nematode families include all individuals that could not be assigned to a genus but were identified to the family level. CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle.

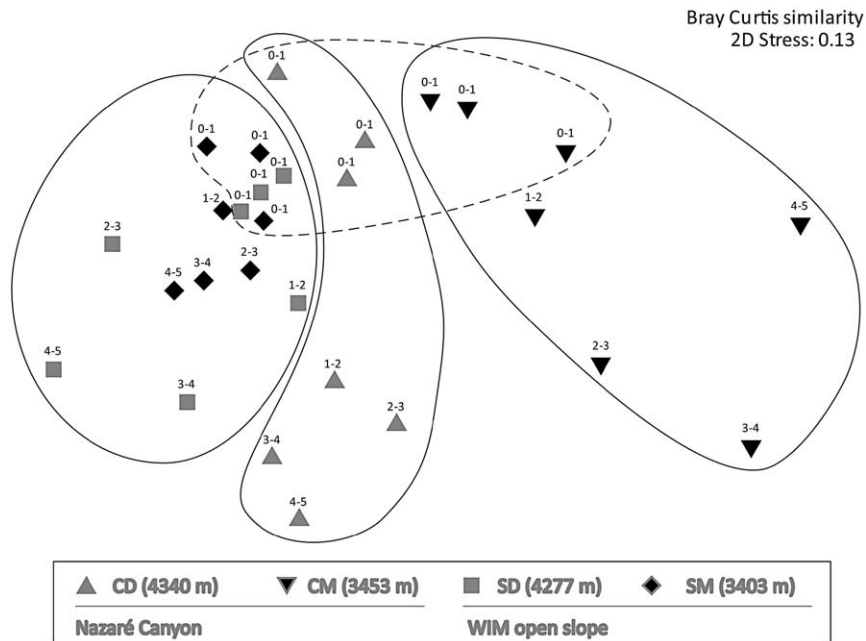


Fig. 6. MDS plot (based on Bray Curtis similarity values of standardised and $\log(X+1)$ transformed genera abundance data), combining all sediment slices and 0–1 cm replicates for all stations. Solid and broken lines indicate supported groups (left solid: open slope stations combined; middle solid: station CD; middle broken: all 0–1 cm sediment slices; right solid: station CM). CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle, WIM: Western Iberian Margin. The numbers in data labels refer to the sediment layers (0–1; 1–2; 2–3; 3–4 and 4–5 cm).

Table 4

Overview of the performed ANOSIM analyses.

ANOSIM	Factors		H_0 -hypothesis	R, ρ	p
	A	B			
1-way ⁰⁻¹	Stations (CD, CM, SD, SM)	–	No station differences*	0.821	0.001
1-way ⁰⁻¹	Depth (D, M)	–	No depth differences	0.119	0.184
1-way ⁰⁻¹	Habitat (C, S)	–	No habitat differences*	0.594	0.002
2-way crossed (no replicates)	Stations (CD, CM, SD, SM)	Slices (0-1, 1-2, 2-3, 3-4, 4-5 cm)	No slice differences across station groups*	0.564	0.001
			No station differences across slice groups*	0.823	0.001

R, ρ : sample statistic; p : significance level; *: significant rejection of H_0 -hypothesis; ⁰⁻¹: only 0–1 cm data were used. CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle, D: deep stations (approx. 4300 m depth), M: middle stations (approx. 3400 m depth), C: canyon stations, S: slope stations.

can be predominantly ascribed to the genera *Thalassomonhystra*, *Acantholaimus*, *Theristus*, *Daptonema*, and *Halalaimus* (with contributions >5%). The average dissimilarity between canyon and slope samples is rather high (52.79%), but is equivalent to the dissimilarity between slices observed within the canyon group ($100 - 47.81 = 52.19$). The differences between canyon and slope were determined by the sum of small contributions (<5%) from a rather large number of genera, with *Theristus*, *Sabatieria*, *Thalassomonhystra*, *Acantholaimus*, *Paralongicyatholaimus*, and *Sphaerolaimus* at the top of the list (>2.5%).

