Author's Accepted Manuscript

Role of spatial scales and environmental drivers in shaping nematode communities in the Blanes Canyon and its adjacent slope

Sara Román, Lidia Lins, Jeroen Ingels, Chiara Romano, Daniel Martin, Ann Vanreusel

PII: S0967-0637(18)30323-6
DOI: <https://doi.org/10.1016/j.dsr.2019.03.002>
Reference: DSRI3012

To appear in: *Deep-Sea Research Part I*

Received date: 5 November 2018
Revised date: 21 February 2019
Accepted date: 4 March 2019

Cite this article as: Sara Román, Lidia Lins, Jeroen Ingels, Chiara Romano, Daniel Martin and Ann Vanreusel, Role of spatial scales and environmental drivers in shaping nematode communities in the Blanes Canyon and its adjacent slope, *Deep-Sea Research Part I*, <https://doi.org/10.1016/j.dsr.2019.03.002>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Role of spatial scales and environmental drivers in shaping nematode communities in the Blanes Canyon and its adjacent slope

Sara Román^a, Lidia Lins^{b,c}, Jeroen Ingels^d, Chiara Romano^{a,e,*}, Daniel Martín^a, Ann Vanreusel^b

^aCentre d'Estudis Avançats de Blanes (CEAB-CSIC), c/ Accés a la Cala St. Francesc, 14, E-17300 Blanes, Spain.

^bMarine Biology Department, Ghent University, Krijgslaan 281 S8, B-9000 Ghent, Belgium.

^cSenckenberg Research Institute and Natural History Museum, Department of Marine Zoology, 60325 Frankfurt am Main, Germany.

^dFlorida State University Coastal and Marine Lab, 3618 Coastal Highway 98, St. Teresa, FL 32358-2702, USA

^eMarine Invertebrate Phylogenetics Lab Scripps Institution of Oceanography, 8750 Biological Grade, Hubbs Hall, La Jolla, CA 92037, USA

*Corresponding author. cromano@ceab.csic.es

ABSTRACT

Understanding community assembly and processes driving diversity in deep-sea environments is a major challenge in marine ecosystems. In this paper, we investigated the importance of environmental gradients at different spatial scales in structuring deep-sea canyon and continental slope meiobenthic nematode communities in the NW Mediterranean Sea. Three scales were investigated 1) Ecosystem: Blanes Canyon vs. adjacent open slope; 2) Water-depth within each ecosystem: 1500, 1750 and 2000 m; and 3) Vertical profile (three layers within the first 5 cm of sediment). Nematode communities were analysed in terms of density, biomass, diversity and community structure. Grain size, Chl *a*, Chl *a*: phaeopigments, CPE, organic carbon and total nitrogen were measured to assess the relationships with nematode assemblages. Blanes Canyon harbours more abundant and diverse assemblages than slope, particularly at 1,750 m and 2,000 m depth respectively. The higher canyon values may be related to the higher food availability observed in the former, which can be a consequence of the so-called “canyon effect”. Slope assemblages were overall more uniform than those in the canyon, where there were greater bathymetrical differences in community structure. Densities in the canyon peaked at 1,750 m depth, which did not correspond with the bathymetric gradient in food availability. The deepest canyon station was the most similar to the slope stations in terms of both environmental conditions and nematode communities, suggesting it lied outside the canyon influence. The higher habitat heterogeneity of the canyon (indicated by its greater vertical sediment profile and water depth differences) played a key role in structuring nematode spatial distribution. Independently of the ecosystem, however, the vertical sediment profile proved to be the most determinative factor for density, community structure, and diversity.

Keywords:

Submarine canyons, NW Mediterranean, Meiobenthos, Nematodes, Diversity, Deep-sea, Anthropogenic impacts.

1. INTRODUCTION

Continental margins comprise the most geologically diverse components of the deep-ocean floor. They show high topographic heterogeneity (Levin and Dayton, 2009; Levin et al., 2010; Levin and Sibuet, 2012) and have been considered major reservoirs of marine biodiversity and productivity (Levin et al., 2001; Levin and Sibuet, 2012). Submarine canyons are among the major sources of this habitat heterogeneity at regional scale (Vetter and Dayton, 1999; Levin et al., 2001; Ismail et al., 2018). They provide an important transport pathway between shelf and deep-ocean environments by trapping, accumulating and funnelling sediments, organic matter and nutrients (Puig et al., 2014) together with pollutants and litter (Palanques et al., 2008; Tubau et al., 2015).

Active canyons are very unstable environments, subject to tidal currents, episodic slumps, sediment gravity flows, turbidity flows and periodic flushing (Canals et al., 2006; Palanques et al., 2006a; de Stigter et al., 2007; Puig et al., 2012). Furthermore, anthropogenic activities such as commercial fish trawling are prevalent around them. The heavy bottom trawl doors from fishing gears cause significant furrows in the seafloor, and lead to the formation of turbid clouds of suspended sediments, resulting in a persistent bottom intermediate nepheloid layer. These processes can affect the seafloor at great depths inside canyon axis, where transported material may accumulate (Palanques et al., 2006b; Martín et al., 2008; Puig et al., 2012; Martín et al., 2014b; Puig et al., 2015a; Puig et al., 2015b; Pusceddu et al., 2014; Wilson et al., 2015; Paradis et al., 2017), thus giving rise to complex ecosystems with specific hydrographic, sedimentological and geochemical characteristics (Flexas et al., 2008; López-Fernández et al., 2013; Amaro et al., 2016) significantly influencing benthic community structure, diversity and abundance (Garcia et al., 2007; Ingels et al., 2009; Schlacher et al., 2010; Ramalho et al., 2014; De Leo et al., 2014; Román et al., 2016).

