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

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Highlights

- Standing stocks were mainly driven by temporal effects such as food pulses and disturbance events, rather than general depth patterns
- Topographical/hydrographical station differences are important for nematode standing stock patterns
- In food-rich environments such as the Blanes Canyon, nematode size distributions seem regulated by food-pulses
- Food pulses may induce the nematode community into a more 'reproductive' state and/or attract or stimulate smaller, more opportunistic species

Abstract

Despite recent advances in the knowledge of submarine canyons ecosystems, our understanding of the faunal patterns and processes in these environments is still marginal. In this study, meiobenthic nematode communities (from 300 m to 1600 m depth) obtained in November 2003 and May 2004 at eight stations inside and outside Blanes submarine canyon were analysed for nematode standing stocks (SSs), feeding types and gender-life stage distributions. Environmental data were obtained by sediment traps and current meters, attached to moorings (April 2003 – May 2004), and sediments samples analysed for biogeochemistry and grain size (May 2004). In November 2003, nematode SSs decreased with increasing depth (367.2 individuals and 7.31 $\mu\text{g C}$ per 10 cm^2 at 388 m water depth to 7.7 individuals and 0.18 $\mu\text{g C}$ per 10 cm^2 at 1677 m water depth), showing a significant negative relation (abundance: $R^2=0.620$, $p=0.020$; biomass: $R^2=0.512$, $p=0.046$). This was not the case in May 2004 (283.5 individuals and 3.53 $\mu\text{g C}$ per 10 cm^2 at 388 m water depth to 490.8 individuals and 4.93 $\mu\text{g C}$ per 10 cm^2 at 1677 m water depth; abundance: $R^2=0.003$, $p = 0.902$; biomass: $R^2=0.052$, $p=0.587$), suggesting a temporal effect that overrides the traditional decrease of SSs with increasing water depth. Both water depth and sampling time played a significant role in explaining nematode SSs, but with differences between stations. No overall differences were observed between canyon and open slope stations. Nematode standing stock (SS) patterns can be explained by taking into account the interplay of phytodetrital input and disturbance events, with station differences such as topography playing an important role. Individual nematode size decreased from November 2003 to May 2004 and was explained by a food-induced genera shift and/or a food-induced transition from a ‘latent’ to a ‘reproductive’ nematode community. Our results suggest that size patterns in nematode communities are not solely governed by trophic conditions over longer periods of time in relatively food-rich environments such as canyons. We hypothesize that food pulses in a dynamic and topographical heterogeneous environment such as canyons regulate nematode size distributions, rather than long-term food availability. Feeding type distributions in the Blanes Canyon did not clearly resemble those from other canyon systems, apart from the spring assemblage at one station in the head of the canyon.

Keywords: meiobenthos, nematodes, biomass, feeding group, particle fluxes, bottom currents, submarine canyon, Blanes, NW Mediterranean

1. Introduction

In contrast to early suppositions of the deep sea as a faunal desert, we now know that the deep sea is diverse, and that its fauna is subjected to many regulating biogeochemical processes and disturbance and productivity regimes (Gage, 1996; Gray, 2001; Snelgrove and Smith, 2002). Particularly the realization that the continental margins and the mid-oceanic sea floors are much more complex ecologically on various spatial scales, and the knowledge that seasonal variability in primary production as perceived at the ocean surface is able to affect community dynamics at great depth, has improved our understanding of deep sea ecosystems (Billett et al., 1983; Vanreusel et al., 2010). However, while for certain deep-sea habitats it is clear that the benthos is affected by seasonal production at the surface (Gooday, 2002), other habitats are less understood in this respect. This is particularly the case for habitats characterized by complex topography and disturbance regimes, such as submarine canyons, where interactions between different regulating processes are responsible for the faunal patterns we observe, and this on different spatial and temporal scales (McClain and Barry, 2010; Ingels et al., 2011a, c). In recent years, our knowledge on sedimentological and hydrological processes in canyon systems has increased significantly (Durrieu de Madron et al., 2008; Lastras et al., 2009; Zúñiga et al., 2009; de Stigter et al., 2011; Masson et al., 2011), but our understanding of the faunal patterns and processes in these environments is still marginal.

In deep-sea sediments, the meiobenthos (typically, individual organism between 32 and 1000 μm in size, but definitions vary between authors) is omnipresent, inhabiting the interstitial spaces between the sediment grains in vast numbers. Nematodes are usually the most abundant metazoan component of deep-sea meiobenthos and, compared to larger size classes, their numerical dominance frequently increases with depth (Thiel, 1975; Vincx et al., 1994; Mokievsky et al., 2007). Nematode communities can be characterized based on abundance and biomass (Standing Stock, SS), feeding types, gender/life stage ratios, and size class distributions which can be used to infer spatial and temporal dynamics of infaunal communities.

It is now well recognised that the SSs of meiobenthos are strongly correlated with trophic conditions in deep-sea environments. The quality of the sinking surface organic matter decreases through water column degradation processes as it descends to deeper waters. Consequently, SSs in the deep-sea decline with increasing water depth; a trend that has been demonstrated for meiobenthos on a global scale (Soltwedel, 2000;

Mokievsky et al., 2007). Food availability and quality on the seafloor are not only indirectly affected by depth; they are also dependent on the magnitude and variability of surface productivity, the hydrographical situation and habitats structure, and other environmental factors such as temperature and salinity as well as biogeochemical and biological processes on the seabed. In this context, also macro-topography should be recognised as a factor affecting the (re-)distribution of food resources, thereby playing an important role in governing SSs of meiobenthic organisms in different deep-sea habitats (Danovaro et al., 2002; Mokievsky et al., 2007). This is particularly the case for canyon and channel ecosystems where often steep topography allow for organic matter to be channelled, trapped and/or transported from shelf waters to the abyssal plains (i.e. “canyon effects”) and is able to shape the distribution of the food sources for the benthos and consequently influences benthic SSs (Ingels et al., 2009; Tyler et al., 2009; De Leo et al., 2010; Ingels et al., 2011c). In addition, canyons undergo more intense disturbance regimes, ranging from small sediment turbidity flows, dense water cascading, to riverine slumps and mass wasting events, which are often induced by storms, climatological conditions, sediment failure, and river floods (Paull et al., 2002; Puig et al., 2004; Canals et al., 2006). These disturbances are not rare events and can strongly affect biogeochemical processes and benthic life in canyons and the deep sea beyond the continental shelf (Thistle, 1988; Woodgate and Fahrbach, 1999; Lambshead et al., 2001; Sanchez-Vidal et al., 2008).

The here presented study fitted in the framework of the RECS project (REN2002-04556-C02-01/MAR), which aimed at investigating the ecology of an important fishing resource, the red shrimp (*Aristeus antennatus*) in relation with environmental and biological variables in submarine canyons. The project operated interdisciplinary by pursuing the integration meiobenthic data, fishery data, and hydrodynamic and geological data (Sarda et al., 2009). To get insight into canyon benthic community dynamics, the nematode assemblages in terms of biomass, feeding types and gender/life stage information was analyzed in the Blanes Canyon (BC) area and on the adjacent slope, and in relation to environmental variables (sediment characteristics, current intensity, and sedimentation regime) through time. Sample locations covered a depth gradient and different topographical and hydrogeological settings. The main objective was to investigate which environmental factors drive nematode community dynamics. The questions we addressed were (1) whether the environmental differences between autumn 2003 and spring 2004 affect nematode assemblages (November 2003, May 2004)

differently; (2) whether there is a depth gradient discernible; (3) whether the conditions inside the canyon affect nematode patterns differently than on the adjacent slope.