3.3.3. Structural and functional nematode diversity

Within station the number of genera was similar for both canyon stations (64 and 63 genera for stations CD

and CM, respectively), yet only 38 genera on a total of 89 were common to both stations. A similar observation was made for the slope where 46 genera were shared between stations out of a total of 122. A comparable pattern emerged when comparing canyon and slope habitats: 31 genera were found to be exclusive to the canyon whilst 68 genera were unique to the adjacent slope. Hence, *alpha* diversity (defined here as the diversity at one station) was noticeably lower than *beta* diversity (defined as diversity in a habitat, i.e. canyon or slope habitat) because of high genus turnover between stations. Station SD was most diverse based on simple genera numbers, followed by station SM. The canyon stations CD and CM had low diversity. The other Hill indices (H_1, H_2, H_∞) indicated that the slope is more diverse compared to the canyon and that the assemblages at the 3400 m stations, CM and SM, were

more dominated by particular genera compared to the deeper 4300 m stations. This pattern corresponded with observations for Pielou's evenness index, and Shannon-Wiener diversity. EG(51) values were highest for station SD, followed by the middle depth stations (CM, SM) and finally station CD with lowest diversity (Table 5). When comparing the data for the canyon and the slope it became clear that the adjacent slope displayed greater diversity and evenness compared to the canyon. However, total canyon-slope diversity is higher than the subtotals for canyon and slope, suggesting that the canyon diversity is not 'included' in the slope diversity but rather contributes to total diversity.

The relative abundances per station of different feeding types, and the trophic diversity index, are shown in Table 6. The slope is characterised by high numbers of selective and non-selective deposit feeders, while the canyon shows a higher abundance of epistratum feeders and scavengers/predators. The trophic diversity index suggests a higher trophic complexity in the canyons stations, particularly station CM. Compared to station CM, station CD shows a shift in the trophic community structure, with more epistratum feeders and fewer non-selective deposit feeders. At station CM, one mouthless nematode with rudimentary gut was found (*Parastomonema*).

Table 5

Diversity measures calculated on genera-abundance numbers which were recomputed for observed nematode abundances.

	H_0	H_1	H_2	H_∞	J'	H'	$E(51)$
CD	64	16.184	6.702	2.848	0.669	2.784	4.015
CM	63	24.563	16.272	7.957	0.773	3.201	8.362
SD	93	27.258	12.760	5.297	0.729	3.305	12.550
SM	75	25.874	15.341	7.111	0.753	3.253	8.361
C	89	28.918	17.004	6.772	0.750	3.364	23.027
S	122	29.380	14.330	6.017	0.704	3.380	23.519
CS	153	35.730	19.179	6.911	0.711	3.576	25.074

CD: canyon station deep; CM: canyon station middle; SD: slope station deep; SM: slope station middle; C: canyon stations combined; S: slope stations combined; CS: all stations combined; H_0 , H_1 , H_2 and H_∞ : Hill (1973) numbers; J' : Pielou's (Pielou, 1969) evenness number; H' : Shannon-Wiener diversity index (Krebs, 1989), $E(51)$: expected number of species.

Table 6

Relative abundance of different nematode feeding types according to Wieser (1953).

Station	Feeding types				Mouth absent	Trophic diversity index
	1A	1B	2A	2B		
CD	29.8	22.4	39.5	8.3	–	0.302
CM	28.1	37.3	23.6	10.9	0.1	0.286
SD	27.1	42.9	25.9	4.1	–	0.326
SM	30.5	41.3	23.4	4.7	–	0.321

1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epigrowth feeders, 2B: predators/scavengers, CD: canyon station deep, CM: canyon station middle, SD: slope station deep, SM: slope station middle.

Table 7

Kendall tau correlation coefficients and p -values for nematode abundance and biomass.