Canyon benthic communities differ in terms of structure and functioning from the adjacent slope fauna located at equivalent depths (Vetter and Dayton, 1998; Duineveld et al., 2001; Garcia et al., 2007; Ingels et al., 2009; Gunton et al., 2015; Rosli et al., 2016; Román et al., 2016). Furthermore, habitat heterogeneity and organic matter accumulation often support higher density and biomass in canyons, both locally and overall, compared to the adjacent open slopes (e.g., Grémare et al., 2002; Curdia et al., 2004; Ingels et al., 2009; De Leo et al., 2010; Huvenne et al., 2011; Romano et al., 2013a; Leduc et al., 2014; Romano et al., 2017). This phenomenon is generally referred to as “canyon effects”. However, the canyon effect may not occur (e.g., Soltwedel et al., 2005; Bianchelli et al., 2010; Vetter et al., 2010),

and some canyons even show lower densities and biomasses than the adjacent slopes (Maurer et al., 1994; Flach, 2002; Garcia et al., 2007; Van Gaeve et al., 2009), thus preventing to generalize. Each canyon can be regarded as unique, showing different habitat complexes and being subject to different physicochemical regimes depending on their location on the World's continental margins (Harris and Whiteway, 2011). Benthic canyon communities, and meiobenthos in particular, have been relatively recently investigated in a number of canyon systems (e.g., Ingels et al., 2009; Bianchelli et al., 2010; De Leo et al., 2010; Amaro et al., 2016; Ingels et al., 2003b; Romano et al., 2013b; Rosli et al., 2016), but these are vastly outnumbered compared to other canyon studies.

Small-scale habitat variability and patchy disturbance in addition to regional and global differences in environmental conditions may play a major role in maintaining deep-sea diversity (e.g., Rex and Etter, 2010; Vanreusel et al., 2010; Bianchelli et al., 2013). Depending on the observed scale, various environmental processes and disturbances emerged as relevant in structuring benthic communities (Rosli et al., 2017, and references therein). These can either be physical and hydrodynamical in nature at large scales, such as at the entire canyon level (Bianchelli et al., 2013; Lins et al., 2014) or determined by local variability in sediment granulometry and food and oxygen availability at a scale of centimetres to 10s of meters (Heip et al., 1985; Gallucci et al., 2009; Fonseca et al., 2010). Moreover, inter- and intra-annual variations in meiofauna assemblages may be particularly significant in canyons systems (Ingels et al., 2013a; Romano et al., 2013b; Ramalho et al., 2014; Román et al., 2016). However, our understanding of the roles attributed to specific environmental conditions and disturbances (including anthropogenic impacts) on submarine canyon systems remains poorly resolved. Advances are thus urgently needed, as they would contribute to the effective management and conservation of these peculiar ecosystems (Fernández-Arcaya et al., 2017).

Blanes Canyon (NW Mediterranean) is arguably one of the most intensively explored active canyons in recent years, from basic geological and hydrological surveys to research on fish trawling impacts (e.g., Company et al., 2008; Zúñiga et al., 2009; Lastras et al., 2011; Ramirez-Llodra et al., 2010). The intensive fisheries, mainly targeting the red shrimp *Aristeus antennatus* (Risso, 1816), are among the main reasons for a growing scientific interest in this area. However, as for other canyons, the meiobenthic component has been neglected in earlier works. More recently, the meiofauna at higher taxon level has been investigated in this canyon along a bathymetric gradient and in comparison with its western adjacent slope, which show clear differences in taxa diversity and density (Román et al., 2016). In addition, there

seems to be a clear zonation pattern inside the canyon related to its hydrodynamic regimes, topography, sedimentary characteristics and food availability, as well as to regular and persistently high sedimentation rates likely caused by nearby trawling activities (López-Fernandez et al., 2013; Paradis et al., 2018; Román et al., 2018).

Marine free-living nematodes are typically the most abundant metazoan meiobenthic taxon in deep-sea environments (Giere, 2009). The Blanes Canyon system is not an exception, with nematodes accounting for 90% of the total meiofauna composition (Romano et al., 2013b; Román et al., 2016). Furthermore, nematodes exhibit fast turnover rates and likely suffer lower mortality rates after physical disturbances than larger benthic organisms (Schratzberger and Jennings, 2002), whilst they are determinatively influenced by sediment grain size structure and food availability (Leduc et al., 2012a). This is, therefore, an ideal taxon to investigate the structural and functional differences between an active canyon and its adjacent open slopes (Ingels et al., 2013a).

The aims of the present study were 1) to compare the nematode communities inhabiting the canyon and its adjacent western slope; 2) to assess which spatial scale (ecosystems, water depth, vertical sediment layers) was more important in shaping nematode assemblages, and 3) to identify the main environmental drivers explaining the nematode distribution patterns.