2. Material and methods

2.1 Regional settings

The BC is located on the Catalan continental margin (NW Mediterranean) where it cuts deep into the continental slope in a NW:SE direction (Fig. 1). Less than 4 km offshore, the canyon head buries its way into the continental shelf plane at about 60 m water depth (ITGE, 1989; Díaz and Maldonado, 1990) and is linked with the old riverbeds of the river Tordera and the streams of Blanes, Lloret and Tossa. The canyon width increases with depth, reaching a maximum of 20 km at its deepest point (Canals et al., 1982). The canyon ends in the Channel of Valencia, at 2400 m deep. The structure of the canyon, similar to those of La Fonera (or Palamós) and Cap de Creus (all in the NW Mediterranean), is defined by fracture lines and is at least partially eroded by subaerial conditions (Canals, 1985). The canyon exhibits a smooth-sloped eastern wall, whilst the western wall is steep and abrupt. Bathymetry and local topography of the BC exerts strong control on the hydrodynamic situation in the area, particularly in deeper waters, with pronounced differences between the eastern and western flanks in terms of current flow and variability (Zúñiga et al., 2009). The cross-section of the BC is V-shaped along the upper course and U-shaped in the lower course, reflecting the prevalence of erosion and accumulation processes, respectively (Fig 1).

2.2. Core sampling

A total of 46 faunal sediment cores (10 cm inner diameter, 78.54 cm²) with undisturbed sediment-water interface were collected in November 2003 and May 2004 at different habitats in the BC and on the adjacent slope with a Multicorer (Table 1, Fig. 1). Each core was obtained from different individual deployments, yielding replicated samples for each station. The sampled stations cover the three different sections of the canyon-slope area (upper canyon and shelf; the continental slope and middle canyon; and the lower canyon or basin flat sea floor). Eight stations were selected for this study: ‘Rocassa’ (canyon head, ca. 400 m water depth), ‘C1’ and ‘Sot’ (entrance of the upper canyon and upper canyon, respectively, between the main canyon axis and the adjacent slope, both at ca. 600 m water depth), ‘C2’ (middle canyon axis, ca. 1600 m water depth), ‘C3’ (west middle canyon wall, ca. 900 m water depth), ‘C4’ (eastern canyon wall, at the

edge of the canyon and the adjacent slope, ca. 900 m deep), and 'Barana' and 'C5' (outside of the canyon, ca. 800 and 1500 m deep, respectively). The sediment cores for the geochemical analyses are limited to those collected in the spring of 2004 during cruise RECS7 (9-11 May 2004); at each station four Multicorer deployments yielded four independent sediment cores, except for station C4 where only two cores were retrieved.

2.3. Meiobenthos processing and analyses

Each faunal sediment core was sliced in 1 cm sections down to 3 cm sediment depth for fixation and extraction procedures. Overlying bottom water was combined with the 0-1 cm section. The samples were fixed in a borax-buffered 4% formaldehyde/filtered sea water solution. Each sediment slice was then filtered over a set of 250 μm and a 32 μm sieves, and the meiobenthos was extracted from the 32 μm fraction by the Ludox flotation method (Heip et al., 1985; Vincx, 1996), stained with Rose Bengal, and counted under a stereoscopic microscope. The presence of meiofauna taxa in the $>250 \mu\text{m}$ fraction was negligible (<10 individuals), rendering them equivalent to a 32-1000 μm size fraction. Density was expressed as number of individuals per 10 cm^2 . A minimum of 120 nematodes (all nematodes when densities < 120) were picked out at random for each slice and mounted on glycerine slides. Individual nematode carbon content ($\mu\text{g C}$) was estimated using the product of volume and specific gravity (Andrassy, 1956), assuming a specific density of 1.13 and a conversion factor of 0.124 was applied to translate wet weight to carbon weight. Biomass size spectra were constructed using X2 geometric weight classes as defined by Warwick (1984), whereby weight class 0 = $0.000218 - 0.000436 \mu\text{g C}$, weight class 1 = $0.000436 - 0.000872 \mu\text{g C}$, and so on. Each individual nematode was assigned to a weight class. All nematodes (ca. 5000 individuals) were identified up to genus level and assigned to trophic groups according to Wieser (1953) and Jensen (1987). Gender and life stage (juvenile/adult) was identified for each specimen. Biomass and abundance data per cm slice was pooled per core to use in the analyses. Average data was calculated based on the mean values of the replicates that contained more than one individual.

2.4. Sediment characteristics

For sedimentological analyses, two cores were taken at each station, whereby the top centimetre was stored in sealed plastic bags at 4°C . Samples were subsequently dried at

50°C until constant weight prior to analyses. See Zúñiga et al. (2009) for a detailed description of the methodology.

2.5. Current meters and sediment traps

An array with 5 moorings (M1 to M5) equipped with a total of 5 pairs of PPS3 sequential-sampling sediment traps and RCM-7/11 current meters were deployed during two six-month periods in and adjacent to the BC, generally covering the period April 2003 – March 2004. The moorings were located near the faunal sampling stations; M1 was located near (0.5-1 km distance) ‘C1’, M2 near ‘C2’, etc. See Zúñiga et al. (2009) for a detailed description of data acquisition and methodology relative to current meters and sediment traps.

Time Weight Fluxes (TWF, total particulate mass caught in sediment traps expressed in $\text{g.m}^{-2}.\text{day}^{-1}$), Total carbon flux (TCF, $\text{mg.m}^{-2}.\text{day}^{-1}$), total organic carbon flux (TOCF, $\text{mg.m}^{-2}.\text{day}^{-1}$), organic carbon/nitrogen weight ratio (OC/ON), total organic matter flux (TOMF, $\text{mg.m}^{-2}.\text{day}^{-1}$), weight percentage of biogenic sediment trap matter (% Biogenics), and weight percentage of lithogenic sediment trap matter (% Lithogenics) derived from the sediment traps at M1-M4, gave an indication of the sediment rate and constitution of the sedimented matter over a given time period. An average of the 60-day sampling period prior to sediment core collection was used in the analysis. Sediment traps were located 30m above the bottom. For a more detailed description refer to Zúñiga et al. (2009).

Current meter data used in the multivariate analyses cover the 60-day period before sediment core sampling for biological analyses, and were integrated to estimate the mean and maximum current intensity. Current meter data at 600 m deep, representative of the lower water column according to Zúñiga et al. (2009), were available from M1, M2, M3 and M4. For M5, no measurements for 600 m water depth were available.

2.6 Data analyses

Sediment trap and current data for stations M1-M4 was analyzed using Principle Component Analyses (PCA) (Clarke and Gorley, 2006) to interpret variability in flux parameters between sampling times for each station (individual station PCA) and for all stations together (global PCA). Data was normalized to account for scale differences. Data transformation was not needed since no skewness was observed and data distribution approached normality (Clarke and Gorley, 2006).

Regression analyses were performed on the density and biomass data plotted versus water depth and grouped per sampling time (November 2003, May 2004).