	Nematode abundance		Nematode biomass	
	tau	p	tau	p
CPE	0.295	0.069	0.547	≤ 0.01
Chl a :phaeophytin	0.354	≤ 0.05	0.578	≤ 0.01
TOC	0.200	0.218	0.474	≤ 0.01

3.4. Relation between nematodes and environmental variables

Kendall's tau correlations are shown in Table 7. Nematode biomass was significantly, positively correlated with TOC, CPE and chl a :phaeopigments. Nematode abundance, on the other hand, showed no significant correlations other than with chl a :phaeopigments. The RELATE analysis revealed that the spatial pattern based on nematode genera assemblages is significantly related to the patterns inherent to the environmental settings ($\rho = 0.33$, $p \leq 0.01$). The BEST analysis indicated the combination of median grain size, TN, TOC, and CPE (separate values for chl a and phaeophytins excluded) as the subset of abiotic variables that best explain the biotic pattern defined by the genera assemblages ($\rho = 0.662$, $p \leq 0.01$).

4. Discussion

4.1. Quantity and quality of OM

The flux of OM from surface productivity to the seafloor exerts a considerable control on meiofaunal benthic standing stocks (Soltwedel, 2000). Indeed, meiofauna densities at both canyon and slope stations showed a positive correlation with TOC and CPE content (data not shown), but organic input and meiofaunal densities were highest in the canyon (Tables 1 and 2). The OM input in the canyon also seemed more labile than on the adjacent slope (higher chl a :phaeopigment ratio). However, C:N ratios were much higher (8.4–13.4, Table 1) in the canyon sediments compared to the slope (6.3–8.1) and correspond with values reported by Garcia et al. (2007) for the canyon axis. This implies either a greater terrestrial component, or more degraded OM, or both. De Stigter et al. (2007) and Kiriakoulakis et al. (unpublished results) reported that the sediments in the Nazaré Canyon had a large terrestrial component and the same is true for other large canyons like the Cap Breton Canyon (Gaudin et al., 2006) and the Palamós Canyon (Palanques et al., 2005a). The high sedimentary fluxes in these canyons appear to be related with their proximity to the shore, favouring the capture of sediments from the near-shore zone. In addition, Oliveira et al. (2007) suggested that the sediments in the upper Nazaré canyon (<2000 m depth; de Stigter et al., 2007) originate from the shelf areas north and south of the canyon, as well as from erosion of the coastal cliffs. Alternatively, the increased C:N ratio found

in the deeper canyon sediments could reflect removal of labile, proteinaceous (i.e. N-rich) marine OM during the decomposition process (Cowie and Hedges, 1992; Aller et al., 1996; Prahil et al., 1997; Aller and Blair, 2004).

Thus, there is more labile marine OM at the upper and mid (2000–3500 m; de Stigter et al., 2007) sections of Nazaré Canyon with terrestrial, more refractory material dominating in the deeper sections, although there are generally higher concentrations of more labile OM in the canyon sediments than at the slope. The implications for the meiobenthos are twofold. First, the higher amounts of labile OM that are available for the meiofauna in the canyon result in higher standing stocks. Second, benthic respiration of the high level OM in the deeper canyon sections generates reducing sedimentary conditions and this can shape the nematode assemblages present (Soetaert et al., 2002).

4.2. Meiofauna densities and environment

Meiofauna abundance at the slope stations fell within magnitude reported in other Iberian Margin meiofauna studies (Rachor, 1975; Dinét and Vivier, 1977) with values ranging from 7 up to 437 ind. 10 cm^{-2} . In contrast, the canyon abundances are high and more comparable with values reported for shallower Iberian shelf areas (779–1802 ind. 10 cm^{-2}) (Vanreusel et al., 1992; Flach et al., 2002). Considering methodological differences, it is clear that a Van Veen grab, Reineck corer, or even a box corer do not produce samples of the same quality as a MUC or MGC, which recovers cores with an undisturbed sediment-water interface. The mesh size used to separate the meiofauna also varies between authors and can result in a biased perception of the actual meiofauna community. These methodological differences mean that comparisons of densities should be made with care. Yet, the large differences in nematode abundance between communities on the slope and in the canyon suggest that other factors play a key role in regulating community densities.

