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Temporal and spatial variation in the Nazaré Canyon (Western Iberian margin): Inter-annual and canyon heterogeneity effects on meiofauna biomass and diversity

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ABSTRACT

The Nazaré Canyon on the Portuguese Margin (NE Atlantic) was sampled during spring-summer for three consecutive years (2005–2007), permitting the first inter-annual study of the meiofaunal communities at the Iberian Margin at two abyssal depths (~3500 m and ~4400 m). Using new and already published data, the meiofauna standing stocks (abundance and biomass) and nematode structural and functional diversity were investigated in relation to the sediment biogeochemistry (e.g. organic carbon, nitrogen, chlorophyll *a*, phaeopigments) and grain size. A conspicuous increase in sand content from 2005 to 2006 and decrease of phytodetritus at both sites, suggested the occurrence of one or more physical disturbance events. Nematode standing stocks and trophic diversity decreased after these events, seemingly followed by a recovery/recolonisation period in 2007, which was strongly correlated with an increase in the quantity and bioavailability of phytodetrital organic matter supplied. Changes in meiofauna assemblages, however, also differed between stations, likely because of the contrasting hydrodynamic and food supply conditions. Higher meiofauna and nematode abundances, biomass and trophic complexity were found at the shallowest canyon station, where the quantity, quality and bioavailability of food material were higher than at the deeper site. The present results suggest that even though inter-annual variations in the sedimentary environment can regulate the meiofauna in the abyssal Nazaré Canyon, heterogeneity between sampling locations in the canyon were more pronounced.

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1. Introduction

In contrast to earlier ideas of the deep sea as a remote faunal desert, we now know that it harbours diverse assemblages of animals and protists. Organisms inhabiting this environment are subjected to variable regulating disturbance and seasonal/episodic productivity regimes related to upper water-column processes (Gage and Tyler, 1991). Understanding benthic community responses to such events allows insights into deep-sea diversity and dynamics (Gage and Tyler, 1991; Gooday, 2002; Billett et al., 2010). There is evidence that smaller

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benthic organisms tend to respond quickly to pulses of organic-rich detritus, with increases in standing stocks and enhanced metabolic responses (Gooday, 2002; Guidi-Guilvard et al., 2009). Nevertheless we are still confronted with a lack of knowledge on the scales (temporal and spatial) at which different processes regulate deep-sea communities, including conclusive insights into the cause–effect relationships (Glover et al., 2010; Ingels and Vanreusel, 2013). In addition, for certain relatively homogeneous deep-sea habitats it is possible to roughly predict faunal response to, for instance, yearly peaks in organic matter (OM) fluxes (Gooday, 2002), while for other, more complex and dynamic habitats, patterns are more challenging to investigate. This is particularly the case for submarine canyons, where different regulating processes and heterogeneous environmental conditions act in concert, in time and space, to structure faunal communities (e.g. Bianchelli et al., 2008; Ingels and Vanreusel, 2013; McClain and Barry, 2010).

Submarine canyons are pervasive, large-scale geological features that cut the continental shelf and slope, and form a direct

pathway from shallow waters to the deep sea. Characterised by complex topography, hydrology, disturbance regimes (e.g. strong near-bottom currents, turbidity flows) and locally enhanced organic matter availability, canyons act as important sediment and organic material conduits to the abyssal plain (Canals et al., 2006; de Stigter et al., 2007; Masson et al., 2010). In general, higher faunal densities, biomass, local diversity and trophic complexity are found in canyons compared to the adjacent slope (e.g. Soetaert and Heip, 1995; Soltwedel, 2000; Danovaro et al., 2009; Ingels et al., 2009, 2011c; De Leo et al., 2010; McClain and Barry, 2010), although occasionally very low densities are also found (Van Gaever et al., 2009; Garcia et al., 2007).

The number of studies on meiofauna in submarine canyons has increased in recent years, providing a better insight into how benthic communities respond to environmental conditions within canyons (e.g. Soetaert et al., 1991; Soltwedel, 2000; Soltwedel et al., 2005; Koho et al., 2007; Bianchelli et al., 2008, 2010, Ingels et al., 2009, 2011a, 2011b, 2011c; Danovaro et al., 2010; Pusceddu et al., 2013). Nematodes, as the most abundant meiobenthic taxon, are considered a useful tool to obtain information on ecosystem characteristics and functioning (Heip et al., 1985; Vincx et al., 1994). Due to their ecological and biological characteristics (high abundance, sensitive to different types of disturbance, short generation time, limited mobility and lack of pelagic life stages), it is expected that the structural and functional diversity of nematode communities reflect variability in habitats, physical disturbance and food availability throughout canyon systems over time (Giere, 2009; Vanreusel et al., 2010). Still, many of the canyon studies only address spatial patterns (e.g. Danovaro et al., 1999, 2009; Garcia et al., 2007; Ingels et al., 2009, 2011b, 2011c; Bianchelli et al., 2010; Ingels and Vanreusel, 2013).

The relative inaccessibility and the logistical challenges of maintaining a long-term monitoring programme are among the main factors restricting temporal studies in canyons. Information on temporal variability of meiofauna within canyons is therefore sparse and generally limited to seasonal studies (Danovaro et al., 1999; Gooday, 2002; Fontanier et al., 2005). The few studies that use nematodes to investigate intra- and inter-annual variability, focus solely on abundances (de Bovée et al., 1990; Soetaert et al., 1991; Guidi-Guilvard et al., 2005) and to our knowledge only one study has investigated patterns based on nematode diversity as well as biomass (Pusceddu et al., 2013) from canyons in the Mediterranean Sea. All studies indicate high variability over time, probably related with fluctuations of the food supply in the context of benthic-pelagic coupling. Additionally, alterations to the sedimentary environment caused by physical disturbance (e.g. turbidity currents, benthic storms, etc.) may be responsible for some of the faunal temporal changes observed (Guidi-Guilvard et al., 2009; Pusceddu et al., 2013). Meiofaunal abundances can decrease markedly after physical disturbance events and are usually followed by a short recovery time (Ingels et al., *in press*; Romano et al., *in press*; Pusceddu et al., 2013). The causes for the evident standing stocks decrease could be the result of one or a set of factors such as an increase in mortality, resuspension and transport of the individuals entrained with sediments, and migration to deep sediment layers (Guidi-Guilvard et al., 2009). Nevertheless, limited information is available on how meiobenthic, and in particular nematode community composition, and structural and functional diversity are altered by temporal changes in canyons.

As part of the HERMES project (Hotspot Ecosystem Research on the Margins of European Seas), the NE Atlantic margin's largest canyon, the Nazaré Canyon, was sampled in three consecutive years (2005–2007), permitting us to perform the first inter-annual meiobenthic study in canyons along the Iberian coast. Using already published (Ingels et al., 2009, 2011b; Kiriakoulakis et al., 2011) and new data, the main aim of this study was to investigate inter-annual patterns of the meiofaunal communities, with emphasis on free-living marine nematodes at two distinct abyssal

canyon locations (representing two different water depths; ca. 3500 m and ca. 4400 m). We hypothesised that potential changes in environmental conditions between the two canyon sites and over the years would be reflected in the meiofauna/nematodes standing stocks and structural and functional diversity. The following null hypotheses were tested for meiofauna and nematode abundance, community composition, biomass, diversity, and trophic composition: (1) there are no significant differences between the different years, 2005, 2006, and 2007; (2) there are no significant differences between the canyon sites (ca. 3500 and ca. 4400 m); (3) there is no relation between environmental conditions and meiofauna and nematode community parameters.

2. Material and methods

2.1. Study area

The Western Iberian Margin in the Northeast Atlantic is characterised by a narrow shelf adjacent to a steep irregular slope and is incised by numerous canyons. The largest canyon along the Western Iberian Margin is the Nazaré Canyon (Fig. 1), originating on the shelf at a water depth of 50 m near the Portuguese coast and extending to 5000 m water depth at the edge of the Iberian Abyssal Plain (Masson et al., 2011). There is no connection to a large river system, but the canyon intersects a significant part of the shelf, and traps large quantities of sediments with high OM content that are moving along the coast (de Stigter et al., 2007; Oliveira et al., 2007; Arzola et al., 2008; Lastras et al., 2009; Masson et al., 2011). The canyon is usually divided into three parts on the basis of its morphology (de Stigter et al., 2007; Lastras et al., 2009). The upper and mid-canyon sections are characterised by the presence of moderately strong tidal currents (maximum of 35 cm/s), causing resuspension, transport and redistribution of particulate matter (de Stigter et al., 2007; Masson et al., 2011). The transport towards the lower part of the canyon takes place predominantly in nepheloid layers or less frequently through the flushing of sediments by gravity flows, providing irregular OM input to the deeper section (Van Weering et al., 2002; de Stigter et al., 2007; Lastras et al., 2009). The mid-canyon site was located in the central part of the canyon on a terraced slope next to the axial channel (thalweg), with high sediment accumulation rates (Arzola et al., 2008; Lastras et al., 2009). The deep-canyon site was located in the flat-floored lower canyon valley.

2.2. Sampling

The sampling was conducted during the late spring/early summer of 2005, 2006 and 2007, at ca. 3500 m and ca. 4400 m, corresponding to the mid and deeper sections of the canyon, respectively (Fig. 1; Weaver, 2005; Billett, 2006; Masson, 2009). At each sampling site and in each year, 6 sediment cores were recovered (3 for meiofauna analysis and 3 for environmental analyses). The sediment samples from 2005 and 2006 were obtained using a multicorer (MUC, Plexiglas tubes with 57 mm internal diameter) and a megacorer (MGC, Ocean Scientific International Ltd, Plexiglas tubes with 100 mm internal diameter), the latter subsampled with a core of 60 mm internal diameter, in order to maintain relative consistency in sample surface area for all replicates. The 2007 samples were taken using push cores (with internal diameter of 57 mm) by the Remotely Operated Vehicle (ROV) ISIS. At each sampling event the top 1 cm of 3 replicate cores (each core from independent deployments) were placed in Petri dishes and frozen at -20°C , for later determination of environmental characteristics in the lab. The other 3 replicate cores from independent deployments, with exception of the deep site in 2006