A three-way crossed permutational analysis of variance (PERMANOVA, Primer v6 and PERMANOVA+) was performed on the univariate density and biomass data per core (Anderson, 2005; Anderson et al., 2008) in a 3-factor design; using water depth (400, 600, 800, 900, 1500, 1600 m), habitat (canyon, open slope), and sampling time (November 2003, May 2004) as factors to gain insight into what influences biomass and density patterns most. Data was square-root transformed and Bray-Curtis similarity was used to calculate resemblance. Subsequently, pair-wise comparisons were made to investigate interactions, notably between water depth and sampling times. To assess differences between density and biomass variables between November 2003 and May 2004 in females, males and juveniles, pairwise PERMANOVA comparisons between sampling times were made of the univariate data for females, juveniles and males at each station. Raw data was used and Bray Curtis was applied to calculate resemblance. The number of permutations was 9999 and Monte Carlo values were used in those PERMANOVA tests where a restriction in number of available permutations (<100) had to be accounted for. PERMANOVA was preferred over traditional ANOVA procedures because it easily allows testing for multiple factors and their interaction effects simultaneously. ANOVA inherently uses Euclidean distance as a resemblance measure and assumes normal distribution of the data. PERMANOVA, on the other hand, relies on permutations to calculate p-values (making it distribution free) and any resemblance measure that is suitable for the data can be used.

3 Results

3.1. Environmental variables

3.1.1. Sediment characteristics

The May 2004 sediments of the topmost cm were mainly fine-grained hemipelagic mud, with high silt contents (57.2 – 63.5 %). Only in ‘Rocassa’ there was a significant amount of sand in the sediments (Table 2), resulting in a higher mean grain size compared to the other stations. Total carbon, organic carbon and nitrogen hardly differed between stations, and the C:N ratio reflected the presence of relatively degraded organic matter compared to the typical values of fresh phytoplankton ~6 (Redfield et al., 1963). At the ‘Rocassa’ site, highest C:N ratio was observed (10.17 weight ratio), reflecting the more degraded nature of the organic matter or indicating possible terrigenous influence from river systems in the vicinity (Table 2).

3.1.2. Sediment traps and Time Weight Fluxes (TWF)

TWF values in the BC at M1 exceeded those at other stations. Spring recordings were higher than observed values in autumn 2003 for stations M1-M3; at M4 autumn 2003 TWF was higher in autumn than in spring (Table 3). This temporal difference was also reflected in the variables total carbon flux (TCF), total organic carbon flux (TOCF) and total organic matter flux (TOMF) (Table 3). The percentage of lithogenic material in the particle flux peaked in autumn 2003 samples at M1-M3, except for M4 where highest % lithogenic material was recorded in spring 2004. At M1, biogenic % content of the flux material peaked in spring 2004 whereas highest values were recorded in autumn 2003 for the other moorings (Table 3). For a detailed description of the sediment traps and the TWF, we refer to Zuñiga et al (2009).

Principal Coordinates Analyses were performed on the available sediment trap data of stations M1-M4 individually (Fig. 2 A-D, data covering period April 2003 – March 2004) and in a global analysis (Fig. 2 E). Cumulative percentages of variation explained by the first two PC axes were 95.6 %, 79.7 %, 92.1 %, 67.9 % for M1, M2, M3, M4, respectively (Fig. 2 A-D). Greatest variability between sampling times was exhibited at station M1 in the BC, with clear differences between the spring, summer and autumn/winter months (Fig. 2A, E). The pattern of variability seemed to progress throughout the year, with high variability in the late autumn and winter months. In spring of 2003, fluxes had high biogenic content and higher OM levels compared to the late autumn and winter months. In November-December 2003, increased particle fluxes were observed, with higher levels of more degraded organic matter and greater lithogenic content. The March 2004 samples lie close to those of April 2003, suggesting a year-round cyclic pattern of flux parameters at M1. Such a pattern, however, needs to be substantiated with multi-annual seasonal data. At station M2, variability between samples is less pronounced than at M1, with a separation between the spring/summer and autumn/winter months expressed by higher lithogenic content in spring/summer fluxes, and higher biogenic content in autumn/winter fluxes. Higher fluxes were observed leading up to spring 2004. At station M3, fewer samples were available and variability between months was lower than at the other stations (Fig. 2C), but fluxes were greater in spring 2004. At station M4, the summer month fluxes contained more degraded organic matter (Fig. 2D, Corg/Norg), and again, fluxes increased towards the spring of 2004. At this station, spring samples showed a generally higher biogenic input than the

autumn/winter months, with the exception of October 2003. In Fig. 2E there is a gradual shift from the shallower station in the head of the BC at the left (M1), towards the deeper canyon stations at the right hand side (M2, M3). Negative correlations between flux parameters indicative for the amount of material contained in the fluxes and the PC1 axis, imply an overall lower mass flux at stations with greater depth. The slope station (M4) lies at the far right-hand side, indicating lowest mass flux values at this station (Fig. 2E).

3.2. Nematode standing stocks

3.2.1. General nematode standing stock patterns

Nematode densities were generally higher in May 2004 than in November 2003, except for 'Rocassa' and 'C3', where density was lower in spring 2004 (Fig. 3). Samples from 'C1' and 'C2' exhibited the highest nematode densities in May 2004 (Fig. 3) and highest differences between May 2004 and November 2003 values; both 'C1' and 'C2' were situated in the axis of the canyon. The regression of mean nematode abundance with depth was significant in November 2003 ($R^2=0.620$, $p=0.020$) but not in May 2004 ($R^2=0.003$, $p=0.902$) (Fig 3).

Total nematode biomass exhibited the same pattern as the density values; generally, biomass per 10 cm² was higher in May 2004 than in November 2003, except for 'Rocassa', 'C3', and 'C4' (Fig. 4). The regression of mean nematode abundance with depth was again significant in November 2003 ($R^2=0.512$, $p=0.0459$) but not in spring 2004 ($R^2=0.052$, $p=0.587$) (Fig 4). The lowest and highest biomass recordings were from the axis of the canyon, at 'C2' in November 2003 and at 'C1' in May 2004, respectively. Together with 'C3', these stations were characterized by marked differences in biomass between both sampling times.

Mean individual nematode biomass trends were difficult to distinguish, with high variability between replicates (Fig. 5). No significant regressions between mean individual nematode biomass and depth were found for either sampling times (Fig. 5). Geometric (X2) biomass relative frequency diagrams generally showed a shift in body-size or weight between November 2003 and May 2004 (Fig. 6A) with higher relative numbers of larger individuals in November 2003. This shift was clear for all stations (Fig. S1), except for 'Rocassa' and 'Sot', which are the two shallowest stations inside the BC. The observed nematode biomass spectra shift between sampling times was consistent for both canyon and slope stations (Fig. 6I, J). Comparing all individuals from canyon sites

with slope sites, regardless of the sampling time, a slight shift in relative frequencies towards larger individuals was exhibited (Fig. S2A).