2. MATERIAL AND METHODS

2.1. Study area and sampling strategy

The N-S oriented Blanes submarine canyon is located on the North Catalan margin and constitutes one of the major structures that incise the shelf in the NW Mediterranean Sea (Fig. 1). The head is 60 m deep and is located at 4 km off the coastline, where the Tordera River reaches the sea. The Blanes Canyon has a complex topography, a V-shaped cross section in its upper course, and a U-shaped cross section along its middle and lower course, where it forms meanders (Lastras et al., 2011). It extends over 184 km and reaches a maximum width of 20 km at its deepest part at about 2000 m (Lastras et al., 2011). Circulation in the wider area is dominated by the Northern Current, a general cyclonic circulation along the NW Mediterranean continental slope, forced by the entrance of Atlantic Water through the Gibraltar strait (Millot, 1999). In addition, a high particle transport is observed in the canyon area, responding to the flooding from the Tordera River and the numerous coastal creeks of its catchment, and to the occurrence of major coastal storms (autumn-winter), as well as to phytoplankton blooms (spring-summer) (Flexas et al., 2008; Zúñiga et al., 2009; López-

Fernández et al., 2013). Sediments in the upper part of the canyon are relatively coarse compared with those further down (Pedrosa et al., 2013; Román et al., 2016).

Like most of the Catalan margin of the Iberian Peninsula, Blanes Canyon and their adjacent margins are important areas for bottom trawling fisheries. Around canyons, these are mainly targeting the deep-sea red shrimp *Aristeus antennatus* (Sardá et al., 2009) and, thus, trawling grounds occur around their heads, rims and flanks up to 800 m depth (Román et al., 2016; Paradis et al., 2018). The engine power of the fishing boats was almost negligible until the 1960s, when the trawling fleet underwent an important technification implying the change of wind-propelled vessels by a fully motorized fleet (Gorelli et al., 2016). This activity supports a specialized commercial fleet (~17 trawling-boats) that have been exploiting the area for over 60 years (Sardá et al., 2009; Ramirez-Llodrà et al., 2010) causing a profound impact on the seafloor (Puig et al., 2012; Martin et al., 2014a, Paradis et al., 2018).

Sampling was conducted in Blanes Canyon and the western open slope areas on board of the R/V *García del Cid* (October 2012) during the Dos Mares II project (Table 1). In the present study, three stations were sampled at ca. 1,500 m, 1,750 m and 2,000 m depth in the canyon (BC1500, BC1750, and BC2000, respectively) and on the western adjacent open slope (OS1500, OS1750, and OS2000) in October 2012 (Table 1, Fig. 1). Sediment samples were collected with a multicorer (KC Denmark A/S), equipped with six tubes of 9.4 cm of internal diameter, yielding virtually undisturbed sediment samples (69.4 cm² surface area). Three multicorer deployments (replicates) were conducted at each sampling station. From each deployment, one core was used for meiofaunal and two for sediment analyses. The upper 5 cm of each core was sliced in three layers: 0-1 cm, 1-2 cm and 2-5 cm.

2.2. Environmental data

The environmental data used in the present study have been described previously in Román et al. (2016). Samples from each sediment layer (1 g each) were preserved at -20 °C prior to granulometry and biogeochemistry analyses. Grain size distribution was measured with a Malvern Mastersizer 2000 (0.02-2000 µm size range) and divided into three categories: clay (<4 µm), silt (4- 63 µm) and sand (63 µm – 2 mm) fractions (volume %). Sedimentary organic carbon (OC, %) and total nitrogen (TN, %), were measured after samples were lyophilised and homogenised, using an elemental analyser Flash 1112 EA interfaced to a Delta C Finnigan MAT isotope ratio mass spectrometer. Measurements were conducted at the “Centres Científics i Tecnològics de la Universitat de Barcelona”. Samples for OC were first decarbonated using repeated additions of 25% HCl with 60°C drying steps in between until no

effervescence was observed (Nieuwenhuize et al., 1994). Chlorophyll *a* (Chl *a*, µg/g) and chlorophyll degradation products in the sediment were measured with Ultra Performance Liquid Chromatography after lyophilisation, homogenization and extraction in 4 ml 90% acetone. Identification of phytopigments was realized by checking the retention times and the absorption spectra against a library based on commercial standard mixtures (DHI, PPS-MiX-1) and extracts from pure cultures of algae and bacteria (modified from Buchaca and Catalan, 2008). Chloroplastic Pigments Equivalents (CPE: sum of Chl *a* and its degradation products as phaeopigments) were used to estimate surface-derived primary productivity at the seafloor (Thiel, 1978). The ratio Chl *a*: phaeopigments (Chl *a*: phaeo) was used as a proxy for the freshness of the organic matter (OM) at the seafloor.

2.3. Meiofauna and nematodes

Samples for meiofauna analyses were preserved in 4% borax-buffered formaldehyde. In the laboratory, samples were washed over a 1000 µm mesh on a 32 µm mesh. The fraction retained on the 32 µm was centrifuged three times using LUDOX HS40 (specific gravity 1.18) as flotation medium and then stained with Rose Bengal (Heip et al., 1985). All metazoan meiobenthic organisms were counted under a stereomicroscope (50 x magnification) and classified at higher taxon level following Higgins and Thiel (1988). For nematode processing, 100-150 individuals (all if density < 100) were randomly picked out from each layer (0-1, 1-2 and 2-5 cm), gradually transferred to glycerine (De Grisse, 1969) and mounted on glass slides. Nematodes were identified under compound microscope (1000 x magnification) to genus level using pictorial keys (Platt and Warwick, 1988), the Nematode Handbook (Schmidt-Rhaesa A, 2013) and the NeMys database (Guilini et al., 2016). Specimens that could not be ascribed to genus level were grouped within the appropriate family to account for its presence in the sample. The percentage presence of each genus in the identified aliquot was multiplied by the total nematode abundance per layer and sampling station to account for core and sediment layer abundance differences. Nematode length (L, µm) (excluding filiform tails tips) and maximum body width (W, µm) were measured for all identified nematodes using a compound microscope and TopView 3.7 imaging software and used to estimate individual body wet weights (WW) using Andrassy's formula (Andrassy, 1956), adjusted for the specific gravity of marine nematodes (i.e. 1.13 g cm⁻³; µg WW= L x W²/1.5 x 10⁶). Wet weight was then converted into carbon weight assuming a 12.4% carbon ratio (Jensen, 1984). To calculate the total nematode biomass for each sediment layer, sampling station and feeding type, average biomass for each nematode genus was multiplied by their respective total densities.