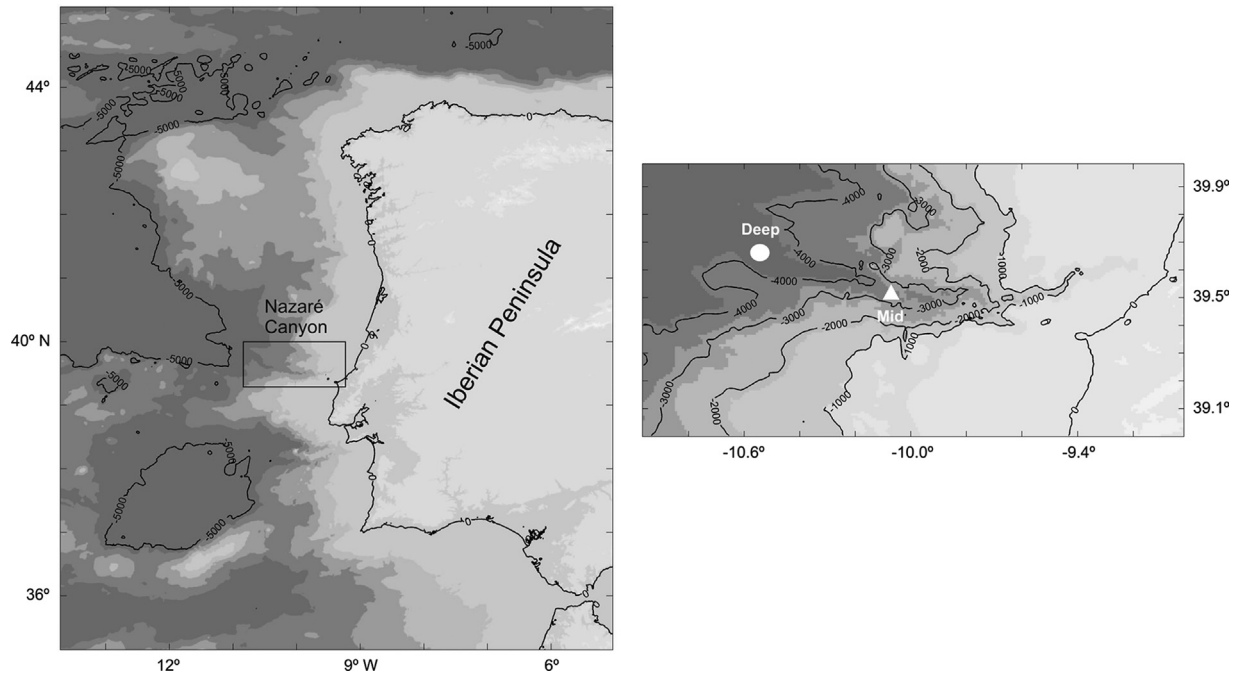


Fig. 1. Left: Overview of the Western Iberian Margin showing the location of the Nazaré Canyon. Right: Detailed map presenting the local geomorphological setting of the Nazaré Canyon sample stations: Mid (ca. 3500 m) and Deep (ca. 4400 m). Bathymetry data compiled from a General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas (IOC et al., 2003) and Mirone software (Luis, 2007, <http://w3.ualg.pt/~jluis/mirone/>).

when only 2 replicates were recovered, were fixed in borax-buffered 4% formalin for further meiofauna analysis.

2.3. Environmental data

In the laboratory, sediments were analysed for grain size, geochemistry and pigment content. In 2007 for the deep station, it was not possible to analyse granulometry and pigment content in the sediment, and for some replicates in 2006 not all variables could be measured. The grain-size distribution of the 4–800 μm sediment fraction was measured using a Coulter Counter LS 100TM Particle Size Analyzer and classified according to Wentworth (1922). Total organic carbon (TOC) and total nitrogen (TN) content was measured using a CEInstruments NC 2500 CHN analyser in duplicate (mean value quoted here; all values were within 10% of the mean). Samples for TOC analyses were acidified according to the acid vapour method of Yamamuro and Kayanne (1995). TN was determined without acidification. To estimate the amount of OM in the sediment that is derived from primary production, the sediment samples were lyophilised and homogenised prior to extracting the pigments in 90% acetone. Pigments were then separated using reverse phase HPLC, and quantified using a fluorescence detector according to Wright and Jeffrey (1997). Chloroplastic Pigment Equivalents (CPE) values were obtained from the sum of chlorophyll *a* (chl *a*) and its degradation products, phaeopigments (phaeo). To estimate the freshness of OM of photosynthetic origin, the ratio chl *a*:phaeo was determined (García and Thomsen, 2008). Additionally, the ratio chl *a*:TOC was used as a measurement to the bioavailability of organic carbon from photosynthetic origin. The environmental data has been published in Ingels et al. (2009, 2011b) and Kiriakoulakis et al. (2011).

2.4. Meiofauna and nematodes

Meiofauna was extracted from the sediment using a density gradient solution in a centrifugation procedure (Heip et al., 1985). The fixed samples were rinsed on a 1000- μm mesh sieve followed

by sieving on a 32- μm mesh. The retained 32–1000 μm fraction was washed and centrifuged three times using the colloidal silica polymer LUDOX TM 40 (specific gravity 1.19). The supernatant of each washing cycle was again collected on a 32- μm sieve. After extraction, the samples were kept in buffered 4% formalin and stained with Rose Bengal. All metazoan meiobenthic organisms were counted and classified at higher taxon level following Higgins and Thiel (1988; all at phylum level apart from nauplius larvae, which are ecologically distinct from their adult counterparts, the copepods) under a Leica S6E stereomicroscope (50 \times magnification). For nematode identification, 100–120 nematodes (or all nematodes when densities were lower than 120 per sample) were picked out randomly and mounted on permanent glycerin slides after stepwise dehydration in a graded series of ethanol: glycerin mixtures (Seinhorst, 1959). Afterwards, the nematodes were identified down to genus level using pictorial keys (Platt and Warwick, 1988) and the online identification keys/literature available on Nemys Database (Deprez et al., 2005, www.nemys.ugent.be). When a specimen could not be assigned to a genus, it was identified at the family level. All identified individuals were also grouped into four feeding-type groups (selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A), and predators/scavengers (2B)) according to the Wieser classification (1953). Nematode length (excluding filiform tail tips; *L*) and maximum body width (*W*) were measured under a Olympus BX-50 compound microscope (1000 \times magnification) with Olympus Cell[^]D software. Biomass of all specimens was calculated by applying Andrassy's formula for calculating the wet weight (Andrassy, 1956). A ratio of 0.25 was assumed to convert nematode wet weight in dry weight (dwt; Heip et al., 1985). Part of the meiofauna and nematode data has been published previously in Ingels et al. (2009) and Ingels et al. (2011b).

2.5. Data analyses

In order to test for significant differences in all investigated environmental and biological data between years and stations, a two-way crossed design (factors: year (fixed) and depth (fixed))

was used to perform either uni- or multivariate analysis of variance by permutation (PERMANOVA Anderson, 2005; Anderson et al., 2008). All analyses, apart from correlations, were performed using PRIMER v6 (Clarke and Gorley, 2006) and PERMANOVA+ (Anderson et al., 2008). To investigate significant differences in all environmental variables over time and depth/stations, uni- and multi-variate PERMANOVA analyses were applied (all environmental variables were analysed univariately, apart from grain-size data, which was analysed multivariately by considering clay, silt and sand as multivariate variables). Additionally, a principal component analysis (PCA) was performed to identify temporal and spatial patterns based on physicochemical data. Prior to the calculation of the Euclidean distance resemblance matrix, the data were checked for uniform distribution (the C:N ratio values were $\log[0.01+X]$ transformed) followed by normalisation (subtracting the mean and dividing by the standard deviation, for each variable) before analysis.

Two-way PERMANOVA analyses were performed to test if the meiofauna and nematode abundance, community composition, and biomass, differed significantly over time and between water depths/habitats. The data were *a priori* standardized, square-root transformed (fourth-root transformed in the case of biomass) and the Bray–Curtis similarity was used for calculating the resemblance matrix. Whenever significant differences were detected, pairwise comparisons were performed. When PERMANOVA permutations numbers were limited (< 100), Monte-Carlo values were used to infer significance. Afterwards, to determine the relative contribution of each genus to the (dis)similarities between years and stations, a two-way crossed similarity percentage analysis procedure (SIMPER; cut-off percentage: 90%) was performed. To determine temporal and spatial patterns between samples based on nematode community structure, a principal coordinate analysis (PCO) plot was drawn. The nematode structural diversity at genus level was calculated using Hill indices (1973) (H_0 , H_1 , H_2 and H_∞), Pielou evenness measure (J) and estimated number of genera (EG (51)). To understand the functional diversity the trophic diversity index was calculated (ITD; Heip et al., 1998) based on the feeding-types from Wieser (1953). The reciprocal value of the trophic index (Θ^{-1}) was used, so that the higher values of the index correspond to higher trophic diversity. As in the case of nematode abundance and biomass, differences in selected structural diversity measures (H_0 , H_1) and a functional diversity measure (trophic index; Θ^{-1}) were tested by means of univariate PERMANOVA (standardized, fourth-root transformed and Bray–Curtis similarity used for resemblance), to test for significant differences between factors.

To assess if and to what extent the physicochemical variables explained changes in nematode community composition, a

DISTLM (distance-based linear model) routine was applied. DISTLM allows for the building of a parsimonious model of variables that explain the nematode genera community patterns and testing the interrelationships by means of permutation. The DISTLM procedure was conducted using adjusted R^2 as selection criterion and a stepwise selection procedure, whereby in each step the routine adds a variable to the model (starting from 0) that improves the selection criterion based on a conditional test, followed by the removal of a variable if the criterion can be increased (Anderson et al., 2008). The dbrDA (distance-based redundancy analysis) plot was computed to illustrate the DISTLM model. To complement these analyses, correlations were calculated between environmental variables and meiofauna/nematode abundance and biomass, and diversity of the nematodes (non-parametric Kendall-tau statistics using Statistica v7).

3. Results

3.1. Characterisation of the environment

The results of the PERMANOVA analyses revealed significant differences between years for sediment grain size and all variables derived from photosynthetic pigment values (Table 1 and Table S1). Significant depth differences were only found for the variables TN, CPE and phaeo.

A high content of clay and silt (79–91%) and low sand content (9–21%) were found in 2005 and 2007, whilst a remarkable increase of sand content (56–75%) was observed in 2006. The total phytopigment concentrations (CPE, chl *a*), freshness (chl *a*:phaeo ratio) and bioavailability (chl *a*:TOC ratio) of the phytodetrital OM were particularly high in 2007 at the mid-canyon station (Table 1). No significant differences were found between years for TOC and TN values (Table S1), but the highest values were consistently found at the mid-canyon station (1.70–2.05 for TOC %, 0.20–0.22 for TN%), with lower values at the deeper station (1.41–1.68 for TOC%, 0.15–0.16 for TN%; Table 1). Only TN values were significantly different between stations ($p < 0.05$, Table S1). Relatively high C:N ratios were observed in all samples (9.2–12.7) compared to literature values for fresh marine OM, particularly at the deeper station (Table 1), but no statistically significant differences were found between years or stations.

The results of the PCA ordination showed a distinct separation of the different sampling years (Fig. 2), in accordance with the PERMANOVA analyses and the physicochemical values (Fig. 2, Table S1). No consistent differences were observed between stations. The first two PC axes explained 71% of the variation (46.3 and 24.6 for PC1 and PC2,

Table 1

Mean \pm standard deviation values of environmental variables for each year at each station. Mid: ca. 3500 m, Deep: ca. 4400 m; Sediment fraction according to Wentworth (1922): clay (%), silt (%), sand (%); total organic carbon (TOC), total nitrogen (TN), molar carbon:nitrogen ratio (C:N); chloroplastic pigments equivalents (CPE), chlorophyll *a* (chl *a*), chlorophyll *a*:phaeopigment ratio (chl *a*:phaeo) and chlorophyll *a*:total organic carbon (chl *a*:TOC).