Few meiofauna data are available for the Nazaré Canyon and findings differ. Garcia et al. (2007) reported very low abundances (9.9–236 ind. 10 cm^{-2}) while the present study and Soetaert et al. (2002) found very high meiofaunal densities (850–1267 and 617–1571 ind. 10 cm^{-2} respectively). Intensive summer upwelling at the Iberian Margin (McClain et al., 1986; Frouin et al., 1990) may induce high levels of primary production (Slagstad and Wassmann, 2001; Joint et al., 2002), resulting in a seasonally elevated phytodetrital input to the deep sea, causing benthic standing stocks to increase. However, since all sampling for these Nazaré Canyon studies occurred during spring/summer, seasonal variability is unlikely to account for this discrepancy. Notwithstanding sampling gear (box corer vs. MUC) and mesh-size differences (32 μm vs. 50 μm), the difference in abundance is likely to be explained by the different localities of the sampling stations within the very heterogeneous canyon and their variable susceptibility to episodic disturbance (de Stigter et al., 2007). Indeed, the low density samples (Garcia et al., 2007) were collected in the canyon axis

whilst the high-density samples for the present study and Soetaert et al. (2002) were collected from the terraces beside the *thalweg* or nearer the canyon walls. There is evidence that meiofauna in disturbed ecosystems, particularly nematodes, can recover rapidly (e.g. Sherman and Coull, 1980; Sun and Fleeger, 1994; Lee et al., 2001a, b), but continuous disturbance by sediment transport and deposition, as observed in the canyon axis, is detrimental for the meiobenthic community. In addition, the sedimentary OM is also likely to play a key role in density differences. Significant, positive correlation of nematode abundances with chl *a*: phaeopigment ratios and positive correlations with CPE values (Table 7), underline the strong dependence of nematode abundance on the quantity and quality of OM. The fact that different localities in the canyon show variations in the freshness and amount of available OM is a factor regulating abundance differences between stations (Epping et al., 2002; Garcia and Thomsen, 2008).

4.3. Nematodes

4.3.1. Nematode biomass

Nematode biomass values in the Nazaré Canyon (93.2 and 343.5 $\mu\text{g dwt } 10\text{ cm}^{-2}$ for stations CD and CM, respectively) were high compared to values for the open slope and other stations along the Iberian Margin (Soetaert et al., 2002). Nematode biomass was significantly and positively correlated with the amount and freshness of the OM. Hence, the high levels and quality of the available food in the canyon support higher standing stocks than on the slope. Other data (Thiel, 1972a, b; Rachor, 1975; Flach et al., 2002; Soetaert et al., 2002; Garcia et al., 2007) generally confirm that nematode biomass is lower along the Iberian Margin slope relative to the Nazaré Canyon. However, comparable biomass values have been reported off the Iberian coast although at much shallower depths (e.g. 334 and 137 $\mu\text{g dwt } 10\text{ cm}^{-2}$ at depths of 190 and 325 m respectively; Vanreusel et al., 1992).

Nematode biomass values reported for the axis of the Nazaré Canyon by Garcia et al. (2007) (~ 4 up to $\sim 44\text{ }\mu\text{g dwt } 10\text{ cm}^{-2}$) are much lower than canyon values reported here but are similar to those for slope sites in this study (29.9–53.7 $\mu\text{g dwt } 10\text{ cm}^{-2}$). Furthermore, Soetaert et al. (2002) found very high values at the canyon head (256 $\mu\text{g dwt } 10\text{ cm}^{-2}$ at 344 m depth) where deposition rates are high (de Stigter et al., 2007), whilst at about 3000 m depth, biomass decreased to approximately half the amount observed at the 3400 m station in present study. So, nematode standing stocks decrease with depth, but heterogeneity and patchiness in canyons can result in variable standing stocks at similar depths as illustrated. The Nazaré Canyon is a very active system (de Stigter et al., 2007; Arzola et al., 2008) and its *thalweg* along the canyon axis, which is the main channel of turbulent flows, may be destructive to nematode communities and lead to low standing stocks.