2.4. Data analyses

Nematode standing stock (density and biomass), diversity, and community structure were analysed by means of non-parametric permutational analyses of variance (PERMANOVA) using PRIMER v6 (Anderson et al., 2005, 2008). Diversity measures (genus level richness, Shannon diversity (Shannon, 1948), and expected number of genera (*EG* (51)) were calculated using the function DIVERSE in PRIMER v6 (Clarke and Gorley, 2006; based on Sanders/Hurlbert rarefaction calculation). Similarity matrices for the univariate descriptors (density, biomass and diversity) were based on Euclidean distance. Community structure matrices were built using Bray-Curtis similarity (Clarke and Gorley, 2006) based on genera abundance (percentage abundance * total abundance in each sample).

The bathymetric trends of canyon and slope nematode assemblages and standing stocks were compared using a two-factor PERMANOVA design with *ecosystem* (*Ec*: canyon and slope) and *water depth* (*WD*: 1,500, 1,750 and 2,000 m) as fixed factors. Since sediment layers were not considered a factor in this design, total abundance of the entire sediment core (0-5 cm) was used. Community structure was analysed by principal correspondence analysis (PCO). When the number of unique permutations was <100, Monte Carlo (P(MC)) *p* values were used (Anderson and Robinson, 2003).

Three spatial scales (i.e., ecosystem, water depth, sediment layer) were analysed using 4-way PERMANOVA design, with factors *ecosystem* (*Ec*, fixed, two levels: canyon, slope), *water depth* (*WD*, fixed, three levels: 1,500, 1,750 and 2,000 m), *sediment layer* (*SL*, fixed, three levels: 0-1, 1-2 and 2-5 cm), and *core* (*Co*, random, nested in *Ec* and *WD*), the latter to account for dependence of sediment layers within the same core. The importance of each spatial scale was assessed using the Estimated of Components of Variation (ECV). ECV for each factor is calculated as its percentage of total variation in the PERMANOVA tests. Variance components were set to zero in case of negative results, assuming they correspond to sampled underestimates of small zero variances (Benedetti-Cecchi, 2001). SIMPER analyses were conducted to assess genera responsible for differences between stations (*Ec* x *WD*) and canyon vs. slope sediment layers (*Ec* x *SL*) (cut-off of 90% for low contributions).

Since PERMANOVA does not distinguish between factor effects and data dispersion, homogeneity of multivariate dispersion was tested using PERMDISP within factors *Ec*, *WD* and *SL*. Non-significant PERMDISP results indicated that the significant differences in the PERMANOVA analyses were indeed factor effects and not caused by heterogenic multivariate

dispersions. Nematode density and biomass results were significant for the univariate variables and were thus square-root transformed prior to the analyses.

All sediment variables were tested for collinearity (Draftsman plot and Spearman correlation); redundant variables ($R^2 > 0.95$) were omitted from the analyses (i.e. Chl-a:OC, phaeopigments). Sediment variable differences were assessed using the same 4-way PERMANOVA design as described for nematode assemblages, based on Euclidean similarity matrices. Environmental variable differences between canyon and slope were assessed by Principal Component Analyses (PCA) based on whole sample (i.e., sediment layers were not considered).

Partial Spearman Rank correlations between the selected environmental variables (clay, silt, sand, OC, TN, Chl α , CPE, and Chl α : phaeo) and univariate descriptors (density, biomass, genus richness, *EG*(51), and Shannon diversity) were performed at water depth and sediment layer scales for canyon and slope separately, using XLSTAT (Addinsoft) software. RELATE and DISTLM (distance-based linear model) routines based on normalized environmental data were also performed (Anderson et al., 2008; Clarke and Gorley, 2006) to analyse and model the relationship between community structure and environmental variables for the canyon and slope. The DISTLM was built using a “step-wise” selection procedure and adjusted R^2 as selection criterion (Anderson et al., 2008). The results were visualized using dbRDA (distance-based redundancy analysis) plots.

3. RESULTS

3.1. Environmental variables

Canyon and slope sediments were dominated by silt (70.1-77%), followed by clay (18.4-24.3%) and sand (4.4- 5.8%) (Fig. 2). There were significant differences for clay and silt content between the canyon and slope (Table 2) at all water depths ($p < 0.01$, Table S1. A-B) with those from the canyon having higher silt content, and those from the slope having higher clay contents (Fig. 2). Clay content increased and silt content decreased with increasing water depth only in the canyon ($p < 0.01$, Table S1.A-B; Fig. 2), while sediments became always finer along the vertical sediment profile (Table 2 and Table S1.A-B; Fig. S1).

OC was significantly higher in the canyon (0.76-0.83%) than at the slope (0.61-0.62%) (Table 2, Table S1-D; Fig. 2), and did not exhibit significant bathymetric trends, but decreased significantly with increasing sediment depth ($p < 0.05$, Table S1-D; Fig. S1).