Year:	2005		2006		2007	
	Mid	Deep	Mid	Deep	Mid	Deep
Clay (%)	12.17 \pm 0.46	10.63 \pm 0.66	16.42 \pm 3.24	12.58 \pm 4.88	13.96 \pm 0.82	–
Silt (%)	78.62 \pm 1.08	68.42 \pm 2.23	8.66 \pm 0.91	31.51 \pm 18.65	76.44 \pm 0.91	–
Sand (%)	9.22 \pm 0.78	20.95 \pm 2.78	74.92 \pm 2.46	55.91 \pm 13.79	9.61 \pm 0.41	–
TOC (%)	1.70 \pm 0.53	1.68 \pm 0.13	1.77 \pm 0.16	1.41 \pm 0.16	2.05 \pm 0.15	1.63 \pm 0.00
TN (%)	0.22 \pm 0.02	0.15 \pm 0.01	0.20 \pm 0.02	0.15 \pm 0.01	0.22 \pm 0.03	0.16 \pm 0.00
C:N	9.2 \pm 3.5	12.7 \pm 0.4	10.2 \pm 0.2	10.8 \pm 0.9	10.8 \pm 1.1	11.7 \pm 0.0
CPE (μ g/g)	1.67 \pm 0.09	1.14 \pm 0.19	0.44 \pm 0.18	0.20 \pm 0.13	1.61 \pm 0.13	–
chl <i>a</i> (μ g/g)	0.12 \pm 0.01	0.11 \pm 0.04	0.10 \pm 0.02	0.05 \pm 0.00	0.26 \pm 0.03	–
phaeo (μ g/g)	0.89 \pm 0.08	0.59 \pm 0.07	0.34 \pm 0.14	0.12 \pm 0.10	0.78 \pm 0.05	–
chl <i>a</i> :phaeo	0.08 \pm 0.01	0.10 \pm 0.02	0.32 \pm 0.11	0.21 \pm 0.00	0.33 \pm 0.02	–
chl <i>a</i> :TOC	0.08 \pm 0.04	0.06 \pm 0.03	0.05 \pm 0.02	0.01 \pm 0.02	0.13 \pm 0.03	–

respectively). The main contributors were CPE (−0.437), sand % (0.414) and silt % (−0.409) for axis PC1 and chl *a*:phaeo (0.559) and clay % (−0.505) for axis PC2 (numbers in parentheses represent eigenvector values).

3.2. Metazoan meiofauna

In total, 19 meiofauna higher taxa were identified; nematodes were always the dominant group (83.4–91.1%) (Table 2, Fig. 3), followed by nauplius larvae (3.3–9.6%) and harpacticoid copepods (3.3–7.8%). The remaining taxa comprised less than 1% of total

abundance. The results of the two-factor PERMANOVA for meiofauna abundance exhibited significant differences between years, stations and the interaction of both factors ($p < 0.01$, Table 3). Differences between stations were more important than the years and interaction differences judging by the higher estimated component of variation of the former. The highest total abundances were recorded in 2005 (509.5 ± 107.5 ind. 10 cm^{-2}), whilst abundances in 2006 and 2007 were ca. 30–40% lower and variable depending on the station (299.0 ± 41.4 ind. 10 cm^{-2} and 363.4 ± 316.6 ind. 10 cm^{-2} , for the 3400 m and 4400 m sites, respectively; Table 3, Fig. 3). Meiofauna community structure was significantly different only when the two stations were compared ($p < 0.05$, Table 3).

3.3. Nematodes

3.3.1. Nematode assemblages

The results of the two-factor PERMANOVA analysis indicated significant differences in nematode communities between years ($p < 0.01$), stations ($p < 0.01$), and the interaction of both factors ($p < 0.05$, Table 3). However, station differences were clearly more important than yearly differences or the interaction for community variability as indicated by the high estimated component of variation (ECV). Overall, the community-based PCO ordination plot (Fig. 4) shows a complete separation of the mid- and deep-stations, but also clear differences between 2005 and samples taken in 2006 and 2007. Subsequent pairwise tests confirmed this, with 2005 assemblages highly distinct from 2006 and 2007 ($p < 0.01$, Table S2). No significant differences were observed between the samples from 2006 and 2007. Additionally, while nematode communities from different stations showed significant differences for 2005 and 2007 ($p < 0.05$), in 2006, differences between the two stations were not significant ($p = 0.068$ level, Table S2).

The most common genera found in all canyon stations were *Halalaimus* ($12.8 \pm 5.9\%$), *Dichromadora* ($8.8 \pm 7.3\%$), *Acantholaimus* ($8.3 \pm 11.8\%$), *Desmoscolex* ($6.9 \pm 7.8\%$), and *Daptonema* ($5.4 \pm 2.3\%$; Table 4). The SIMPER analysis showed a maximum dissimilarity between mid-station and deep-station assemblages (60%), mainly through the presence of *Desmoscolex* (6.5%) and *Acantholaimus* (5.6%), which are typically found at the deep station. The highest between-year dissimilarities in the assemblages were found

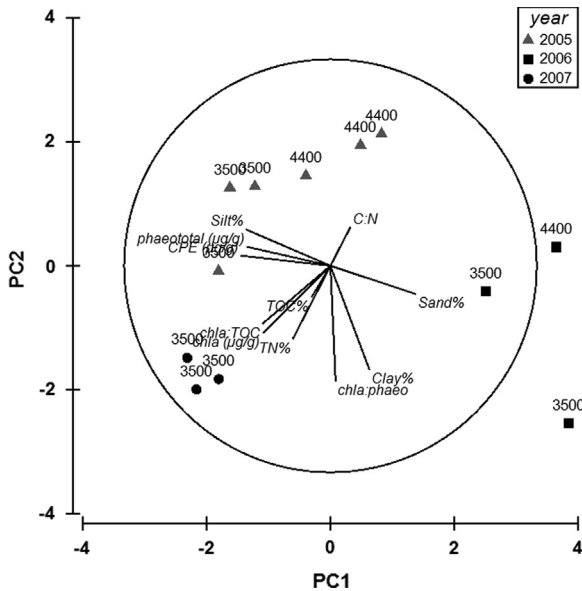


Fig. 2. Principal component analysis (PCA) ordination based on environmental data per year at the two studied stations (Mid: ca. 3500 m and Deep: ca. 4400 m). Data untransformed (except log (0.01 + X) transformation for C:N ratio) and normalised. Euclidean distance used as measurement for resemblance. Parameters included in the analysis are: Sediment fraction according to Wentworth (1922): clay (%), silt (%), sand (%); total organic carbon (TOC), total nitrogen (TN), molar carbon:nitrogen ratio (C:N); chloroplastic pigments equivalents (CPE), chlorophyll *a* (chl *a*), chlorophyll *a*:phaeopigment ratio (chl *a*:phaeo) and chlorophyll *a*:total organic carbon (chl *a*:TOC).

Table 2
Mean \pm standard deviation of meiofauna higher taxa abundance (ind. 10 cm^{-2}) for each year (2005, 2006 and 2007) and station (Mid: ca. 3500 m, Deep: ca. 4400 m).

Year:	2005		2006		2007	
	Mid	Deep	Mid	Deep	Mid	Deep
Bivalvia	–	0.4 \pm 0.0	0.8 \pm 0.2	0.2 \pm 0.2	0.4 \pm 0.3	–
Gastropoda	0.3 \pm 0.4	–	–	–	–	–
Gastrotricha	0.1 \pm 0.2	0.1 \pm 0.2	0.4 \pm 0.3	–	0.9 \pm 0.5	0.3 \pm 0.2
Gnathostomulidae	0.1 \pm 0.2	0.1 \pm 0.2	–	–	–	–
Halacarida	–	0.1 \pm 0.2	0.1 \pm 0.2	–	–	–
Harpacticoida	28.6 \pm 15.6	20.4 \pm 3.2	26.5 \pm 2.4	5.8 \pm 2.7	29.7 \pm 2.7	3.7 \pm 1.6
Holothuroidea	–	–	–	–	0.1 \pm 0.2	–
Isopoda	0.1 \pm 0.2	0.1 \pm 0.2	–	–	0.1 \pm 0.2	–
Kinorhyncha	12.0 \pm 4.3	0.3 \pm 0.2	6.7 \pm 4.9	0.4 \pm 0.4	7.8 \pm 1.4	0.4 \pm 0.4
Nauplii	26.5 \pm 16.4	28.5 \pm 4.6	17.1 \pm 3.9	6.0 \pm 1.4	60.9 \pm 14.0	5.0 \pm 1.8
Nematoda	515.1 \pm 60.2	372.2 \pm 60.0	314.7 \pm 106.3	175.3 \pm 33.6	535.6 \pm 102.2	74.7 \pm 35.2
Oligochaeta	0.1 \pm 0.2	0.1 \pm 0.2	0.1 \pm 0.2	0.2 \pm 0.2	0.1 \pm 0.2	–
Ostracoda	0.4 \pm 0.3	0.4 \pm 0.6	0.6 \pm 0.4	0.2 \pm 0.2	–	–
Polychaeta	2.2 \pm 1.0	1.2 \pm 0.6	2.5 \pm 1.5	1.4 \pm 0.7	3.5 \pm 0.6	0.5 \pm 0.4
Priapulida	0.3 \pm 0.4	0.1 \pm 0.2	0.1 \pm 0.2	–	0.3 \pm 0.4	–
Rotifera	3.5 \pm 0.5	3.8 \pm 0.8	0.6 \pm 0.4	0.9 \pm 0.9	–	–
Tanaidacea	0.1 \pm 0.2	0.3 \pm 0.4	0.1 \pm 0.2	0.2 \pm 0.2	0.5 \pm 0.5	0.1 \pm 0.2
Tardigrada	–	–	0.1 \pm 0.2	–	–	–
Turbellaria	0.9 \pm 0.7	0.4 \pm 0.3	0.4 \pm 0.3	0.5 \pm 0.2	–	0.3 \pm 0.4
Total (ind. 10 cm^{-2})	590.4 \pm 43.1	428.5 \pm 65.5	371.0 \pm 114.8	191.0 \pm 27.7	640.0 \pm 108.9	84.9 \pm 36.2