Nematode biomass values (74.7–249.8 $\mu\text{g dry weight } 10\text{ cm}^{-2}$) for the Gulf of Lions canyon system (de Bovee and Labat, 1993; Grémare et al., 2002) lie within the same order of magnitude as values for the Nazaré Canyon, but

again, they reflect the situation at much shallower depths (240, 910, 1000 and 1200 m). Nevertheless, the data indicate that nematode biomass is higher in canyon systems than on the slope, providing that regular intense hydrodynamic activity does not prevent meiobenthic communities from settling.

At the canyon stations average individual biomass increased with sediment depth. As a consequence, total nematode biomass peaked in the 1–3 cm layer, below which densities decreased considerably and total biomass was reduced. This was not the case at the slope stations where average individual biomass diminished immediately below the surface layer. The increasing nematode size with sediment depth and the high nematode numbers in the canyon are responsible for the high biomass values observed in canyon systems and mostly reflect high rates of sedimentation and availability of OM.

4.3.2. Nematode community structure and function, and their relation with environmental conditions

The generic assemblages were distinctly different between canyon and adjacent slope stations and between canyon stations. Furthermore, in the canyon a discrepancy down the vertical profile was notable (Figs. 3 and 6). The 2-way crossed ANOSIM test results demonstrated that there are indeed significant differences between sediment layers among all stations and that this vertical discrepancy is responsible for a large part of the variability between stations (Table 4). The deeper layers of the Nazaré Canyon sediments showed higher nematode abundances and biomass relative to the slope because of the higher CPE contents and the presence of relatively labile OM throughout the vertical profile (high chl *a*:phaeopigment ratios in deeper layers), which allows the nematode community to penetrate deeper into the sediment. This was supported by the significant correlation between nematode abundance and biomass and the freshness of the OM (Table 7). Moreover, nematode biomass was significantly correlated with TOC and CPE indicating that the quantity and quality of OM drives nematode biomass at the surface and in the deeper layers. Deep vertical colonisation of the sediment by meiobenthos was also observed by Vivier (1978a) in the Canyon de Cassidaigne off the coast of Marseille. However, Vivier (1978a) related the deep colonisation to the fluidity of the mud, which enabled the meiobenthos to thrive in that environment. Mud fluidity has not been quantified in the Nazaré Canyon, but ROV exploration of the sampling sites showed that these terraces are draped in very soft, easily resuspendable muds (pers. obs.) and possibly comparable to those described by Vivier (1978a). Unpublished data of de Stigter (pers. comm.) confirm that surface sediments on the canyon terraces are very watery and uncompacted, with porosity values of 70–80% in the upper 5 cm.

Sediment depth can affect nematode shape and structural composition much more profoundly than water depth (Soetaert and Heip, 1989; Soetaert et al., 2002). Along the Iberian Margin and in the Nazaré Canyon nematodes tend to be longer and more slender deeper in the sediment (Fig. 5). This can be partially explained by