The PERMANOVA results for the nematode density and biomass data indicated that there were significant effects for the factors water depth (WD) and sampling time (ST), but also the interaction factor, WD x ST, was significant (Table 4, 5). No significant canyon effect was observed for these variables. Estimated components of variation of the PERMANOVA test (Table 4) showed that water depth was responsible for more variability in nematode density and biomass than a temporal effect (November 2003-May 2004 contrast). Subsequent pairwise comparisons for the density data indicated that sampling time differences were apparent for all water depths except for 400 and 900 m. For both sampling times, depth differences were only significant in a limited number of depth comparisons (600-1600, 400-1600, 800-1500, 900-1600 for autumn, and 400-600, 600-900, 600-1500, 900-1600 for spring; Table 4). Arguably, one could take into account significant results at the $p < 0.1$ level for other comparisons, such as the 600-1600 m comparison in May 2004, which exhibited a p-level of ca. 0.07 (Table 4). Due to the omission of certain comparisons because of insufficient degrees of freedom for specific WD levels, the possibility of other depth differences cannot be excluded. Pairwise comparisons for the biomass data indicated a significant temporal difference at 600 and 1600 m water depth – and arguably at 1500 m water depth as well ($p = 0.054$, Table 5). In November 2003, depth contrasts in biomass are significant between 600 and 1600 m, 400 and 1600 m, and 900 and 1600 m water depth. In May 2004, the following depth comparisons were significant: 400-600, 600-800, 600-900, and 600-1600 m water depth (Table 5).

3.2.2. Gender, life-stage, and feeding type patterns

Going into more detail, and looking at the density and relative abundance differences between nematode females, males and juvenile stages for each station and both November 2003 and May 2004, it is clear that juveniles outnumber male and female individuals across all stations and both sampling times (Fig. 7A-F), and consequently account for a large share of total biomass values (Fig. 7G-I). The general trend of increasing densities from November 2003 to May 2004 is also found when separating the female, male and juvenile data (including the inverse trend for stations ‘Rocassa’ and ‘C3’) as seen on Fig. 7A-F. Noteworthy is the clear increase from near-zero densities in November 2003 to above-average densities in May 2004 at station ‘C2’ across all gender/life-stage

categories (Fig. 7A-C). Differences between sampling times of relative abundances of the three gender/life-stage categories at each station were only obvious for stations 'C1' and 'Barana', where there is a turnover from juvenile individuals to females from November 2003 to May 2004 (Fig. 7D-F), and 'Sot' and 'C2', where an increase in, respectively, females and males occurred between sampling times. No other significant relative abundance trends were observed.

Total biomass for each gender/life-stage category reflects the patterns of their respective densities (Fig. 7A-C, G-I). As is the case for total nematode biomass, total female and juvenile biomass decreases from November 2003 to May 2004 for the stations 'Rocassa', 'C3' and 'C4'. Although low in total biomass, females have clearly the highest individual biomass followed by juveniles or males depending on the sampling time and the station. Average individual nematode biomass values were generally lower in May 2004 than in November 2003, with a few exceptions (data not shown). Biomass size spectra indicated that juvenile, female and male nematodes were generally larger in November 2003 compared to May 2004, as shown by the shift to the right of the relative frequency curves (Fig. 6B-D), implying greater relative numbers of individuals in the larger geometric size classes. Disregarding sampling time differences, juvenile nematodes are somewhat larger in the canyon compared to the adjacent slope as judged from the shift of the biomass size spectra curve towards the larger weight classes (Fig. S2D). For male and female nematodes this canyon-slope difference is not clear (Fig. S2B, C)

The relative abundance of each feeding type is little different between stations, often with great variability between replicates (Fig. 8). Generally, the nematode community is dominated by the 1A group, the selective deposit feeders. Ratios between the different feeding groups are very similar at each station, except for 'C5', where the number of epistratum feeders exceed the non-selective deposit feeders in November 2003, and for 'Rocassa' in May 2004, where the non-selective deposit feeders greatly dominate the assemblage (Fig. 7). Density values for the different feeding types are similar to patterns observed for the relative abundance of each feeding group.

Generally, 1B, 2A and 2B nematodes are larger in size than the 1A nematodes, resulting in relatively greater biomass per 10cm^{-2} for these feeding types, than expected based on their relative abundances and densities (Fig. 8). Despite the smaller size of the selective deposit feeders, 1A, they are responsible for the largest share of total nematode biomass, except at station 'Rocassa', where the non-selective deposit feeders (1B) contribute most to total biomass. The size differences between feeding types are apparent

in Fig. S3. For all feeding types, nematodes are generally larger in November 2003, compared to May 2004 (Fig. 6E-H). The 1B and 2B nematodes are generally larger in the slope samples compared to the canyon samples (Fig. S2 F, H); no weight spectrum shift was observed between canyon and slope samples for the other feeding types (Fig. S2 E, G).

4. Discussion

4.1. Productivity-disturbance effects on nematode standing stocks and the role of depth, sampling time and habitat

In the BC-slope system, there is evidence that nematode SSs are affected by water depth (PERMANOVA results, Table 4, 5). The classical decrease of SSs with increasing water depth as observed for oceans worldwide was not distinct in this study for the pooled dataset. Such a negative relation only became apparent when treating November 2003 and May 2004 samples separately, suggesting a substantial temporal role in regulating nematode SSs. In November 2003, the linear decrease of the SSs with increasing water depth was significant (Fig. 3, 4) whilst in May 2004 there was no indication of such a negative relation (Fig. 3, 4). These results suggest that spring 2004 events (e.g. storm-induced turbidity currents or dense shelf water cascading) may have affected the nematode community, whilst the normally observed negative relation between depth and nematode SS is maintained in autumn 2003. So, the decrease of SSs with increasing water depth is only meaningful under November 2003 conditions. This confirms the observation that there is a significant interaction effect between water depth and sampling time on nematode SSs (Table 4, 5). Sediment trap and current meter data indicated that in spring 2004, there was generally a much greater influx of particulate matter (Fig. 2A-D) due to spring blooms and that the region experienced more intense storm-induced current activity and riverine inputs in spring compared to autumn (Table 3) (Zúñiga et al., 2009). Currents were consistently larger in magnitude (with higher maxima) in spring 2004 compared to autumn 2003, with the average current speed two months prior to the faunal sampling ranging $5.40 - 6.50 \text{ cm.s}^{-1}$ and $3.00 - 4.93 \text{ cm.s}^{-1}$, respectively (Table 3). In addition, hydrodynamic processes can be intensified by the ‘channelling’ nature of the canyon topography (Hotchkiss and Wunsch, 1982; El-Gawad et al., In Press). It is likely that dense shelf water cascading has had an important influence, with possibly disturbance effects on the seafloor and benthic assemblages. A particular energetic event in March 2004 resulted in current speeds up to 20 cm s^{-1} , concomitant with a

drop in water temperature, suggesting a dense water cascade had occurred. For the winter-spring period in 2003-2004, moderate dense shelf water cascading events have been reported for the Cap de Creus Canyon just north of the BC area (Palanques et al., 2009) and the BC may be particularly susceptible to dense shelf water cascading with subsequent changes in deep water biological communities (Company et al., 2008; Ulses et al., 2008). The intense storm event in late February 2004 induced down-welling reinforced with dense shelf water cascading, causing massive off-shelf transport of the re-suspended sediment (Palanques et al., 2009). Intense down-welling of sediments containing reworked phytodetrital food is very likely to have played an important role in driving benthic SSs. In addition, increased spring surface productivity and increased frequency and volume of riverine inputs should have contributed to greater food influx for the benthic environment, with a positive effect on nematode SSs. Previous studies have indicated that the meiobenthos, and nematodes as its dominant component, are more responsive to temporal variations in particulate organic carbon fluxes in the relatively eutrophic north-western Mediterranean compared to the oligotrophic Cretan Sea (Danovaro et al., 1999). Increased quantity and availability of food resources, concomitantly with effective transport or flushing of food-rich sediments into deeper canyon areas because of the more intense and more frequent currents in spring 2004, is likely to have overridden the classical pattern of decreasing SSs with increasing water depth as observed in the preceding autumn.