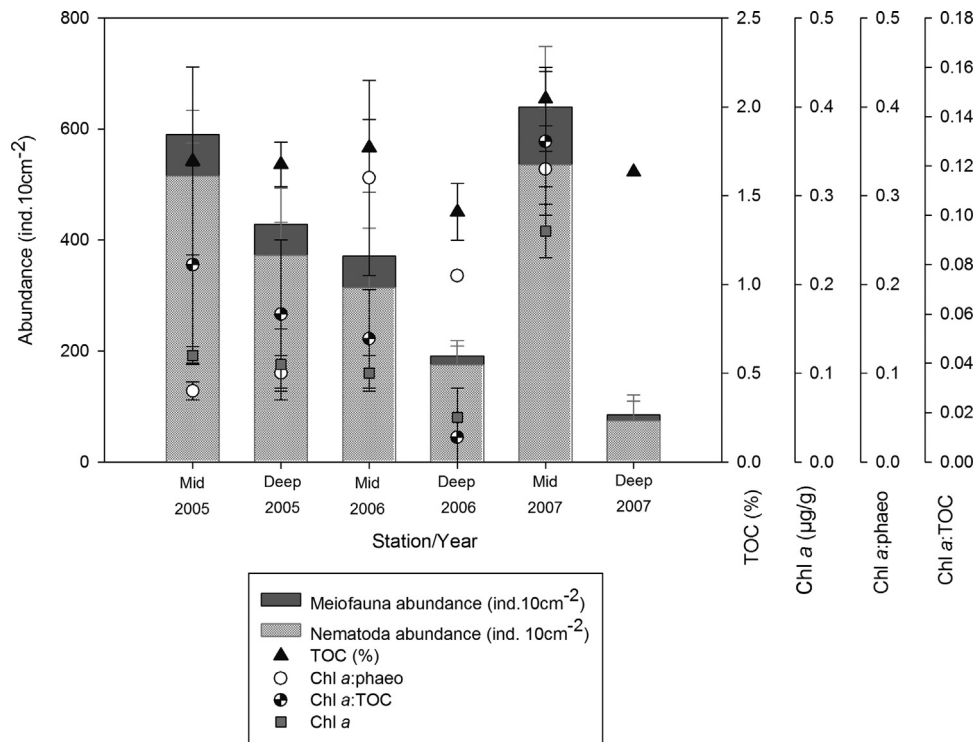


Fig. 3. Mean \pm standard deviation of the meiofauna and nematode abundances, total organic carbon (TOC), chlorophyll a (chl a), freshness (chl a:phaeo) and bioavailability (chl a:phaeo) in the sediment for all studied years at both stations (Mid: ca. 3500 m and Deep: ca. 4400 m).

between 2005 and 2007 (51.6%) followed by the comparison between 2005 and 2006 (50.8%), with *Acantholaimus* (3.4–4.1%), *Thalassomonhystera* (4.1%), *Metadesmolaimus* (5.3%), and *Molgolaimus* (3.0–3.7%) as the main contributors (Table 5).

3.3.2. Structural and functional diversity

Ninety-four nematode genera were identified among the 2088 individuals investigated (Table 6). Genus richness (H_0) and structural diversity based on H_1 differed significantly between years ($p < 0.05$; Table 3). Diversity at the deep station was greater in 2006 and 2007 compared to the mid-station; the inverse was true for 2005. Highest diversity values were observed at the deep station in 2006. The variable differences between stations for each year may explain the significant interaction in the PERMANOVA test ($p < 0.05$, based on H_0 and H_1 ; Table 3). The trophic diversity (θ^{-1}) changed significantly over time ($p < 0.05$, Table 3), but not between stations. The lower trophic diversity was found in 2006 (3.01 ± 0.30) followed by 2005 (3.22 ± 0.22) and the highest values were observed in 2007 (3.50 ± 0.17 ; Fig. 5). At the mid-station, the non-selective deposit feeders (1B) dominated the assemblages in all years, while at the deep site epistrate feeders dominated the assemblages in 2005, but were overtaken by the deposit feeders (1A, 1B) in 2006 and 2007. The predator/scavenger group (2B) was the least abundant feeding type in assemblages at both sites and in all sampling years (Fig. 5).

3.3.3. Biomass

The results of the univariate PERMANOVA analysis of biomass data indicated highly significant differences between years and stations ($p \leq 0.01$, Table 3; Fig. 6). The interaction of factors was not significant. Highest total nematode biomass (dwt) was observed in 2005 ($67.9 \pm 41.8 \mu\text{g dwt } 10 \text{ cm}^{-2}$), followed by 2006 and 2007 with $33.0 \pm 22.3 \mu\text{g dwt } 10 \text{ cm}^{-2}$ and $23.5 \pm 17.3 \mu\text{g dwt } 10 \text{ cm}^{-2}$, respectively. The general trend was that total biomass declined over the years at both stations. Additionally, the biomass was much higher at the

mid-canyon station ($35.4\text{--}85.2 \mu\text{g dwt } 10 \text{ cm}^{-2}$) than at the deeper station ($11.6\text{--}38.6 \mu\text{g dwt } 10 \text{ cm}^{-2}$). The estimated components of variation resulting from the PERMANOVA test indicate that greater biomass differences exist between stations than between years. The non-selective deposit feeders (1B) contributed the most to total biomass at the mid-station, whilst predators/scavengers dominated the biomass at the deep site.

3.4. Relation between nematode communities and environmental variables

The marginal (individual variables) tests on the DISTLM analysis indicated that chl a:phaeo, Clay% and TN% explain a significant amount of the variation in nematode genera composition ($p < 0.05$; 21.2%, 18.7%, 22.7% of variation explained, respectively). The sequential tests using the stepwise selection procedure indicated that the combination of TN%, chl a:phaeo, Silt%, CPE ($\mu\text{g/g}$), phaeo total ($\mu\text{g/g}$), and chl a:TOC constituted the best explanatory model for the nematode community patterns (ca. 73% of total variability explained). These results imply that the bioavailability of the OM in the sediments explain a large part of the variability observed in the nematode community. No separation was observed in the dbrDA plot between the years 2006 and 2007, but the 2005 samples were separated from the 2006–2007 group (Fig. 7). The environmental vectors on the plot give an indication of the importance of the environmental variable differences between different samples. The first two dbrDA axes explained 56.7% of the variation contained in the nematode genera composition.

The Kendall-Tau correlations are shown in Table 7. Both meiofaunal and nematode abundances were positively correlated with quantity and bioavailability of the OM (CPE, chl a, and chl a:TOC), whilst TN(%) was positively correlated with meiofauna abundance only ($p=0.019$). None of the environmental factors showed a correlation with nematode biomass nor with any diversity measurements (data not shown), except for the trophic

Table 3
Results of the two-way PERMANOVA test (factor “Year” with 3 levels, and factor “Station” with 2 levels, both fixed) for all biological variables analysed: meiofauna abundance and composition, nematode community structure, structural (H_0 and H_1) and functional diversity (θ^{-1}) and biomass ($\mu\text{g } 10 \text{ cm}^{-2}$; dwt) between years (2005, 2006 and 2007), water depths stations (Mid: ca. 3400 m and Deep: ca. 4400 m) and interaction of factors. A—meiofauna composition; B—nematodes descriptors. *Significance at the $p < 0.05$ level and ** $p < 0.01$. Data were standardised and square root transformed; resemblance was calculated using Bray–Curtis similarity.

Factors	df	SS	MS	Pseudo-F	P (perm)	Perms	Estim. of comp. of variation
A. Meiofauna							
Abundance							
Year	2	2220.8	2220.8	31.946	0.0003**	9941	258.96
Station	1	1353.5	676.73	9.7345	0.0009**	9942	108.99
Year \times Station	2	1349.9	674.97	9.7091	0.0018**	9956	217.34
Residual	11	764.7	69.519				69.519
Total	16	5766.8					
Community							
Year	2	211.32	211.32	2.071	0.0788	9953	13.154
Station	1	421.29	210.65	2.0643	0.0378*	9931	19.493
Year \times Station	2	176.32	88.161	0.86398	0.5356	9949	4.9824
Residual	11	1122.5	102.04				102.04
Total	16	1928.1					
B. Nematode							
Community							
Year	2	4932.6	2466.3	3.1135	0.0004**	9917	300.49
Station	1	8061.6	8061.6	10.177	0.0001**	9938	875.03
Year \times Station	2	2601.6	1300.8	1.6422	0.0247*	9911	182.6
Residual	11	8713.4	792.12				792.12
Total	16	24,791					
Genera richness (H_0)							
Year	2	34.945	17.473	4.9375	0.0322*	9946	2.5009
Station	1	5.2685	5.2685	1.4888	0.2362	9881	0.2082
Year \times Station	2	38.103	19.052	5.3837	0.0255*	9958	5.5687
Residual	11	38.926	3.5388				3.5388
Total	16	111.56					
Structural diversity (H_1)							
Year	2	34.955	17.473	4.9375	0.0304*	9958	2.5009
Station	1	5.268	5.2685	1.4888	0.2457	9904	0.2082
Year \times Station	2	38.103	19.052	5.3837	0.0281*	9953	5.5687
Residual	11	38.926	3.5388				3.5388
Total	16	111.56					
Trophic diversity (θ^{-1})							
Year	2	10.007	5.0036	5.8784	0.0198*	9946	0.7453
Station	1	0.2934	0.2934	0.3447	0.5792	9885	0.0672
Year \times Station	2	1.4047	0.7023	0.8251	0.4638	9953	0.0534
Residual	11	9.363	0.8511				0.8511
Total	16	21.263					
Biomass							
Year	2	3950.1	1975.1	2.2434	0.0016**	9880	196.48
Station	1	5995.3	5995.3	6.8099	0.0002**	9929	615.69
Year \times Station	2	2239.6	1119.8	1.2719	0.164	9900	85.94
Residual	11	9684.3	880.39				880.39
Total	16	22,119					

diversity, which was positively correlated ($p=0.039$) with the bioavailability of the sedimentary carbon pool (chl a :TOC).

4. Discussion

4.1. Sedimentary environment

Nazaré Canyon sediments at the studied sites are usually dominated by high fractions of clay and silt (Garcia et al., 2007; Ingels et al., 2009; Kiriakoulakis et al., 2011). Nevertheless, a striking rise in sand content in 2006 at both stations was observed compared to the previous and following year (2005 and 2007). The increase was not restricted to the surface layer but was established over at least 5 cm depth (unpublished data). This suggests the

occurrence of one or more deposition events, such as slumps or very rapid settlement of coarse sediment displacements, prior to the 2006 sampling event. Alternatively, the erosion of fine sediments may have occurred, which would have removed the top layer of the sediment and exposed the coarser sediment layers underneath. However, sediment cores recovered by Arzola et al. (2008) from the same locations as the present study show the prevalence of turbiditic mud in the top metre of the sediment. Another argument for proposing that the occurrence of one or more deposition events is likely to explain our observations is that mass deposition events, likely associated with sediment gravity flows, are not rare in the areas we investigated (de Stigter et al., 2007). The sedimentary environment in canyons is subjected to heterogeneous processes, characterised by cycles of suspension, transport and deposition that may be the result of one or a set of

the physical disturbance processes occurring with a distinct frequency and intensity over time (e.g. tidal currents, turbidity currents, occasional sediment gravity flows; Arzola et al., 2008; de Stigter et al., 2007; Lastras et al., 2009).

The observed changes in granulometry during the study period were possibly associated with changes in food supply and OM bioavailability. The significant drop of phytopigment concentrations (CPE, chl *a*) and phytodetrital OM bioavailability (chl *a*:TOC ratio) in 2006 compared to the years before and after is most likely linked to a dilution or covering effect caused by deposited layers of sediment with low OM phytodetritus concentrations, since the changes are consistent over a vertical profile of at least 5 cm depth (unpublished data). Still, there remains the possibility that erosion of the top sediment layers and re-deposition has occurred, particularly at the shallower station where strong tidal and turbidity currents are more common than at the deep site (de Stigter et al., 2007). Also changes in the sea surface productivity may have contributed to the observed changes in OM parameters in 2006.