oxygen availability (Soetaert et al., 2002). Deeper than 2000 m on the slope, oxygen concentrations decline steadily until exhausted at ~4–5 cm sediment depth (Epping et al., 2002), whereas oxygen penetration depth is reduced in the canyon to between 1 and 3 cm at 3100 and 4300 m, respectively (Epping et al., 2002; Soetaert et al., 2002). In addition, Kiriakoulakis et al. (unpublished results) report that the oxic/anoxic boundary in Nazaré Canyon sediments is close to the surface (< 1 cm). Limited oxygen penetration depth in the canyon sediments is caused by decomposition of the large amounts of OM deposited there. Reduced, anoxic conditions are harmful to nematodes, and although they can be rather tolerant to anoxia, nematodes cannot survive long-term exposure (Moodley et al., 1997). Soetaert et al. (2002) proposed vertical migration in the sediment as a solution to escape temporarily reduced conditions, and stated that mobility is enhanced by a long and slender nematode body shape. Alternatively, increasing nematode slenderness and size with sediment depth may be an adaptation to recurring hydrodynamic disturbance. Several authors have suggested that certain morphological adaptations are characteristic of nematodes living in high energy environments. Individuals may use their long, slender body and long, retractable tail to escape into the deeper sediment layers to avoid resuspension in hydrodynamically active deep-sea areas (Thistle and Sherman, 1985 and references therein), such as the Nazaré Canyon. Our results show an increase in the abundance of slenderer and larger nematodes (higher individual biomass) with increasing sediment depth (Figs. 3 and 5), especially in the canyon, where only the surface layers are oxygenated and hydrodynamic disturbance is high. The dominance of *Sabatieria* in the canyon and its absence in the slope sediments (Table 3 and SIMPER test results) is striking in this respect. Species of *Sabatieria* thrive in disturbed environments (Steyaert et al., 1999, 2007) and near-anoxic muddy sediments (Vanreusel, 1990; Vincx et al., 1990). It is also suggested that some *Sabatieria* species have developed adaptation mechanisms to survive episodes of anoxia (Steyaert et al., 2007). In addition, Soetaert and Heip (1995) pointed out the preference of *Sabatieria* species for suboxic or anoxic environments and suggested that these species thrive only in those environments where a substantial fraction of OM becomes incorporated below the oxic zone of the sediment, as seems to be the case in the Nazaré Canyon (Epping et al., 2002; Fig. 3). Furthermore, *Sabatieria* species have long and slender body forms, well adapted to their thiotrophic lifestyle.

The canyon was characterised by more predatory/scavenging (e.g. *Sphaerolaimus*, *Pomponema*, see Table 3) nematodes and fewer non-selective deposit feeders compared to the adjacent slope. Together with a decreasing trophic index, this suggests that the canyon sediments harbour a more complex nematode community with a predominance of higher trophic groups such as predators and scavengers. These nematodes are naturally larger and longer compared to other feeding types, which makes them more agile in disturbed canyon sediments and enhances their survival rate. Inputs of abundant and relatively fresh food at the surface and deeper in the

canyon sediment compared to the slope will help to sustain the trophic complexity of the community living there. In addition, there was a shift in the abundance of different feeding types between canyon stations. In particular station CM (highest quality and quantity of OM) was characterised by more non-selective deposit feeders and less epistrate feeders compared to station CD leading to a more evenly distributed trophic diversity.

The environmental patterns revealed by PCA agree well with the MDS results. Generic assemblage patterns can be explained largely by the quantity and quality of the OM (i.e. TN, TOC, and CPE concentrations and freshness) and the median grain size, which seem to be the main structuring factors for the nematode community and can be related to the assemblages observed at the studied stations and along vertical profiles. In addition, the dynamics of water and sediment transport and the morphology of the canyon may have an important role to play in controlling the biota. Levin and Gooday (2003) concluded that the 'distinctiveness' of canyon fauna from the nearby slope was a function of a variety of canyon attributes. Canyons with low topographic relief and mainly soft sediments had a fauna closely resembling the nearby slope. Conversely, canyons that are narrow and deep with much exposed rock will have a fauna quite distinct from the surrounding slope. The Nazaré Canyon is characterised by a complex hydrography, involving tidal and turbidity currents, and intermittent sediment gravity flows transporting sediments along its axis. These processes shape its complex and heterogeneous habitat morphology. Our results indicate that the generic assemblages were as dissimilar between the two canyon stations as they were between the canyon and the adjacent slope. Also, comparing axis samples (Garcia et al., 2007) with samples from other canyon locations indicated large differences in meiofauna and nematode assemblages. Since the quality and quantity of the deposited OM was similar, these differences were most likely due to the contrasting hydrodynamic disturbance and sedimentation regime. Thus, within-canyon heterogeneity plays an important role in structuring its inhabiting fauna. Whether OM quality prevails over habitat heterogeneity in shaping meiofauna distributions within the canyon remains poorly resolved. Quality and quantity of OM were correlated with higher abundances and biomass within the canyon and relative to the open slope, but within-canyon heterogeneity had a large effect on the nematode assemblages. These two factors are most likely closely intertwined in their role as ecosystem drivers since morphological heterogeneity in combination with the canyon hydrography regulate grain-size distributions, the OM patchiness and to an extent OM quality in the canyon. When the hydrodynamic disturbance diminishes at less disturbed canyon sites (as opposed to the harsh canyon axis), then OM quantity and quality are again the main factors controlling the benthos, either directly or indirectly.