TN was significantly higher in the canyon (0.9-0.11%) than on the slope (0.9%) at 1,500 and 1,750 m depth ($p < 0.05$, Table S1-E, Fig. 2; Table 2). There were significant differences between sediment layers (Table 2), but no clear trends along the vertical sediment profile, neither in the canyon nor on the slope (Table S1-E, Fig. S1).

Chl *a* was significantly higher in the canyon (0.02-0.04 $\mu\text{g/g}$) than on the slope (0.0-0.007 $\mu\text{g/g}$) (Table 2, Table S1-F, Fig. 2) at 1,500 and 1,750 m depth, and did not show any clear bathymetric trend, neither in the canyon nor in the slope (Table S1-F, Fig. 2). Chl *a* was significantly higher at 1,500 m depth compared to 2,000 m depth in the canyon ($p < 0.05$, Table S1-F, Fig. 2). There were no overall significant differences in Chl *a* along the vertical sediment profile, neither in the canyon, nor at the slope (Table 2, Fig. S1).

CPE were significantly higher in the canyon (0.8-2.0 $\mu\text{g/g}$) than on the slope (0.2-0.6 $\mu\text{g/g}$) (Table 2, Table S1-G, Fig. 2), showing a bathymetric decrease along the canyon and no clear bathymetric trend on the slope (Fig. 2). There were no significant differences between sediment layers (Table 2), but a decrease along the vertical sediment profile was noticeable at 1,750 and 2,000 m depth in the canyon and on the slope (Fig. S1).

Chl *a*: phaeo did not differ significantly between canyon (0.01-0.07) and slope (0.00-0.04) (Table 2, Fig. 2), nor between sediment layers (Table 2, Fig. S1).

Canyon and slope stations were clearly separated in the PCA plot (Fig. 3), the latter showing less environmental variability than the former. BC2000 was more similar to slope stations than to the other canyon stations, likely owing to greater clay content (Fig. 2). The first two PCA axes explained 76.3% of the variation (Fig. 3). Main contributors were clay (0.426), silt (-0.426), Chl *a* (-0.404) and TN (-0.403) for PC1, and sand (-0.858) and CPE (-0.344) for PC2 (numbers in parenthesis represent eigenvector).

3.2. Canyon vs Slope – Two-way analyses

Nematode densities were significantly different between stations ($Ec \times WD$, Table 3), but a significant bathymetric decrease in density was only observed along the slope (Fig. 4). In the canyon, the highest densities occurred at 1,750 m depth (Fig. 4, Table S2-A). While average densities were higher in the canyon than on the slope for each water depth, pair-wise tests

showed this was only significant for 1,750 m depth (owing to high variability, Table S2-A, Fig. 4). Nematode biomass was significantly higher in the canyon compared to the slope (Table 3, Fig. 4). Similar to densities, biomass decreased with increasing water depth on the slope, but not in the canyon (Fig.4).

One hundred ten genera were identified out of 3,479 nematode specimens (Table S3). In general, the canyon showed higher richness (92 genera) compared to the slope (75 genera). Significant richness differences were found between stations ($Ec \times WD$, Table 3). Similar to density and biomass, richness decreased with increasing water depth on the slope, but not in the canyon (Table 4). Fifty-seven genera were shared between canyon and slope, while 36 exclusively appeared in the canyon and 17 on the slope. Thirty-eight genera appeared in all canyon stations and 30 were shared between all slope stations.

EG (51) only differed significantly between canyon and slope, but there were no bathymetric trends (Tables 3, 4). The Shannon diversity was significantly higher in the canyon compared to the slope, and differed significantly between water depths (Table 3, 4), showing a bathymetric decrease in the canyon, but not on the slope (Table 4, Table S2-C).

Sabatieria dominated in slope sediments followed by *Acantholaimus*, *Halalaimus*, and *Tricoma*, particularly at OS1500 (Table 5). In the canyon, these genera were also abundant, but differed in relative abundance between water depths. *Sphaerolaimus* and *Molgolaimus* occurred in both the canyon and slope stations (absent at OS2000), but were more abundant at BC1500 (8%) and BC1750 (9.6%) (Table 5). There were significant community structure differences between stations ($Ec \times WD$, Table 3). Slope communities were relatively similar, with no clear difference between stations, while canyon communities differed between stations (Fig. 5). This was confirmed by the station dissimilarities being higher in the canyon than on the slope (SIMPER, Table 6). *Sabatieria* contributed most to the dissimilarities in the canyon, followed by *Sphaerolaimus* and *Molgolaimus* (more abundant at BC1500 and BC1750, respectively) (Table 6).

3.3. Spatial scale variability of nematode assemblages – Four-way analyses

There were significant interactions between the three main spatial scale factors for nematode density, biomass, genus richness and community structure (Table 7, Table S4). This means that differences at the level of the three spatial scales interact, with the effects of one factor changing across the levels of the others.

Pair-wise comparisons for densities showed that significant differences between canyon and slope occurred at the deeper 1,750 and 2,000 m sites, for the 0-1 and 1-2 cm sediment layers, respectively (Table S5A, Fig. 6). In the canyon, the only significant difference

in density was a decreased along the vertical sediment profile at 1,750 m depth (Table S5C, Fig. 6). On the slope, there were no significant differences between sediment layers at any depth (Table S5C, Fig. 6). According to ECV, sediment layers explain most of the total density variation in the sample pool (39.7%, Table S4), particularly in the canyon (Table S5-B-C).