The highest values of sediment OM content were consistently found at the mid-canyon station, which supports the view that

this site is a deposition center, whereas OM quantity and quality were consistently higher when compared to greater depths (Garcia et al., 2007; Ingels et al., 2009; Kiriakoulakis et al., 2011). The high C:N ratios in all samples confirm that the organic component of the sediments consists of (degraded) phytoplanktonic material, with variable contributions of terrigenous matter along the canyon. Particularly at the deeper station there is more refractory material from terrigenous origin present (de Stigter et al., 2007; García and Thomsen, 2008; Ingels et al., 2009, Kiriakoulakis et al., 2011).

4.2. Meiofauna densities in relation to the environment

The decrease in meiofauna abundance from 2005 to 2006 at both stations was highly related with sedimentary environmental parameters. The subsequent abundance increase at the mid-station in 2007 implies recovery of the meiofauna community that is able to thrive on the increased levels of OM. The meiobenthic response to environmental change linked to physical disturbance observed here is similar to that reported in the Mediterranean Sea (Guidi-Guilvard et al., 2005, 2009; Pusceddu et al., 2013). Following disturbance, meiofaunal abundances may decrease as animals are flushed away with the sediment or are diluted in the extra sediments transported and deposited along the canyon, or driven by increased mortality caused by the physical stress (Guidi-Guilvard et al., 2009). Also a key factor to consider is how granulometry determines spatial and structural conditions for endobenthos directly and indirectly via the regulation of the chemical environment (Giere, 2009). Grain size has profound effects on meiobenthic communities, which are often related to the oxygen and organic content in the sediments (Schratzberger et al., 2004). Significant inter-annual differences in meiofaunal abundance were related with changes of the quality (CPE and chl *a*) and bioavailability of the OM (chl *a*:TOC) in the sediment over time. Supporting this is the fact that meiofauna standing stocks are highly dependent on the food quantity that arrives at the deep-sea floor, but also on the nutritional value of the OM supplied (e.g. Gage and Tyler, 1991; Vincx et al., 1994; Smith and Druffel, 1998). The effect of OM quantity and quality was also expressed in the differences between stations, with meiofaunal abundance being consistently lower at the deeper station compared to the mid-canyon station. This is in agreement with OM being of lesser quality or more degraded when more time is needed for it to reach the deeper areas of the canyon. The topographical differences between the two sites and their position in the canyon would also contribute to the variability (e.g. Ingels et al., 2013 for the Blanes Canyon in the Mediterranean). The mid-canyon site is characterised by

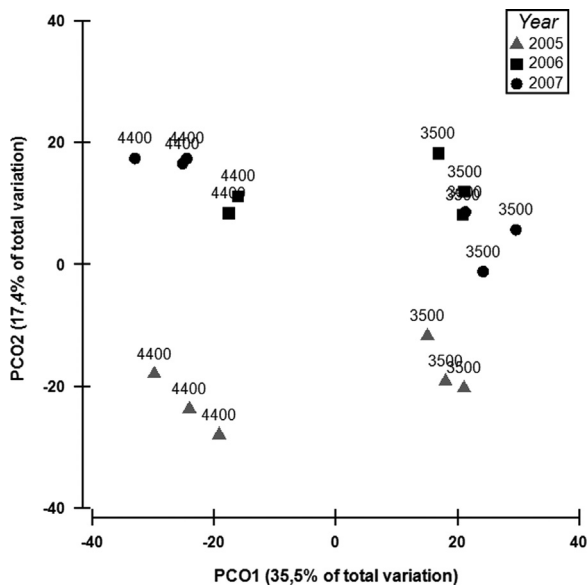


Fig. 4. Principal coordinates analysis (PCO) plot based on standardized and square-root transformed nematode genera relative abundance data and Bray-Curtis similarity measurement for each year (2005, 2006 and 2007) and station (Mid: ca. 3500 m and Deep: ca. 4400 m).

Table 4

Mean relative abundance of the abundant nematode genera ($\geq 3\%$) per year (2005, 2006 and 2007) and station (Mid: ca. 3500 m and Deep: ca. 4400 m). Nematode individuals that could not be identified to the genus level were grouped in the appropriate families.

2005			2006			2007					
Mid	%	Deep	%	Mid	%	Deep	%	Mid	%	Deep	%
<i>Halalaimus</i>	17.7	<i>Acantholaimus</i>	31.6	<i>Dichromadora</i>	17.5	<i>Halalaimus</i>	14.5	<i>Halalaimus</i>	17.9	<i>Desmoscolex</i>	17.8
<i>Daptonema</i>	9.6	<i>Halalaimus</i>	12.3	<i>Halalaimus</i>	12.7	<i>Desmoscolex</i>	12.2	<i>Dichromadora</i>	17.4	<i>Molgolaimus</i>	9.3
<i>Dichromadora</i>	9.3	<i>Desmoscolex</i>	11.1	<i>Metadesmolaimus</i>	12.0	<i>Acantholaimus</i>	7.5	<i>Pomponema</i>	10.3	<i>Acantholaimus</i>	7.2
<i>Paralongicyatholaimus</i>	8.8	<i>Tricoma</i>	5.7	<i>Pomponema</i>	6.2	<i>Campylolaimus</i>	7.4	<i>Retrotheristus</i>	8.5	<i>Campylolaimus</i>	6.3
<i>Pomponema</i>	7.5	<i>Daptonema</i>	5.7	<i>Daptonema</i>	5.7	<i>Tricoma</i>	6.1	<i>Actinonema</i>	5.2	<i>Oncholaimellus</i>	5.6
<i>Elzalia</i>	6.8	<i>Dichromadora</i>	5.3	<i>Retrotheristus</i>	5.0	<i>Sphaerolaimus</i>	4.7	<i>Elzalia</i>	4.6	<i>Thalassomonhystera</i>	4.8
<i>Actinonema</i>	5.1	<i>Sphaerolaimus</i>	3.4	<i>Aegialolaimus</i>	4.7	<i>Metadesmolaimus</i>	4.3	<i>Thalassomonhystera</i>	4.3	<i>Xyalidae</i>	4.3
<i>Axonolaimus</i>	4.9			<i>Actinonema</i>	3.5	<i>Daptonema</i>	4.2	<i>Eleutherolaimus</i>	3.7	<i>Daptonema</i>	4.1
				<i>Molgolaimus</i>	3.5	<i>Thalassomonhystera</i>	4.2			<i>Paracanthochus</i>	3.5
				<i>Monhystrella</i>	3.2					<i>Greeffiella</i>	3.2
										<i>Tricoma</i>	3.1

Table 5
Results of similarities and species contribution (SIMPER) analysis indicating (dis)similarity between years and water depths and distinguishing the genera that contributed to the (dis)similarity. Individual genus cut-off level for similarity was 5% and 3% for dissimilarity.

Year 2005	56.3	Year 2006	64.5	Year 2007	62.2	Mid	61.1	Deep	59.9
SIMPER similarity (% contribution > 5%)									
<i>Halalaimus</i>	12.9	<i>Halalaimus</i>	10.0	<i>Dichromadora</i>	8.7	<i>Halalaimus</i>	12.3	<i>Acantholaimus</i>	13.9
<i>Acantholaimus</i>	12.0	<i>Dichromadora</i>	8.7	<i>Halalaimus</i>	7.9	<i>Dichromadora</i>	11.9	<i>Desmoscolex</i>	12.1
<i>Daptonema</i>	10.0	<i>Metadesmolaimus</i>	8.6	<i>Desmoscolex</i>	7.0	<i>Pomponema</i>	7.9	<i>Halalaimus</i>	7.5
<i>Dichromadora</i>	9.6	<i>Daptonema</i>	7.0	<i>Campylaimus</i>	5.9	<i>Daptonema</i>	7.4	<i>Daptonema</i>	7.1
<i>Sphaerolaimus</i>	5.6	<i>Pomponema</i>	6.3	<i>Thalassomonhystera</i>	5.8	<i>Retrotheristus</i>	6.0	<i>Campylaimus</i>	6.1
<i>Desmoscolex</i>	5.6			<i>Daptonema</i>	5.0	<i>Actinonema</i>	6.0	<i>Tricoma</i>	5.6
						<i>Elzalia</i>	5.4	<i>Dichromadora</i>	5.2
Years 2005 vs. 2006	50.8	Years 2005 vs. 2007	51.6	Years 2006 vs. 2007			41.5	Mid vs. Deep	60.0
SIMPER dissimilarity (% contribution > 3%)									
<i>Metadesmolaimus</i>	5.3	<i>Thalassomonhystera</i>	4.1	<i>Metadesmolaimus</i>			5.8	<i>Desmoscolex</i>	6.5
<i>Acantholaimus</i>	3.4	<i>Acantholaimus</i>	4.1	<i>Molgolaimus</i>			5.0	<i>Acantholaimus</i>	5.6
<i>Molgolaimus</i>	3.0	<i>Molgolaimus</i>	3.7	<i>Halalaimus</i>			4.3	<i>Pomponema</i>	4.2
		<i>Halalaimus</i>	3.6	<i>Xyalidae</i>			3.4	<i>Dichromadora</i>	3.9
				<i>Aegialoalaimus</i>			3.4	<i>Retrotheristus</i>	3.2
								<i>Halalaimus</i>	3.2

Table 6
Mean \pm standard deviation of structural diversity indices per year (2005, 2006 and 2007) and station (Mid: ca. 3500 m and Deep: ca. 4400 m). H_0 , H_1 , H_2 and H_∞ : Hill (1973), J' : Pielou's evenness (Pielou, 1969), H' : Shannon–Wiener index (Krebs, 1989), EG(51): expected number of genera.