In a study comparing different canyon systems, Pusceddu et al. (2010) reported that the trophic status of deep-sea sediments is mostly controlled by surface production rather than local topography. We argue here, however, that local topography in canyons plays a crucial role in controlling benthic densities and biomass. Topography may alter current intensity and direction, the frequency and magnitude of disturbance effects, and hence also the (re)distribution of organic matter as it settles from surface waters or arrives from other canyon areas. Our results suggest initially that seasonally high surface production and subsequent export (modulated by down-welling events) to the deep sea may indeed override depth effects, but the variable interaction effect between water depth and sampling time (not all pairwise comparison tests are significant, Table 4, 5) suggests differences at the station scale. The variability in sediment trap parameters observed through time for several stations (Fig. 2) emphasizes the importance of station differences, which are related to the position of each station in the BC-slope system.

The BC system is not uniform; its sinuous nature and topographical heterogeneity means that there is environmental variability on a local scale, whereby the currents are

altered by the canyon morphology. As the seafloor descends, the northern current bounces off the east wall and is “guided” out of the canyon through the axis, resulting in more unidirectional currents with a higher intensity compared to the adjacent slope (Zúñiga et al., 2009). While the increased influx in spring 2004 compared to the preceding autumn provided more food for the benthos in the BC-slope system, resulting in generally higher nematode SSs in May 2004, this increase is not consistent for all sampling locations. At ‘Rocassa’ and ‘C3’ nematode SSs were lower in spring compared to autumn. Situated at the head of the canyon and on the western flank, respectively, it is likely that these stations experience more intense sediment disturbance compared to the other locations. At the western flank of the BC, a more active and persistent current has been identified (Zúñiga et al., 2009) and the hydrodynamic activity in the canyon channel may be responsible for the reduced nematode SSs at ‘Rocassa’ and ‘C3’, especially for the spring time sampling, which was preceded by more intense current activity compared to the previous autumn. Localized events related to these currents, e.g. mass wasting or sediment slumps, may have added to this effect by reworking the sediment, creating unfavorable conditions for the benthos, or simply removal through sediment displacement. During the study period, several intense current pulses occurred, lasting for several days at a time and often reaching the seafloor (Romano et al., this volume). Downward particle fluxes exhibited abrupt changes throughout the 2003-2004 study period, indicating the event-dominated nature of these events, and are related to river flood events, high-wave energy processes associated with local meteorological forcing and margin circulation (Zúñiga et al., 2009).

Despite the temporal effects observed for the BC-slope system SSs, the factors related to topography are also important, and both stress the importance of keeping in mind the environmental variability and heterogeneity among stations in trying to infer general patterns within canyon systems.

4.2. Productivity-disturbance effects on nematode size and gender/life-stage ratios

Globally, meiofauna, and especially nematodes, may exhibit reduced size when recovered from deeper waters because the food input is lower when distance from the surface where the food is produced increases (Vanreusel et al., 1995; Soltwedel et al., 1996; Vanaverbeke et al., 1997; Udalov et al., 2005; Soetaert et al., 2009). Recognizing the existence of a depth-related size reduction, many explanations that have been evoked have been based on trophic conditions including the amount of food that is available to

the benthic community on longer time scales (Thiel, 1975; Sibuet et al., 1989; Vanreusel et al., 1995; Soetaert et al., 2002). In summary, smaller organisms that have reduced energy costs compared to larger organisms are better adapted to persistent food-poor conditions (Thiel, 1975). Fig. 5 shows a slightly decreasing individual nematode biomass with increasing water depth, but high variability between replicates renders the regressions non-significant. Considering the relatively high food input over space and time in the BC-slope system – and many other canyons - this is not surprising, since nematode communities are not consistently confronted with low amounts of food input as traditionally encountered in deep-sea sediments. Instead, the seasonal pattern of food availability in combination with the variable current regimes and topographical ‘food traps’, create a heterogeneous environment with high background food levels, in which no explicit nematode size relation with water depth is exhibited. The importance of temporal variables, such as post-bloom influx and disturbance regimes, rather than depth itself, is clear in Fig. S1, showing size class distribution shifts between both sampling times. In addition, there are other factors that influence organism size. It has been postulated that the traditional depth-size relation may be an indirect one, with variables such as sediment biochemistry (e.g. oxygen) and grain size (linked to food availability), which may themselves bear a relation with depth, having greater power in explaining size patterns of organisms than depth in itself (Udalov et al., 2005; Soetaert et al., 2009).

In the BC-slope region, there is a notable decline of average individual nematode biomass for adults (both genders) and juveniles from November 2003 to May 2004 (Fig. 6B-D), indicating an overall shift in the nematode communities towards smaller species and/or smaller individuals of the same species. Stations C1 to C4 exhibit this shift clearly (Fig. S1). An explanation may lie in the increased food influx shortly before the May 2004 faunal sampling as implied by the position of the spring sediment trap samples on the PCAs relative to the flux vectors correlated with the PC axes in Fig. 2. The sudden availability of increased food levels in spring 2004 compared to autumn 2003 may instigate transition of the nematode community into a more ‘reproductive’ state, whereby newly produced nematode generations with mainly younger and smaller individuals cause an overall size reduction. Added support for this supposition lies in the general increase of the relative abundance of females from November 2003 to May 2004, indicating a ‘turn-over’ from juveniles (and males) to female adults in the assemblages; especially at ‘C1’ and ‘Barana’, where the increase of females is significant between sampling times (Fig. 7A, D, G). These observations suggest that the increased availability of food resources

may have induced the community to turn into a more reproductive state, with more females and overall smaller individuals.

Alternatively, or rather complementary, the phytodetrital pulse may have attracted or stimulated smaller species. Vanaverbeke et al. (2004) demonstrated in shallow-water environments that the community can shift towards an opportunistic community specialized in exploiting the seasonal phytodetrital input. Opportunistic nematode species are often smaller and have shorter life cycles compared to more specialized species (Bongers, 1990; Bongers et al., 1991), enabling them to produce offspring quickly and thrive in food-rich environments. Preliminary insights into the community data (Romano et al., in preparation) indicate the likelihood of this hypothesis. May 2004 samples contain substantial densities of chromadorids and desmoscolecids – which include genera generally smaller and similar to the ones observed in Vanaverbeke et al. (2004), whilst these are often absent in November 2003. However, detailed community structure research is needed to assess the validity of this food-induced genera-shift hypothesis (Romano et al., in preparation).

The assemblages at the BC-slope system are characterized by a very high percentage of juvenile individuals (roughly between 70 and 90%, Fig. 5). Previous Mediterranean studies have reported much lower values; Vivier (1978) found between 43-65 % juveniles and Soetaert (Soetaert, 1983) found 48-61 % juveniles in September. Interestingly, juvenile relative abundances in the Blanes region were comparable to those encountered in the Atacama trench at 7800 m water depth (77%) (Gambi et al., 2003). Environmental comparisons can be drawn between the two regions in the sense that both are characterized by relatively high amounts of nutritional food available to the benthos (irrespective of season), compared to other deep-sea sites. It seems likely that the favorable conditions allow the opportunistic species to exploit the food-rich habitat and increase the population with new, smaller, and faster maturing generations of nematodes.