4.4. Nazaré canyon diversity

The numbers of nematode genera indicated a high turnover rate between stations and habitats (Table 6). It is

possible that the harsh and unpredictable conditions of the canyon axis shape the infauna, lead to aberrant nematode assemblages, and consequently contribute to the total diversity in the canyon. With those of Garcia et al. (2007), the numbers of genera total 112, 165, and 191 for the Nazaré Canyon, adjacent slope and both habitats combined, respectively. Again, this leads to higher generic turnover rates. Few studies have documented nematode diversity along the Iberian Margin (Dinet and Vivier, 1979; Vanreusel et al., 1992; Garcia et al., 2007), but when comparing the data between canyon and slope, the Nazaré Canyon seems to display a lower diversity. Hill's diversity indices are variably dependent on the dominance of genera; going from H_0 , which is a simple reflection of genera numbers and is abundance independent, to H_∞ or "dominance index", which is the reciprocal of the proportional abundance of the most dominant genus. Hill's higher order numbers (H_2 , H_∞) indicate that the middle canyon has the highest diversity. Alternatively, the lower order Hill numbers (H_0 , H_1) designate the slope stations as being most diverse. Diversity at station CM is thus higher when it takes into account generic abundances, which will be important in the case of high dominance assemblages. In the present study, Shannon Wiener diversity was higher and Pielou's J' values lower than values put forward by Garcia et al. (2007), apart from two axis stations (1121 and 2847 m) which displayed lower evenness.

In conclusion, we found that the Nazaré Canyon has lower *alpha* diversity values, but its diversity contributes to total Iberian Margin diversity because of the high generic turnover or *beta* diversity observed between stations and habitats. The canyon's heterogeneity and its unique characteristics separate this ecosystem from the adjacent slope.

5. Conclusions

The Nazaré Canyon is one of the largest near-shore canyons on Earth and is considered a depo-centre for a mixture of fresh marine and more recalcitrant terrigenous OM with episodic flushing to the deeper canyon parts and the abyssal plain. Despite the fact that the OM in the canyon was largely of terrestrial origin and refractory, the amount and quality of OM available for direct consumption was higher in the canyon. Together with the positive correlation of nematode abundance and biomass with quantity and freshness of the OM, this explains the high standing stocks observed in the canyon sediments. Furthermore, canyon assemblages showed particular adaptations (e.g. higher trophic complexity, variable nematode morphology, and the presence of opportunistic genera such as *Sabatieria*) to the prevailing conditions, particularly in the deeper sediment layers. Strong hydrodynamic activity, as found in the canyon axis, is likely to be detrimental to the meiobenthic community. Thus, both the quantity and quality of the sedimentary OM drive metazoan meiobenthos standing stocks and regulate the nematode assemblages directly and indirectly, and in concordance with canyon heterogeneity and hydrography.

Nazaré Canyon's diversity was slightly lower than that of the adjacent slope and its communities were characterised by higher dominance of certain genera. Hydrodynamic disturbance in the canyon is likely to have a negative impact on the establishment of meiobenthic communities and hence its diversity, even when the canyon's physical and geochemical (with respect to OM) heterogeneity suggests a high diversity. Nevertheless, the Nazaré Canyon contributes considerably to total Western Iberian Margin nematode diversity because of the high turnover rate and presence of assemblages that are different from those found on the slope.

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