Year	Station (depth)	H_0	H_1	H_2	H_∞	J'	EG(51)
2005	Mid	32 \pm 1	15.42 \pm 1.79	9.47 \pm 1.57	4.59 \pm 1.30	0.79 \pm 0.03	18.71 \pm 1.16
	Deep	27 \pm 1	12.04 \pm 1.07	6.81 \pm 0.31	3.17 \pm 0.10	0.76 \pm 0.02	16.77 \pm 1.45
	Total	76	24.72	13.72	6.37	0.74	21.59
2006	Mid	26 \pm 4	16.14 \pm 3.31	11.06 \pm 2.73	5.10 \pm 1.25	0.85 \pm 0.03	18.90 \pm 2.67
	Deep	33 \pm 4	20.57 \pm 3.18	14.53 \pm 2.02	6.69 \pm 1.18	0.86 \pm 0.01	22.22 \pm 2.29
	Total	54	26.61	17.20	7.35	0.82	23.00
2007	Mid	24 \pm 3	14.35 \pm 2.97	10.13 \pm 2.59	5.24 \pm 0.78	0.83 \pm 0.06	17.54 \pm 2.27
	Deep	28 \pm 3	18.50 \pm 1.68	13.17 \pm 1.27	5.63 \pm 0.42	0.88 \pm 0.02	21.38 \pm 0.88
	Total	58	29.14	20.03	9.46	0.83	23.88
Total		94	31.90	18.92	7.46	0.76	24.24

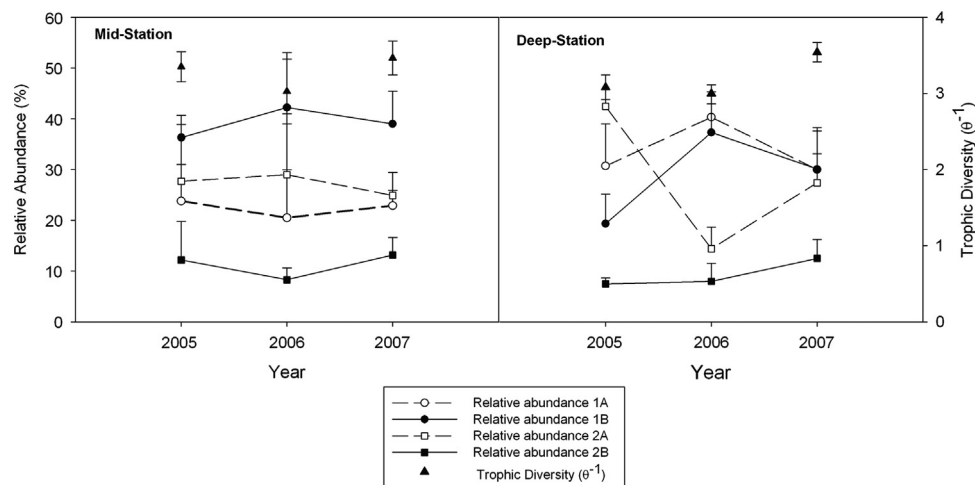


Fig. 5. Relative abundance of trophic groups according to Wieser (1953) and trophic diversity index (θ^{-1}) per each year (2005, 2006 and 2007) and station (Mid: ca. 3500 m, Deep: ca. 4400 m). 1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epigrowth feeders, 2B: predator/scavengers and dwt: dry weight.

much higher sedimentation rates and is likely to recover from any occurring disturbance event that is associated with the canyon axis more quickly compared to the deep site, which is positioned in the middle of the canyon floor. At the deeper site, meiofauna standing stocks did not recover as fast as the middle

site. Meiofauna in the deeper parts of the canyon are not regularly subjected to physicochemical stress and disturbance as in the middle part, and therefore the community may not be as resilient as the one inhabiting the more regularly disturbed sediments in the upper canyon.

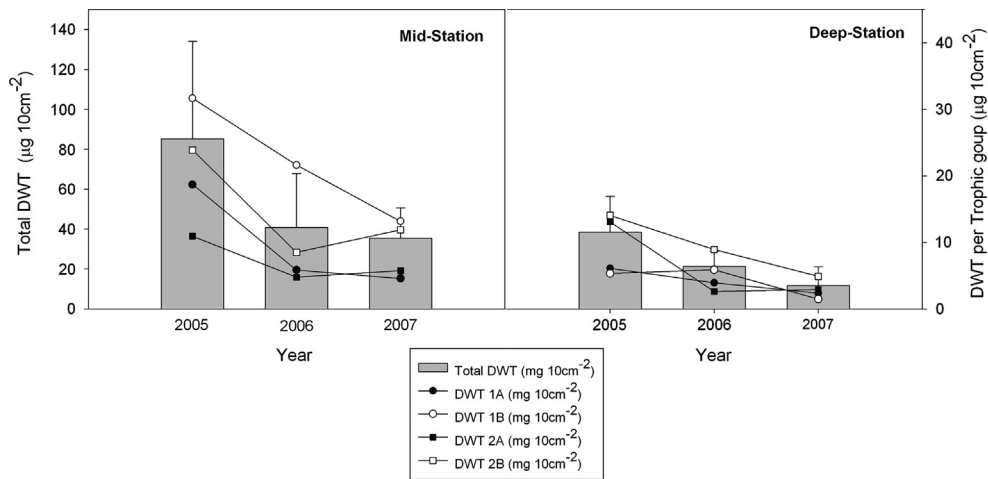


Fig. 6. Total and trophic group biomass values for each year (2005, 2006 and 2007) and station (Mid: ca. 3500 m, Deep: ca. 4400 m). 1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epigrowth feeders, 2B: predators/scavengers and dwt: dry weight.

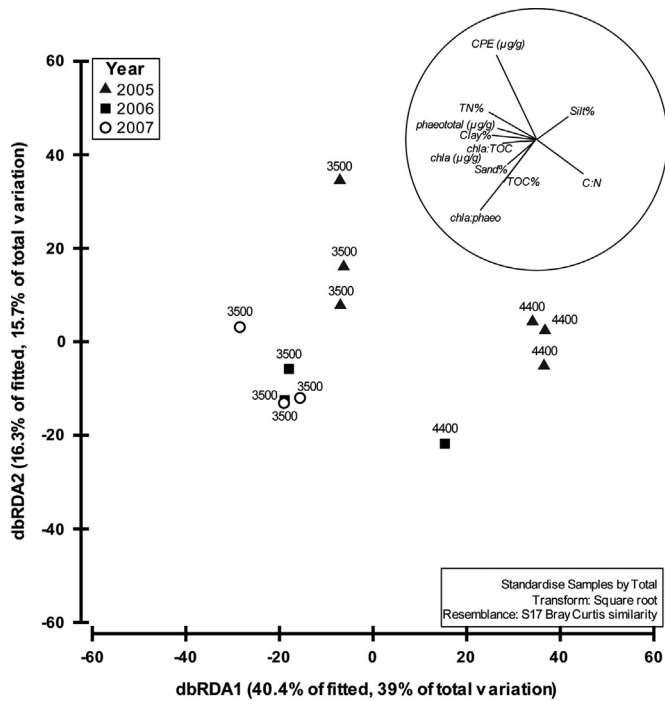


Fig. 7. Distance-based redundancy (dbRDA) plot illustrating the DISTLM model based on the nematode genera assemblages and the fitted environmental variables as vectors. Parameters included in the analysis were: Sediment fractions according to Wentworth's classification (1922): clay (%), silt (%), sand (%); total organic carbon (TOC), total nitrogen (TN), molar carbon:nitrogen ratio (C:N); chloroplastic pigments equivalents (CPE), chlorophyll *a* (chl *a*), chlorophyll *a*:phaeopigment ratio (chl *a*:phaeo) and chlorophyll *a*:total organic carbon (chl *a*:TOC).

4.3. Nematodes

4.3.1. Nematode community structure and diversity in relation to the environmental conditions

When comparing different nematode studies from canyons and slopes at the Western Iberian margin (Dinet and Vivier, 1979; Danovaro et al., 2000; Vanreusel et al., 1992; Garcia et al., 2007; Ingels et al., 2009, 2011a, 2011b), it is clear that the Nazaré Canyon exhibits lower local diversity (α diversity). However, Ingels et al. (2009) reported that despite their lower diversity, the nematodes assemblages in the Nazaré Canyon are distinct from the

Table 7

Kendall-Tau correlation coefficients between the abiotic and biotic factors with significance values (*p*). Abiotic factors are total organic carbon (TOC), total nitrogen (TN), molar carbon:nitrogen ratio (C:N); chloroplastic pigments equivalents (CPE), chlorophyll *a* (chl *a*), chlorophyll *a*:phaeopigment ratio (chl *a*:phaeo) and chlorophyll *a*:total organic carbon (chl *a*:TOC). Biotic factors shown are meiofauna abundance (ind. 10 cm⁻²), nematode abundance (ind. 10 cm⁻²), trophic diversity (θ^{-1}). The remaining other biotic factors (biomass, structural diversity (H_0 and H_1)) were also analysed but showed no correlation with the physicochemical variables. Significance at the **p* < 0.05 level and ***p* < 0.01.

Environmental variables	Meiofauna abundance		Nematode abundance		Trophic diversity (θ^{-1})	
	Kendall tau	<i>p</i>	Kendall tau	<i>p</i>	Kendall tau	<i>p</i>
TOC	0.027	0.217	0.182	0.411	0.182	0.411
TN	0.515	0.019*	0.424	0.054	0.303	0.170
C:N	-0.303	0.170	-2.212	0.337	-2.273	0.217
CPE	0.697	0.002**	0.545	0.014*	0.303	0.170
chl <i>a</i>	0.697	0.002**	0.606	0.006**	0.424	0.055
chl <i>a</i> : phaeo	-0.030	0.890	-1.121	0.583	-0.061	0.784
chl <i>a</i> : TOC	0.606	0.006**	0.576	0.009**	0.455	0.039*

assemblages on the continental slope and shelf, resulting in a high turn-over or β diversity, and hence an overall higher diversity for the Iberian Region (Danovaro et al., 2009). This phenomenon is probably related to the greater bioavailability of the OM and its nutritional value as well other environmental conditions that enhance faunal diversity (Dell'Anno et al., 2013).

No correlation was found between the structural or trophic diversity indices and the environmental variables. The H_1 index, based on relative abundances of the different genera, increased from 2005 to 2007 suggesting a rise in evenness over the three years. Considering the assumed disturbance event between 2005 and 2006, these results agree with other recent findings, whereby high nematode diversity occurred following recolonisation of defaunated sediments (Gallucci et al., 2008; Pusceddu et al., 2013). The high nematode densities in canyon sediments, and possibly their aggregation resulting from the often patchy distribution of phytodetrital material, are likely to constitute ideal conditions to recolonise sites that have been affected by a physical disturbance event (Gallucci et al., 2008; Guilini et al., 2011). Looking at the diversity indices for each station separately, we consistently observed higher values at the mid-canyon site compared to the deep site in 2005, whilst the opposite was true for 2006 and 2007. Possibly, the disturbance event(s) caused the

decrease in diversity at the middle site, and led to a reduced disturbance–productivity relation (Paterson et al., 2011; Leduc et al., 2012) persisting in 2006 and 2007, despite the recovery to a more diverse and evenly distributed community in these years at each station individually. However, we cannot exclude the possibility of downward vertical migration of nematodes in response to such disturbance episode. Increased abundance of nematodes in subsurface layers has been reported in previous canyon studies as a result of greater amounts of bioavailable OM in subsurface sediments (Ingels et al., 2009).