The main significant differences in biomass between canyon and slope occurred at 1,750 m depth in the 0-1 cm and 2-5 cm layers and at 2,000 m depth for 2-5 cm layers (Table S5A, Fig. 6). There were no significant differences in biomass between sediment layers at the slope and canyon stations, except at 1,750 m depth between the 0-1 and 1-2 sediment layers in the canyon (Table S5C, Fig. 6).

Genus richness differed significantly between canyon and slope, but only in specific sediment layers at 1,500 m (2-5 cm), 1,750 m (0-1 cm) and 2,000 m (1-2 cm) depth (Table S5A). Genus richness in canyon samples only decreased significantly along the vertical sediment profile at each water depth, but did not differ between water depths (Tables S5B, S5BC). On the slope, genus richness differed significantly between sediment layers at each water depth, but also between water depths (Table S5BC).

The Shannon diversity index, showed significant interactions (i.e., $Ec \times WD$ and $Ec \times SL$, Table 7). The differences between canyon and slope were significant for all water depths (Table S6), and sediment layer differences were significant in both canyon and slope (Table 7, Table S6). Water depths only differed significantly at the slope, not in the canyon.

The differences between sediment layers explained most overall variability in diversity, based on ECV: genus richness (49%), Shannon diversity (57%) and community structure (46%) (Table S4).

The main differences between canyon and slope community structure were mainly found at 1,500 and 1,750 m depth for the 1-2 and 2-5 cm layers (Table S5A). The chemosynthetic mouthless genus *Astomonema* (Table S2), only occurred in the deep sediment layer in the canyon, especially at 1,750 m depth, and is a main contributor to the observed differences (Fig. 7). Significant differences between water depths in each ecosystem (canyon, slope) mainly occurred for the 1-2 cm layers (Table S5B). Along the vertical sediment profile, significant differences mainly occurred between the 0-1 cm and 2-5 cm layers in the canyon, as well as on the slope (except for OS2000, Table S5B). Significant community differences were mainly caused by the 0-1 cm and 2-5 cm layers (SIMPER, Table 8, Fig. 7). The deposit feeding genus *Sabatieria* was the main contributor to community dissimilarity between sediment layers, showing the highest abundance in the 2-5 cm layer. *Acantholaimus* was the second most important contributor, and was more abundant in the 0-1 cm layer. The average canyon vs. slope dissimilarity for each sediment layer was 55.5%. *Molgolaimus*, *Acantholaimus* and

Tricoma were the main responsible genera for the dissimilarities between the 0-1 cm layers, while those between canyon and slope for the 1-2 and 2-5 cm layers were respectively caused by *Sabatieria*, *Sphaerolaimus* (higher in the canyon, 5.2 %), and by *Hopperia* and *Syringolaimus* (higher on the slope, 5.6% and 5.3%, respectively) (Table 8).

3.4. Relationship between nematode descriptors and environmental variables

Significant correlations between environmental variables and univariate nematode descriptors at the water depth scale (stations in each ecosystem) were only observed in the canyon (Spearman rank correlations, Table 9). Genus richness was negatively correlated with Chl *a* (-0.695) and CPE (-0.812), while Shannon diversity was positively correlated with CPE (0.750) and silt (0.900).

All univariate descriptors exhibited significant correlations with silt and clay along the vertical sediment profile in the canyon, while biomass was positively correlated with TN (Table 9). No correlations with pigment-related variables were observed. On the slope, density was correlated with CPE (0.413), sand (0.421), and clay content (-0.440). Genus richness was negatively correlated with Chl *a*, Chl *a*: phaeo, TN and OC, and *EG*(51) and Shannon diversity were negatively correlated with clay, and OC and with TN, respectively (Table 9).

The relationships between environmental variables and community structure were only significant for the 1-2 cm and the 2-5 cm layers (RELATE, 1-2 cm: $\rho=0.30$, $p<0.01$; 2-5 cm: $\rho=0.45$, $p<0.05$). In the best fitting model, silt explains nearly 20% of the variation observed for the 1-2 cm layers, while Chl *a* explains nearly a 15% for the 2-5 cm layers (DISTLM, Table S7, Fig. 8).

4. DISCUSSION

4.1. Comparing Blanes Canyon with the adjacent western slope

Canyons are often characterized by higher faunal abundance and biomass, but lower diversity, compared to the adjacent slopes (Vetter and Dayton, 1998; Curdia et al., 2004; Danovaro et al., 2009; Ingels et al., 2009; Romano et al., 2013b; Leduc et al., 2014; Gunton et al., 2015; Gambi and Danovaro, 2016). However, this is not always the case, as there are opposite observations (Danovaro et al., 1999; Bianchelli et al., 2013). This cast some doubts on what really drive infaunal communities in canyon sediments, as well as on to what extent canyon heterogeneity interplays with environmental and ecological processes. Currently, we still have limited mechanistic understanding on how abundance, biomass and biodiversity are regulated in these highly heterogeneous environments.