Our observations stand in contrast with the reports of several authors (Vanreusel et al., 1995; Soltwedel et al., 1996; Sommer and Pfannkuche, 2000; Brown et al., 2001; Udalov et al., 2005) who compared the nematode size spectra from regions with different trophic regimes and documented a reduction of mean nematode individual size and a relatively high proportion of small individuals in oligotrophic areas. Persistent food limitation does not allow the high energy consumption of larger species. We suggest that the size distribution of the nematode communities in the BC system is not driven by long-term food-limitation as is the case in other deep-sea habitats, but put forward the

hypothesis that in addition to generally high food availability on the background, the disturbance regimes in the BC (recurrent food pulses, hydrodynamic disturbance) drive a community with no specific size restrictions/allowances in the long term. Instead, the community is governed by cycles of food-input and sediment disturbance on a shorter time scale from weeks to months. The implications of this are that size patterns of deep-sea nematodes, and perhaps meiobenthos in general, should not just be seen as a result of trophic conditions over longer periods of time, but rather driven by the interaction of long-term food conditions and sporadic or recurrent food pulses.

4.3. Productivity-disturbance effects on nematode feeding type ratios

In the BC-slope system, no marked differences in feeding type distribution occur between both sampling times, except for station ‘Rocassa’, where in November 2003 there is a community dominated by selective deposit feeders (i.e. 1A group, characterised by lack of teeth, and possessing small buccal cavities (or buccal cavity is absent) feeding mainly on microbiota or sufficiently small particles), and in May 2004, the community is dominated by non-selective deposit feeders (i.e. 1B group, no teeth, large buccal cavity and able to feed on larger particles than the 1A group). All other stations harbour communities dominated by 1A nematodes, in autumn as well as in spring (Fig. 8). Dominance of selective deposit feeders is somewhat uncharacteristic for canyon environments. In several nematode canyon studies, communities were characterised by a relative dominance of the 1B group, the non-selective deposit feeders, which constituted sometimes nearly half of the community (Garcia et al., 2007; Ingels et al., 2009; Ingels et al., 2011a, b). The 1B group comprises quite large nematodes (Fig. S3), and they are often opportunistic in nature because they are able to exploit a wider range of food particles with their large mouth and buccal cavity. In addition, they are able to move relatively rapidly within sediments, especially in sediments with a coarse grain structure. Their ‘non-selective’ feeding abilities allow them to exploit food attached to and lying in between larger sediment grains, as opposed to selective deposit feeders that are not able to do so. The link between nematode feeding types, individual nematode size and grain size structure is well established (Tietjen, 1984; Udalov et al., 2005; Soetaert et al., 2009). The fact that at ‘Rocassa’ the sediment composition in spring is characterised by a high sand content compared to the other stations in this study (Table 2), but similar to locations in other canyons such as the Nazaré Canyon (Garcia et al., 2007; Ingels et al., 2009; Ingels et al., 2011b) gives further evidence for this link, with 1B-dominated communities in

‘sandy’ sediments. Additional support is also given by the fact that epistrate feeders (2A), characterised by teeth which allow them to scrape of food from larger sediment grains and found as dominant group in coarse sediments, are the second most abundant group at ‘Rocassa’ in spring.

Temporal differences did not have any drastic effect on feeding type composition at the BC-slope stations. Relative abundances between feeding types remained similar when comparing November 2003 and May 2004 values for each station (Fig. 8), except for the ‘Rocassa’ station which we have already discussed. The different feeding types were all able to exploit the increased food availability that came with spring conditions, as indicated by the equitable increase of densities for each feeding type (Fig. 8). In addition, the shift to smaller nematode individuals from November 2003 to May 2004 manifests itself for all feeding types.

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Table 1. Location, depth and number of sediment cores used for meiofaunal analyses. * indicates stations located in the Blanes Canyon

Station	Latitude	Longitude	Depth (m)	Number of cores	
				Autumn 6/11/2003	Spring 9-11/05/2004
C1*	41°30'94"N	02°55'01"E	(563) 600	2	3
C2*	41°22'34"N	02°51'04"E	(1677) 1600	2	3
C3*	41°54'60"N	02°48'19"E	(865) 900	2	3
Rocassa*	41°36'29"N	02°50'35"E	(388) 400	3	3
Sot*	41°29'20"N	03°00'54"E	(556) 600	4	3
C4	41°19'30"N	02°57'10"E	(906) 900	1	5
C5	41°20'06"N	03°12'54"E	(1430) 1500	3	3
Barana	41°22'40"N	03°22'08"E	(806) 800	3	3

Table 2. Mean values of sediment biogeochemical variables. TC: total percentage carbon weight content; TN: total percentage nitrogen weight content, TOC: total percentage organic carbon weight content, CaCO₃: total percentage calcium-carbonate weight content, C:N: carbon – nitrogen ratio based on weight percentages, MGS: mean grain size, %Clay: Weight percentage clay, %Silt: volume percentage silt, %Sand: Volume percentage sand. Clay, silt and sand percentage are based on the uppermost 3 cm. * indicate canyon locations. All values are based on measurements from spring 2004 samples.

Station	TC (%)	TN (%)	TOC (%)	CaCO ₃ (%)	C:N	MGS (μm)	%Clay	%Silt	%Sand
Rocassa*	4.23	0.06	0.61	30.11	10.17	20.95	28.43	62.63	8.95
C1*	3.69	0.09	0.81	23.99	8.97	11.64	35.60	63.53	0.87
C3*	3.61	0.09	0.75	23.84	8.31	7.91	41.08	58.85	0.08
C2*	3.63	0.09	0.81	23.51	8.94	8.68	40.98	58.90	0.12
Sot*	3.88	0.09	0.78	25.78	8.97	10.88	38.90	60.50	0.60
C4	3.84	0.09	0.81	25.24	8.94	7.80	42.05	57.85	0.10
C5	3.98	0.09	0.73	27.03	8.17	8.38	40.53	59.10	0.38
Barana	3.86	0.08	0.64	26.78	7.76	9.97	42.40	57.20	0.40

Table 3: Data from sediment traps and current meters of moorings M1-M4 (Data M5 not available). Av.: Average values for autumn 2003 and spring 2004 sampling period (10-29 days). Average values of current speeds are based on the two months preceding the biotic sampling. Max.: maximum values during period of two months prior to sampling of sediment cores for faunal analysis. TWF: time weight flux ($\text{g.m}^{-2}.\text{day}^{-1}$), TCF: total carbon flux ($\text{mg.m}^{-2}.\text{day}$), TOCF: total organic carbon flux ($\text{mg.m}^{-2}.\text{day}$), OC/ON: organic carbon/nitrogen weight ratio, TOMF: total organic matter flux ($\text{mg.m}^{-2}.\text{day}$), %Biogenics: weight percentage of biogenic sediment trap matter, %Lithogenics: weight percentage of lithogenic sediment trap matter, Current: current speed in cm.s^{-1} . Bold values denote the highest value between spring and autumn values. NA: not available.