It was clear that nematode assemblage composition differed significantly between years and stations. This suggests that community composition may have changed significantly after the proposed disturbance(s), initially as a persistence response or resilience (2006) and afterwards perhaps as an early recolonisation process (2007). Despite the temporal effect on nematode assemblages, the differences between the two sites comprised the most important source of variability and are indicative of canyon heterogeneity playing a substantial role in shaping communities. This is supported by the SIMPER results, with community dissimilarity between both stations being greater (60%) than the dissimilarity between years (41.5–51.6%). Our analysis indicated strong links between environmental variables and nematode community characteristics, with variables that describe the quality of the food contributing most to the nematode community variability (e.g. C: N, chl *a*:TOC, chl *a*:phaeo, TN). The differences in food quality are likely to be responsible for the contrast between the stations and the observed differences between sampling years. The dominant genera at the deeper site (*Acantholaimus* and *Desmoscolex*), which are mainly responsible for the dissimilarities among depths, have ecological characteristics that support our suggestions of a recovery period. The genus *Acantholaimus* is known to be dominant in deep-sea sediments, and its relative abundance usually increases with increasing water depth, and hence diminishing food availability. It is usually associated with very low amounts of chl *a* in the sediments and is considered a “persister” (Bongers et al., 1991; Lee et al., 2001; De Mesel et al., 2006). The second most important genus contributing to dissimilarity values between sites was *Desmoscolex*, being more abundant at the deeper station. Vanaverbeke et al. (2004) suggested that members of the family Desmoscolecidae were more prominent in offshore deeper areas as an opportunistic group, which would explain their high relative abundance at the deep site in the Nazaré Canyon.

4.3.2. Nematode functional structure and biomass in relation to the environment

Canyon communities tend to be more complex in comparison to the adjacent slope in terms of trophic composition, particularly in the upper layers of the sediments, due the higher levels of bioavailable OM and recurrent hydrodynamic disturbance allowing the coexistence of different ecological groups (Bianchelli et al., 2008; Ingels et al., 2009, 2011a, 2011b, 2011c). The inter-annual variability in trophic composition suggests an effect of variability in food supply and/or physical disturbance event(s). The changes observed in the relative abundance of the nematode feeding groups between the 2005 and 2006 are in accordance with the occurrence of a disturbance event. The increase of non-selective deposit feeding (1B) nematodes and selective deposit feeders (1A) at the deeper site in 2006, support the hypothesis of recolonisation/recovery. The 1B nematodes are known to exhibit recolonisation ability after disturbance and are usually considered opportunistic and able to exploit a wider range of food sources compared other groups (Gallucci et al., 2008; Lee et al., 2001). In 2007, an increase in trophic diversity was observed with a more equal distribution of all trophic groups, likely resulting in a more

efficient exploitation of all available niches. Considering, the event (s) in 2006, it is likely that the trophic composition in 2007 is the result of the nematode assemblage reverting to the pre-disturbance state in terms of functional composition. Such a scenario would explain the shifts over time in terms of trophic group structure and genus diversity.

Trophic diversity was not different between stations, but there were station differences in relative abundance of feeding types. At the deep station, the higher abundance of selective-deposit feeders (1A) and epigrowth feeders (2A) was possibly linked to their food selectivity and the lower availability of OM. However, despite sediments at the deep station containing lower amounts and quality of OM than at the mid-canyon site, they are still enriched compared to the adjacent slope, and allow for the presence of a more complex trophic community compared to non-canyon systems (García and Thomsen, 2008; Ingels et al., 2009).

The nematode biomass decrease during the study period at both stations deviates from the meiofauna/nematode abundance patterns. For 2007, no biomass increase was observed at the mid-canyon station, whilst abundance clearly increased at this station that year. The explanation for this may lie in the fact that only the 0–1 cm sections of the collected cores were analysed in this study. Canyon sediments tend to have different vertical nematode distribution patterns than other deep-sea sediments (e.g. abyssal plain), with occasionally higher abundance and biomass in subsurface layers compared to the continental slope (Ingels et al., 2009, 2011a). Ingels et al. (2009) reported increased individual biomass deeper in the sediment, with the highest total biomass occurring between 1 and 3 cm sediment depths.

The station contrasts were the most important factor for nematode biomass (based on ECV values). Biomass values at the mid-canyon station exceeded those of the deeper site consistently, following the typical decrease of biomass with increasing water depth concomitant with diminishing food input and quality (Soetaert and Heip, 1989; Udalov et al., 2005; Rex et al., 2006). When studying the variations of nematode dimensions based on *L/W* ratios, it becomes clear that stout, shorter nematodes, with lower individual biomass, are commonly found at the deep station. In contrast, more slender and longer nematodes are found at the mid-canyon station. These findings support the view that smaller nematodes need less energy to sustain them compared to larger nematodes which is possibly explained by considering adaptation to low-food environments in deeper ocean areas (Thiel, 1975; Vanaverbeke et al., 2004).

5. Conclusions

Based on our findings we conclude that there was an inter-annual effect on meiofaunal communities and nematode functional and structural diversity and biomass. The results suggest the occurrence of one or more physical disturbance events, prior to the 2006 sampling, which shaped the environmental conditions (grain size and food resource quantity and quality) and consequently the benthic communities. Nevertheless, despite the observed abiotic and biotic changes over time, the differences in the meiofauna and particularly nematode community composition between stations (or water depths) were greater than the observed temporal differences. In conclusion, we suggest that inter-annual variations occur (e.g. physical disturbances and yearly variations in food supply) and are important in driving endofaunal assemblages in the Nazaré Canyon, but they can be overridden by the variability caused by habitat heterogeneity and water depth differences, which may influence food supply and availability.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2013.09.010>.

References

- Anderson, M., 2005. PERMANOVA: Permutational Multivariate Analysis of Variance. Department of Statistics, Auckland.
- Anderson, M.J., Gorley, R., Clarke, K., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth.
- Andrassy, I., 1956. The determination of volume and weight of nematodes. *Acta Zoologica (Hungarian academy of Science)* 2, 1–15.
- Arzola, R.G., Wynn, R.B., Lastras, G., Masson, D.G., Weaver, P.P.E., 2008. Sedimentary features and processes in the Nazaré and Setúbal submarine canyons, west Iberian margin. *Marine Geology* 250 (1), 64–88.
- Bianchelli, S., Gambi, C., Pusceddu, A., Danovaro, R., 2008. Trophic conditions and meiofaunal assemblages in the Bari Canyon and the adjacent open slope (Adriatic Sea). *Chemistry and Ecology* 24 (S1), 101–109.
- Bianchelli, S., Gambi, C., Zeppilli, D., Danovaro, R., 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on the rare taxa. *Deep-Sea Research Part I: Oceanographic Research Papers* 57 (3), 420–433.
- Billett, D., 2006. RRS Charles Darwin Cruise CD179, 14 April–17 May 2006. Hostpot ecosystem research in the Setúbal, Lisbon, Cascais and Nazaré Canyons on the Portuguese Continental Margin. National Oceanography Centre, Southampton p. 65.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, M., 2010. Long-term change in the abyssal NE Atlantic: the 'Amperima Event' revisited. *Deep-Sea Research Part II* 57, 1406–1417.
- Bongers, T., Alkemade, R., Yeates, G., 1991. Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of maturity index. *Marine Ecology Progress Series* 76, 135–142.
- Canals, M., Puig, P., de Madron, X.D., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. *Nature* 444, 354–357.
- Clarke, K., Gorley, R., 2006. PRIMER v6. User manual/tutorial. Plymouth Routine in Multivariate Ecological Research. Plymouth Marine Laboratory.
- Danovaro, R., Bianchelli, S., Gambi, C., Mea, M., Zeppilli, D., 2009. Alpha-, beta-, gamma-, delta- and epsilon-diversity of deep-sea nematodes in canyons and open slopes of Northeast Atlantic and Mediterranean margins. *Marine Ecology Progress Series* 396, 197–209.
- Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C., Olu, K., Polymenakou, P., Ramirez-Llodra, E., Sabbatini, A., Sardà, F., Sibuet, M., Tselepidis, A., 2010. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. *PLoS One* 5 (8), e11832.
- Danovaro, R., Dinet, A., Duineveld, G., Tselepidis, A., 1999. Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions-Catalan Sea (western-Mediterranean) and the Cretan Sea (eastern-Mediterranean). *Progress in Oceanography* 44 (1–3), 287–312.
- Danovaro, R., Tselepidis, A., Otegui, A., Della Croce, N., 2000. Dynamics of meiofaunal assemblages on the continental shelf and deep-sea sediments of the Cretan Sea (NE Mediterranean): relationships with seasonal changes in food supply. *Progress in Oceanography* 46 (2–4), 367–400.
- de Bovée, F., Guidi, L.D., Soyer, J., 1990. Quantitative distribution of deep-sea meiobenthos in the northwestern Mediterranean (Gulf of Lions). *Continental Shelf Research* 10 (9), 1123–1145.
- De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the Royal Society B: Biological Sciences* 277 (1695), 2783–2792.
- De Mesel, I., Lee, H.J., Vanhove, S., Vincx, M., Vanreusel, A., 2006. Species diversity and distribution within the deep-sea nematode genus *Acantholaimus* on the continental shelf and slope in Antarctica. *Polar Biology* 29 (10), 860–871.
- de Stigter, H.C., Boer, W., de Jesus Mendes, P.A., Jesus, C.C., Thomsen, L., van den Bergh, G.D., van Weering, T.C.E., 2007. Recent sediment transport and deposition in the Nazaré Canyon, Portuguese continental margin. *Marine Geology* 246 (2–4), 144–164.
- Dell'Anno, A., Pusceddu, A., Corinaldesi, C., Canals, M., Heussner, S., Thomsen, L., Danovaro, R., 2013. Trophic state of benthic deep-sea ecosystems from two different continental margins off Iberia. *Biogeosciences* 10, 2945–2957.
- Deprez, T., Steyaert, M., Vanaverbeke, J., Speybroeck, J., Raes, M., Derycke, S., De Smet, G., Ingels, J., Vanreusel, A., Van Gaever, S., 2005. NeMys. World Wide Web electronic publication. nemys.ugent.be.. Department of Marine Biology, Ghent University.
- Dinet, A., Vivier, M., 1979. Le méiobenthos abyssal du Golfe de Gascogne 2. Les peuplements de nématodes et leur diversité spécifique. *Cahiers de biologie marine* 20 (1), 109–123.
- Fontanier, C., Jorissen, F.J., Chaillou, G., Anschutz, P., Grémare, A., Griveaud, C., 2005. Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: faunal response to focusing of refractory organic matter. *Deep-Sea Research Part I* 52 (7), 1189–1227.
- Gage, J.D., Tyler, P.A., 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, UK.
- Gallucci, F., Moens, T., Vanreusel, A., Fonseca, G., 2008. Active colonisation of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model. *Marine Ecology Progress Series* 367, 173–183.
- García, R., Koho, K., De Stigter, H., Epping, E., Koning, E., Thomsen, L., 2007. Distribution of meiobenthos in the Nazare canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *Marine Ecology Progress Series* 340, 207–220.
- García, R., Thomsen, L., 2008. Bioavailable organic matter in surface sediments of the Nazaré canyon and adjacent slope (Western Iberian Margin). *Journal of Marine Systems* 74 (1–2), 44–59.
- Giere, O., 2009. *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*. Springer-Verlag, Berlin, Heidelberg.
- Glover, A., Gooday, A., Bailey, D., Billett, D., Chevalloné, P., Colaco, A., Copley, J., Cuvelier, D., Desbruyeres, D., Kalogeropoulou, V., 2010. Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. *Advances in Marine Biology* 58, 1–95.
- Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography* 58 (2), 305–332.
- Guilini, K., Soltwedel, T., van Oevelen, D., Vanreusel, A., 2011. Deep-sea nematodes actively colonise sediments, irrespective of the presence of a pulse of organic matter: results from an in-situ experiment. *PLoS One* 6 (4), e18912.
- Guidi-Guilvard, L.D., Dallot, S., Labat, J., 2005. Variations in space and time of nematode abundances at 2347 m depth in the North-Western Mediterranean. *Meiofauna Marina* 14, 33–40.
- Guidi-Guilvard, L.D., Thistle, D., Khrifounoff, A., Gasparini, S., 2009. Dynamics of benthic copepods and other meiofauna in the benthic boundary layer of the deep NW Mediterranean Sea. *Marine Ecology Progress Series* 396, 181–195.
- Heip, C., Herman, P., Soetaert, K., 1998. Indices of diversity and evenness. *Oceanis* 24, 61–87.
- Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. *Oceanography and Marine Biology* 23, 399–489.
- Higgins, R.P., Thiel, H., 1988. *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, London, UK.
- Ingels, J., Billett, D.S.M., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2011a. Structural and functional diversity of Nematoda in relation with environmental variables in the Setúbal and Cascais canyons, Western Iberian Margin. *Deep-Sea Research Part II: Topical Studies in Oceanography* 58, 2354–2368.
- Ingels, J., Billett, D.S.M., Van Gaever, S., Vanreusel, A., 2011b. An insight into the feeding ecology of deep-sea canyon nematodes—results from field observations and the first in-situ ¹³C feeding experiment in the Nazaré Canyon. *Journal of Experimental Marine Biology and Ecology* 396, 185–193.
- Ingels, J., Tchesunov, A.V., Vanreusel, A., 2011c. Meiofauna in the Gollum Channels and the Whittard Canyon, Celtic Margin—how local environmental conditions shape nematode structure and function. *PLoS One* 6 (5), e20094.
- Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazaré Canyon, Western Iberian Margin. *Deep-Sea Research Part I: Oceanographic Research Papers* 56 (9), 1521–1539.
- Ingels, J., Vanreusel, A., 2013. The importance of different spatial scales in determining structural and functional characteristics of deep-sea infauna communities. *Biogeosciences* 10 (7), 4547–4563.
- Ingels, J., Vanreusel, A., Romano, C., Coenjaerts, J., Mar Flexas, M., Zúñiga, D., Martin, D. Spatial and temporal infaunal dynamics of the Blanes submarine canyon-slope system (NW Mediterranean); changes in nematode standing stocks, feeding types and gender-life stage ratios. *Progress in Oceanography*. <http://dx.doi.org/10.1016/j.pocean.2013.07.021>, in press.