Our results showed that all community descriptors differed significantly between canyon and slope ecosystems (Table 3). Density and biomass were higher in the canyon than on the slope, as reported in previous studies (e.g., Ingels et al., 2009; Romano et al., 2013b; Leduc et al., 2014; Gambi and Danovaro, 2016; Rosli et al., 2016). The greater availability of food (i.e., Chl *a*, CPE or OC) in Blanes Canyon compared to that along the slope is likely the main reason explaining the highest canyon standing stocks, which has been also reported for other canyons (Grémare et al., 2002; Ingels et al., 2009; Leduc et al., 2014; Rosli et al., 2016). Bathymetric density gradients were expressed differently in canyon and slope ecosystems; in agreement with the whole meiofauna data along a broader bathymetric gradient (500 to 2,000 m depth) in the same area (Román et al., 2016). Accordingly, we here confirm that the “classical” density decrease with increasing water depth postulated as an overall basic principle in deep-sea ecosystems (Thiel, 1983 and Tietjen, 1992; Soltwedel, 2000) does not necessarily hold for canyon settings, as it does for the nearby slope. Similar exceptions have also been reported for the Gulf of Lions (de Bovée et al., 1990; Grémare et al., 2002) and the Arctic Ardencaple Canyon (Soltwedel et al., 2005). High canyon habitat heterogeneity, owing to a complex topography, hydrography and variable sediment processes (e.g. Canals et al., 2006; Levin and Sibuet, 2012), often disturbs a linear bathymetrical density decrease, leading to a dual canyon/slope trend that seems to be common for Mediterranean and NE Atlantic systems (Bianchelli et al., 2010; Gambi and Danovaro, 2016).

Diversity indicators (except the Shannon index) did not exhibit a clear bathymetric pattern along the canyon either, while a decrease in genus richness with increasing water depth occurred along the slope. Deep-sea nematodes have been found to either decrease or increase in diversity with increasing water depth (Tietjen, 1976; Soetaert et al., 1991; Danovaro et al., 2008), suggesting that diversity patterns may differ in different areas depending more on the local conditions than on any fundamental response to depth (Gage et al., 2000; Muthumbi et al., 2004; Gambi and Danovaro, 2016). Lacking bathymetric diversity pattern for meiofauna higher taxa, as well as for nematodes, has been observed in several other canyons, being apparently independent of the geographical region or the regional environmental conditions, thus pointing on habitat type as a major driver for nematode diversity distribution (Danovaro et al., 2009; Bianchelli et al., 2010; Ingels et al., 2013a; Romano et al., 2013b; Pusceddu et al., 2013; Leduc et al., 2014; Román et al., 2016). Considering that meiofauna and nematode communities may respond to relatively small environmental changes, particularly at the scale of centimetres to meters, it is not surprising that the characteristically high heterogeneity expressed along canyon paths from shallow to deep, does not exhibit the regular bathymetric diversity declines observed along the more

uniform slope environments. Water and sediment transport dynamics, as well as morphology, may play an important role in controlling canyon biota. In the Blanes area, the velocity of particle fluxes is higher in the canyon than on the adjacent slope, particularly in the upper canyon where it is reinforced by an increased lateral transport in the mid axis region (Zuniga et al., 2009; López-Fernández et al., 2013). Also distinct seafloor morphologies in deep-sea environments have revealed higher diversity and turnover in associated nematode assemblages than those sharing a similar and more homogenous seabed (Zeppilli et al 2016).

Until recently, it was generally assumed that slopes would have higher meiobenthic and nematode diversity than canyons. It was hypothesized that by having higher organic matter availability, and more frequent and intense disturbance regimes, canyons would favour colonizer and opportunist species leading to a reduced diversity of the resident communities (Garcia et al., 2007; Danovaro et al., 2009; Ingels et al., 2009; Bianchelli et al., 2010; Bianchelli et al., 2013; Leduc et al., 2014; Gambi and Danovaro, 2016). Our Blanes Canyon findings contradicts such reasoning since it harbours more diverse assemblages than its adjacent western slope, yet its sediment contain higher CPE and OM levels suggesting higher organic matter input into the system. This certainly raises the question of why is diversity higher in Blanes Canyon? An explanation can likely be found in the heterogeneity of the studied system combined with the range of sampling sites. Comprehensive sampling in canyons (i.e., including contrasting sites such as the axis, terraces, recently disturbed, and relatively undisturbed sites) is likely to produce a sample collection with a higher diversity than a set of samples from more similar sites along a bathymetric slope transect. A case in point is, for instance, the observations along the disturbed axis of the well-studied Nazaré Canyon that reported very low meiobenthos and nematode density and diversity levels (Garcia et al., 2007). In contrast, more diverse meiofauna (Bianchelli et al., 2013; Román et al., 2016), nematode (Danovaro et al., 1999; Bianchelli et al., 2013), macrofauna (Romano et al., 2013a; De Leo et al., 2014; Romano et al., 2017) and megafauna (Vetter et al., 2010; Ramirez-Llodra et al., 2010) communities in canyons than in the respective adjacent slopes have been observed. These studies (including our) are likely the result of having included a suitably diverse range of sites that well-represent the canyon landscape heterogeneity, together with the diversity of habitats one can find therein. Our findings thus support the idea of submarine canyons being considered *hot spots* of benthic biodiversity and biomass, particularly if their heterogeneity is taken into consideration.

Nematode community structure at the Blanes canyon system was certainly affected by the “canyon effect”, with clear canyon vs. slope differences at 1,500 and 1,750 m depth. Canyon assemblages showed pronounced bathymetric differences, in contrast to the more

similar slope ones (Fig. 5), which agrees with NE Atlantic (Ingels et al., 2009; Gambi and Danovaro, 2016) and Pacific Ocean-New Zealand (Leduc et al., 2014; Rosli et al., 2016) systems. Thus, canyons showing different characteristics harbour relatively unique meiofauna compared to their slope counterparts (Zeppilli et al., 2018). The community patterns based on genera abundances (PCO, Fig. 5) are relatively similar to those based on environmental variables (PCA, Fig. 3), with the respective differences being reflected in the distances between stations in the plots, which suggest an overall greater similarity between slope than between canyon stations. This corresponds with the general dual idea of homogeneous slope vs. highly heterogeneous canyon environments (Vetter and Dayton, 1999; Garcia et al., 2007; Romano et al., 2013b; Román et al., 2016) and provides additional support to the influence of topographic features on deep-sea meiofauna distribution (Rosli et al., 2016; Zeppilli et al., 2018). Only the deepest, less active Blanes Canyon (BC2000) resembled the slope stations more closely than any other canyon station, meaning that being at 2,000 m depth, it lied outside the range of disturbances and heterogeneity characterising the middle and shallow canyon reaches (López-Fernandez et al., 2013; Román et al., 2016).