Station	Variables	Av. Autumn	Av. Spring	Max. Autumn	Max. Spring
M1/C1	TWF	8.97	19.34	8.97	29.58
	TCF	254.48	898.48	254.48	1299.43
	TOCF	88.16	333.16	88.16	457.15
	OC/ON	9.36	9.21	9.36	9.98
	TOMF	176.31	666.32	176.31	914.29
	% Biog	17.4	27.8	17.41	27.79
	% Lithog	82.6	72.2	82.59	73.19
	Current	3.00	5.40	5.91	38.66
M2/C2	TWF	4.60	8.66	4.60	9.22
	TCF	195.21	371.41	195.21	371.41
	TOCF	61.67	126.06	61.67	126.06
	OC/ON	8.85	8.29	9.14	8.29
	TOMF	123.34	252.11	123.34	252.11
	% Biog	26.8	26.5	28.65	26.52
	% Lithog	73.2	73.5	83.05	73.48
	Current	3.53	5.93	11.88	22.26
M3/C3	TWF	4.37	6.23	5.37	10.76
	TCF	117.88	360.81	159.51	360.81
	TOCF	42.01	129.35	56.96	129.35
	OC/ON	5.82	7.79	9.11	7.79
	TOMF	84.02	258.70	113.91	258.70
	% Biog	16.4	20.3	26.50	20.31
	% Lithog	83.6	79.7	83.61	79.69
	Current	4.69	6.50	12.76	19.61
M4/C4	TWF	5.23	2.39	5.23	2.39
	TCF	209.65	33.01	209.65	33.01
	TOCF	78.22	50.03	78.22	50.03
	OC/ON	6.47	4.18	13.32	4.18
	TOMF	156.43	100.03	156.43	100.06
	% Biog	27.7	23.9	27.74	22.19
	% Lithog	72.3	76.1	76.50	77.81
	Current	4.93	6.30	13.24	14.82

Table 4. Univariate PERMANOVA test to test for nematode density (ind.10cm⁻²) differences between water depths (WD), sampling time (ST: November (Nov) 2003, May 2004) and habitat (Ha: canyon, slope). Including pairwise comparison tests to investigate the interaction factor WDxST. Data was square root transformed and Bray Curtis similarity was used. df: degrees of freedom, SS: sums of squares, MS: means of squares, Un.perm.: unique permutations, Sq. rt. ECV: square root of estimates of components of variation, P(MC): P value after Monte Carlo procedure. Bold values denote p<0.05, bold and underlined values denote p<0.01.

Source	df	SS	MS	Pseudo-F	P(perm)	Un. perm.	Sq. rt. ECV
WD	5	5032.9	1006.6	8.9135	<u>0.0001</u>	9932	11.932
ST	1	2230.4	2230.4	19.751	<u>0.0001</u>	9933	10.426
Ha	1	27.724	27.724	0.2455	0.6542	9925	
WDxST	5	6895.4	1379.1	12.212	<u>0.0001</u>	9942	20.086
WDxHa	1	165.92	165.92	1.4692	0.2239	9937	
STxHa	1	161.93	161.93	1.4339	0.2310	9931	
WDxSTxHa	1	359.11	359.11	3.18	0.0796	9938	
Res	30	3387.8	112.93				
Total	45	16932					

Within level	Comparison	t	P(perm)	perms	P(MC)
400	Nov 2003, May 2004	0.6992	0.6972	10	0.5240
600	Nov 2003, May 2004	2.4291	<u>0.0280</u>	9565	<u>0.0316</u>
800	Nov 2003, May 2004	4.2655	0.1004	10	<u>0.0152</u>
900	Nov 2003, May 2004	0.96713	0.2993	8441	0.3695
1500	Nov 2003, May 2004	8.3117	0.0958	10	<u>0.0010</u>
1600	Nov 2003, May 2004	11.294	0.1009	10	<u>0.0003</u>
Nov 2003	600, 400	0.16023	0.9529	1259	0.9411
Nov 2003	600, 800	0.84804	0.4298	1260	0.4354
Nov 2003	600, 900	0.2174	0.8675	3527	0.8495
Nov 2003	600, 1600	5.2448	<u>0.0045</u>	192	<u>0.0013</u>
Nov 2003	600, 1500	0.43107	0.7922	1259	0.7086
Nov 2003	400, 800	df = 0			
Nov 2003	400, 900	0.34293	0.8250	60	0.7732
Nov 2003	400, 1600	8.1843	0.0984	10	<u>0.0018</u>
Nov 2003	400, 1500	df = 0			
Nov 2003	800, 900	2.3812	0.0828	54	0.0929
Nov 2003	800, 1600	df = 0			
Nov 2003	800, 1500	3.0998	0.0989	10	<u>0.0372</u>
Nov 2003	900, 1600	25.464	0.0708	15	<u>0.0010</u>
Nov 2003	900, 1500	0.80133	0.5813	54	0.4910
Nov 2003	1600, 1500	df = 0			
May 2004	600, 400	7.9747	<u>0.0012</u>	829	<u>0.0003</u>
May 2004	600, 800	1.9939	0.0821	830	0.0848
May 2004	600, 900	3.2462	<u>0.0050</u>	9874	<u>0.0068</u>
May 2004	600, 1600	2.2118	<u>0.0430</u>	830	0.0679
May 2004	600, 1500	2.4982	<u>0.0374</u>	830	<u>0.0426</u>
May 2004	400, 800	df = 0			
May 2004	400, 900	1.434	0.1482	4082	0.1834
May 2004	400, 1600	2.4572	0.1016	10	0.0738
May 2004	400, 1500	df = 0			
May 2004	800, 900	0.4045	0.7807	6074	0.7328
May 2004	800, 1600	df = 0			

May 2004	800, 1500	7.69E-02	1	10	0.9553
May 2004	900, 1600	2.261	0.0476	4065	0.0486
May 2004	900, 1500	0.42727	0.7686	6083	0.7114
May 2004	1600, 1500	df = 0			

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Table 5. Univariate PERMANOVA test to test for nematode biomass ($\mu\text{gC} \cdot 10\text{cm}^{-2}$) differences between water depths (WD), sampling time (ST: November (Nov) 2003, May 2004) and habitat (Ha: canyon, slope). Including pairwise comparison tests to investigate the interaction factor WDxST. Data was square root transformed and Bray Curtis similarity was used. df: degrees of freedom, SS: sums of squares, MS: means of squares, Un.perm.: unique permutations, Sq. rt. ECV: square root of estimates of components of variation, P(MC): P value after Monte Carlo procedure. Bold values denote $p < 0.05$, bold and underlined values denote $p < 0.01$.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	Sq. rt. ECV
WD	5	4896.2	979.23	9.1927	<u>0.0001</u>	9952	11.791
ST	1	1169	1169	10.974	<u>0.0009</u>	9947	7.3848
Ha	1	68.177	68.177	0.64002	0.4494	9926	
WDxST	5	5981	1196.2	11.229	<u>0.0001</u>	9948	18.633
WDxHa	1	176.49	176.49	1.6568	0.1972	9923	
STxHa	1	59.044	59.044	0.55429	0.4837	9933	
WDxSTxHa	1	82.188	82.188	0.77155	0.3940	9937	
Res	30	3195.7	106.52				
Total	45	14524					