- IOC, IHO, BODC, 2003. Centenary Edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans. British Oceanographic Data Centre, Liverpool, UK.
- Kiriakoulakis, K., Blackbird, S., Ingels, J., Vanreusel, A., Wolff, G.A., 2011. Organic geochemistry of submarine canyons: the Portuguese Margin. *Deep-Sea Research Part II: Topical Studies in Oceanography* 58, 2477–2588.
- Koho, K., Kouwenhoven, T., De Stigter, H., Van Der Zwaan, G., 2007. Benthic foraminifera in the Nazaré Canyon, Portuguese continental margin: Sedimentary environments and disturbance. *Marine Micropaleontology* 66 (1), 27–51.
- Lastas, G., Arzola, R., Masson, D., Wynn, R., Huvenne, V., Huhnerbach, V., Canals, M., 2009. Geomorphology and sedimentary features in the Central Portuguese submarine canyons, Western Iberian margin. *Geomorphology* 103 (3), 310–329.
- Leduc, D., Rowden, A.A., Bowden, D.A., Probert, P.K., Pilditch, C.A., Nodder, S.D., 2012. Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity. *Marine Ecology Progress Series* 454, 53–64.
- Lee, H., Gerdes, D., Vanhove, S., Vincx, M., 2001. Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biology* 24 (12), 926–933.
- Luis, J.F., 2007. Mirone: a multi-purpose tool for exploring grid data. *Computers & Geosciences* 33, 31–41.
- Masson, D., 2009. RRS James Cook Cruise 36, 19 Jul–28 Jul 2009. The Geobiology of Whittard Submarine Canyon, 90.
- Masson, D., Huvenne, V., de Stigter, H., Arzola, R., LeBas, T., 2011. Sedimentary processes in the middle Nazaré Canyon. *Deep Sea Research Part II: Topical Studies in Oceanography* 58, 2388–2400.
- Masson, D., Huvenne, V., De Stigter, H., Wolff, G., Kiriakoulakis, K., Arzola, R., Blackbird, S., 2010. Efficient burial of carbon in a submarine canyon. *Geology* 38 (9), 831–834.
- McClain, C.R., Barry, J.P., 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91 (4), 964–976.
- Oliveira, A., Santos, A., Rodrigues, A., Vitorino, J., 2007. Sedimentary particle distribution and dynamics on the Nazaré canyon system and adjacent shelf (Portugal). *Marine Geology* 246 (2–4), 105–122.
- Paterson, G.L.J., Glover, A.G., Cunha, M.R., Neal, L., de Stigter, H., Kiriakoulakis, K., Billett, D.S.M., Wolff, G.A., Tiago, A., Ravara, A., 2011. Disturbance, productivity and diversity in deep-sea canyons: a worm's eye view. *Deep-Sea Research Part II: Topical Studies in Oceanography* 58, 2448–2460.
- Platt, H.M., Warwick, R.M., 1988. Free-living Marine Nematodes. Part II. British Chromadorids: Pictorial Key to World Genera and Notes for the Identification of British Species. E.J. Brill, W. Backhuys, Leiden.
- Pusceddu, A., Mea, M., Canals, M., Heussner, S., Durrieu de Madron, X., Sanchez-Vidal, A., Bianchelli, S., Corinaldesi, C., Dell'Anno, A., Thomsen, L., Danovaro, R., 2013. Major consequences of an intense dense self water cascading event on deep-sea trophic conditions and meiofauna biodiversity. *Biogeosciences* 10 (4), 2659–2670.
- Rex, M.A., Etter, R.J., Morris, J.S., Crouse, J., McClain, C.R., Johnson, N.A., Stuart, C.T., Deming, J.W., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series* 317, 1–8.
- Romano, C., Coenjaerts, J., Mar Flexas, M., Zúñiga, D., Vanreusel, A., Company, J.B., Martin, D., Spatio-temporal variability of meiobenthic density in the Blanes submarine canyon (NW Mediterranean). *Progress in Oceanography*. <http://dx.doi.org/10.1016/j.pocean.2013.07.026>, in press.
- Schratzberger, M., Bolam, S.G., Whomersley, P., Warr, K., Rees, H.L., 2004. Development of a meiobenthic nematode community following the intertidal placement of various types of sediment. *Journal of Experimental Marine Biology and Ecology* 303 (1), 79–96.
- Seinhorst, J., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* 4 (1), 67–69.
- Smith, J.K.L., Druffel, E., 1998. Long time-series monitoring of an abyssal site in the NE Pacific an introduction. *Deep-Sea Research Part II: Topical Studies in Oceanography* 45 (4–5), 573–586.
- Soetaert, K., Heip, C., 1989. The size structure of nematode assemblages along a Mediterranean deep-sea transect. *Deep-Sea Research Part I: Oceanographic Research Papers* 36 (1), 93–102.
- Soetaert, K., Heip, C., 1995. Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. *Marine Ecology Progress Series* 125, 171–183.
- Soetaert, K., Heip, C., Vincx, M., 1991. The Meiobenthos along a Mediterranean Deep Sea Transect off Calvi (Corsica) and in an adjacent canyon. *Marine Ecology* 12 (3), 227–242.
- Soltwedel, T., 2000. Metazoan meiobenthos along continental margins: a review. *Progress in Oceanography* 46, 59–84.
- Soltwedel, T., Hasemann, C., Quéric, N., von Juterzenka, K., 2005. Gradients in activity and biomass of the small benthic biota along a channel system in the deep Western Greenland Sea. *Deep-Sea Research Part I* 52, 815–835.
- Thiel, H., 1975. The size structure of the deep-sea benthos. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 60, 575–606.
- Udalov, A., Azovsky, A., Mokievsky, V., 2005. Depth-related pattern in nematode size: what does the depth itself really mean? *Progress in Oceanography* 67 (1–2), 1–23.
- Van Weering, T.C.E., De Stigter, H., Boer, W., De Haas, H., 2002. Recent sediment transport and accumulation on the NW Iberian margin. *Progress in Oceanography* 52 (2–4), 349–371.
- Van Gaever, S., Galéron, J., Sibuet, M., Vanreusel, A., 2009. Deep-sea habitat heterogeneity influence on meiofaunal communities in the Gulf of Guinea. *Deep-Sea Research Part II: Topical Studies in Oceanography* 56 (23), 2259–2269.
- Vanaverbeke, J., Soetaert, K., Vincx, M., 2004. Changes in morphometric characteristics of nematode communities during a spring phytoplankton bloom deposition. *Marine Ecology Progress Series* 273, 139–146.
- Vanreusel, A., Vincx, M., Vangansbeke, D., Gijssels, W., 1992. Structural analysis of the Meiobenthos communities of the shelf break Area in 2 stations of the Gulf-of-Biscay (Ne Atlantic). *Belgian Journal of Zoology* 122 (2), 185–202.
- Vanreusel, A., Fonseca, G., Danovaro, R., Da Silva, M.C., Esteves, A.M., Ferrero, T., Gad, G., Galtsova, V., Gambi, C., da Fonseca Genevois, V., 2010. The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. *Marine Ecology* 31 (1), 6–20.
- Vincx, M., Bett, B., Dinert, A., Ferrero, T., Gooday, A., Lamshead, P., Pfannkuche, O., Soltwedel, T., Vanreusel, A., 1994. Meiobenthos of the deep Northeast Atlantic. *Advances in Marine Biology* 30, 1–88.
- Weaver, P., 2005. RRS "Discovery" Cruise D297, 27 Jul–16 Aug 2005. The Geobiology of the Nazare and Setubal Canyons, Portuguese Continental Margin. HERMES Reports. National Oceanography Centre, Southampton p. 41.
- Wentworth, C., 1922. The Wentworth scale of grain size for sediments. *Journal of Geology* 30, 381.
- Wieser, W., 1953. Beziehungen zwischen Mundholengestalt, Ernahrungswiese und Vorkommen bei freilebenden marinen Nematoden. *Arkiv For Zoologie* 2, 439–484.
- Wright, S.W., Jeffrey, S.W., 1997. High-resolution HPLC system for chlorophylls and carotenoids of marine phytoplankton. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), *Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods*. United Nations Educational, Scientific and Cultural organization, Paris, pp. 327–341.
- Yamamoto, M., Kayanne, H., 1995. Rapid direct determination of organic carbon and nitrogen in carbonate-bearing sediments with a Yanaco MT-5 CHN analyzer. *Limnology and Oceanography* 40, 1001–1005.