Within level	Comparison	t	P(perm)	perms	P(MC)
400	Nov 2003, May 2004	0.8219	0.7993	10	0.4588
600	Nov 2003, May 2004	3.0361	0.0185	9590	0.0149
800	Nov 2003, May 2004	0.51974	0.696	10	0.6381
900	Nov 2003, May 2004	1.8551	0.1251	8340	0.1015
1500	Nov 2003, May 2004	2.5837	0.1999	10	0.0586
1600	Nov 2003, May 2004	7.0446	0.1081	10	<u>0.0024</u>
Nov 2003	600, 400	0.52711	0.7029	1258	0.6632
Nov 2003	600, 800	0.15189	0.9193	1259	0.9212
Nov 2003	600, 900	1.5532	0.1661	3500	0.1707
Nov 2003	600, 1600	7.5362	<u>0.0060</u>	192	<u>0.0001</u>
Nov 2003	600, 1500	0.31603	0.7969	1257	0.7847
Nov 2003	400, 800	df = 0			
Nov 2003	400, 900	0.34445	0.7701	60	0.7724
Nov 2003	400, 1600	6.488	0.1011	10	<u>0.0033</u>
Nov 2003	400, 1500	df = 0			
Nov 2003	800, 900	1.2124	0.3270	54	0.3122
Nov 2003	800, 1600	df = 0			
Nov 2003	800, 1500	0.15268	0.8986	10	0.9147
Nov 2003	900, 1600	9.2308	0.0637	15	<u>0.0050</u>
Nov 2003	900, 1500	2.1142	0.0971	54	0.1189
Nov 2003	1600, 1500	df = 0			
May 2004	600, 400	6.4078	<u>0.0019</u>	829	<u>0.0011</u>
May 2004	600, 800	4.1034	<u>0.0015</u>	829	<u>0.0057</u>
May 2004	600, 900	3.1601	<u>0.0058</u>	9907	<u>0.0080</u>
May 2004	600, 1600	3.0018	0.0272	829	0.0202
May 2004	600, 1500	0.67273	0.5442	830	0.5332
May 2004	400, 800	df = 0			
May 2004	400, 900	1.595	0.1385	4063	0.1418
May 2004	400, 1600	0.39218	0.700	10	0.7264
May 2004	400, 1500	df = 0			
May 2004	800, 900	0.46378	0.7193	6025	0.6800
May 2004	800, 1600	df = 0			

May 2004	800, 1500	1.9854	0.1967	10	0.1169
May 2004	900, 1600	1.2915	0.2208	4065	0.2247
May 2004	900, 1500	1.0081	0.3691	6094	0.3438
May 2004	1600, 1500	df = 0			

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Figure 1

Figure 1. Overview of the Blanes canyon with indication of sample locations.

Fig. 2: Principal Component Analysis (PCA) for stations M1-M4, A-D, respectively based on environmental data from the sediment trap samples. Superimposed are the vectors for selected variables. Lines connect the sediment trap samples through time; labels denote the month of sampling. Nematode density and biomass bar charts (average data of replicates including standard deviation) were inserted for graphs A-D for the individual stations (C1-C4) and linked to the closest sediment trap sample in time. The left Y-axis of the inserts pertains to the left bar (density in ind. 10cm⁻²; 0-1000), the right Y-axis pertains to the right bar (biomass in µgC. 10cm⁻²; 0-10). Graph E presents the global PCA for all four stations, with environmental variables superimposed (Spearman correlation > 0.8, circle denotes correlation with axes = 1).

Fig. 3

Figure 3. Nematode densities (ind.10cm⁻²) including standard deviation (based on replicates) at each station in autumn and spring along the water depth gradient. Black symbols represent autumn samples and white symbols represent spring samples. Interrupted regression line for spring samples ($R^2=0.003$, $p = 0.902$), full regression line for autumn samples ($R^2=0.620$, $p = 0.020$). Symbols in grey areas indicate that the station is located in the canyon system.

Figure 4

Figure 4. Total nematode biomass ($\mu\text{g C } 10\text{cm}^{-2}$) and standard deviation (based on replicates) at each station in autumn and spring along the water depth gradient. Black symbols represent autumn samples and white symbols represent spring samples. Interrupted regression line for spring samples ($R^2=0.052$, $p = 0.587$), full regression line for autumn samples ($R^2=0.512$, $p = 0.046$). Symbols in grey areas indicate that the station is located in the canyon system.

Figure 5

Figure 5. Mean individual nematode biomass ($\mu\text{g C individual}^{-1}$) and standard deviation (based on replicates) at each station in autumn and spring along the water depth gradient. Black symbols represent autumn samples and white symbols represent spring samples. Interrupted regression line for spring samples ($R^2=0.081$, $p = 0.496$), full regression line for autumn samples ($R^2=0.181$, $p = 0.295$). Symbols in grey areas indicate that the station is located in the canyon system.

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Figure 6

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Figure 6. Relative abundance of each X2 geometric weight class based on individual nematode biomass data (class 0 = 0.000218 to 0.000436 $\mu\text{g C}$, class 1 = 0.000436 to 0.000872 $\mu\text{g C}$, and so on). Full lines represent values for the November 2003 samples, dashed lines represent the values for the May 2004 samples. Top chart is based on all individuals ($n=5002$), lower charts are based on subsets of individual biomass data for each group represented; 1A = selective deposit feeders, 1B: non-selective deposit feeders, 2A: epistratum feeders, 2B: scavengers/predators/omnivores.

Figure 7. Densities (top row; a-c; ind. 10 cm⁻²), relative abundances (middle row; d-f; %), and total biomass (bottom row; g-i; µgC 10 cm⁻²) for male (♂), female (♀) and juvenile (juv) nematodes for spring and autumn, including standard deviation for each station (shallow to deep from left to right). * indicates significant differences between November (Nov) 2003 and May 2004 values at p<0.05 level, ** indicates significant differences at the p<0.01 level (PERMANOVA pairwise comparisons between seasons for females, juveniles, males at each station). Bars in grey areas indicate that the station is located in the canyon system.

Figure 8. Mean relative abundances (top row; a,b; %), densities (middle row; c, d; ind. 10 cm⁻²), and total biomass (bottom row; e, f; µg C 10 cm⁻²) for the four different nematode feeding types for November (Nov) 2003 and May 2004, including standard deviation for each

981 station (shallow to deep from left to right). 1A: selective deposit feeders, 1B: non-selective
982 deposit feeders, 2A: epistratum feeders, 2B: predators/scavengers/omnivores. Bars in grey
983 areas indicate that the station is located in the canyon system

984 Figure S1.

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987 **Fig. S1.** Relative abundance of each X2 geometric weight class based on individual nematode
988 biomass data for each station (class 0 = 0.000218 to 0.000436 $\mu\text{g C}$, class 1 = 0.000436 to
989 0.000872 $\mu\text{g C}$, and so on). Full lines represent values for the November 2003 samples,
990 dashed lines represent the values for May 2004 samples. Charts are based on individual
991 biomass data for each station .

Fig. S2. Relative abundance of each X2 geometric weight class based on individual nematode biomass data (class 0 = 0.000218 to 0.000436 $\mu\text{g C}$, class 1 = 0.000436 to 0.000872 $\mu\text{g C}$, and so on). Full lines represent values for the canyon samples; dashed lines represent the values for slope samples. Top left chart is based on all individuals ($n=5002$), other charts are based on subsets of individual biomass data for each group represented; 1A = selective deposit feeders, 1B: non-selective deposit feeders, 2A: epistratum feeders, 2B: scavengers/predators/omnivores.

1004 Fig. S3
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1008 Fig. S3. Relative abundance of each X2 geometric weight class based on individual nematode
1009 biomass data ($\mu\text{g C}$) for all samples. Charts are based on subsets of individual biomass data
1010 for each feeding type represented (total $n = 5002$); 1A = selective deposit feeders, 1B: non-
1011 selective deposit feeders, 2A: epistratum feeders, 2B: scavengers/predators/omnivores
1012