The nematode genera being abundant in our study have been reported as so in other Mediterranean slopes and canyons, including the dominant *Sabatieria* (e.g. Vivier, 1978; Soetaert et al., 1995; Soetaert and Heip, 1995). The average nematode assemblages from canyons often shared several dominant genera with those in slopes (Vanreusel et al., 2010), which held true for the Blanes Canyon. In fact, the dominant genera *Sabatieria*, *Acantholaimus* and *Halalaimus* showing similar relative abundances both at the slope and in the canyon.

Blanes Canyon communities at 1,500 m depth were characterized by a relatively high abundance of predatory/scavenging genera, such as *Sphaerolaimus* and *Pomponema*, while non-selective deposit feeders such as *Sabatieria* (Wieser, 1953) were less numerous compared to the slope. A similar dominance pattern was found in the Nazaré Canyon, where it was suggested that increased mobility of large-sized predatory nematodes (Ingels et al., 2009), enabled them to penetrate deeper into the sediment. Therefore they were better at avoiding resuspension in case of sediment disturbance, thereby enhancing their survival rate.

The higher food inputs in the canyon relative to those reaching the slope may be one of the main reasons explaining the peculiarities of canyon communities. In this context we should pay particular attention to the presence of the chemotrophic nematode *Astomonema* (Table S2). This genus is characterized by lacking mouth opening and having a degenerated alimentary canal, which is transformed into a rudimentary gut containing prokaryote micro-organisms (Austen et al., 1993; Musat et al., 2007; Tchesunov et al., 2012). These endosymbionts have been identified as sulphur-oxidising bacteria, which use sulphur

compounds reduction as energy source to nourish their nematode hosts (Ott et al., 2004; Musat et al., 2007). The exclusive presence of *Astomonema* in the canyon, particularly at 1,500 and 1,750 m depth, suggests the presence of reduced sediments, likely due to the very high sedimentation rates, burial, and subsequent change from oxygenic to anaerobic conditions (Paradis et al., 2018). *Astomonema* occurred in other canyons systems (De Leonardis et al., 2008; Ingels et al., 2011a; Tchesunov et al., 2012), which supports its preference by high-deposition, organically-enriched canyon environments (Lins et al., 2013; Ingels et al., 2015) where benthic chemotrophic food webs may likely develop (Zeppilli et al., 2018). Further support to the postulated organic enrichment at 1,750 m depth inside the canyon can be found in the enhanced abundance of *Molgolaimus*, which is often associated with organic enrichment, but also to recent disturbing events (Vanhove et al., 1999; Lee et al., 2001) such as previous depositional episodes leading to consequent increases in OM (Román., 2018). Accordingly, this could likely be an additional driver explaining the singularity of the canyon ecosystem.

4.2. Role of spatial scale in shaping nematode assemblages

Nematodes are known for their patchy distribution at small (cm) spatial scales, both horizontally and vertically (e.g., Eckman and Thistle, 1988; Gallucci et al., 2009). Our results have shown that small-scale variability along the vertical sediment profile was more important for nematode community structure, density and diversity, compared to bathymetry, both in the canyon and at the slope. Consistently, small-scale (cm) variability has been reported as more important than larger-scale (km) differences in explaining meiofaunal and nematode patterns (Ingels et al., 2009; Ingels et al., 2011a, b; Ingels and Vanreusel, 2013; Rosli et al., 2016). Centimetre-scale effects were also illustrated by the occurrence of particular genera in different sediment layers (SL), which lead to a high generic turnover between the 0-1 cm and the 2-5 cm layers, both in the canyon and in the slope. The nematodes showed clear vertical profile gradients in community structure, with genera such as *Acantholaimus* being more common in the surface than in deep sediments (e.g., Leduc et al., 2015). In turn, *Sabatieria* thrives in the deep sediment layers suggesting reduced oxygen availability (Soetaert and Heip, 1995; Vanreusel et al., 1997; Muthumbi et al., 2004). Furthermore, the relationship between nematode descriptors and environmental parameters were much more obvious at the vertical sediment profile scale than at water-depth scale. Significant correlations between community descriptors and environmental variables along the vertical sediment were absent on the slope, likely as a consequence of a higher sedimentary homogeneity compared to canyon settings (Fig. 2).

Substrate heterogeneity seems a key factor contributing to the highly diverse faunal assemblage in submarine canyons (De Leo et al., 2014), and has often been considered a possible cause of spatial variability in deep-sea benthic organisms that acts on various spatial scales and mostly in concert with food availability (Eckman and Thistle, 1988; Rex and Etter, 2010; Vanreusel et al., 2010; Zeppilli et al., 2016). Food availability is particularly relevant for nematode distribution and can vary significantly between different spatial scales, e.g. from patchy distributions in between the micro-topographic features of the seafloor to areas that stretch hundreds of square kilometres and are under the influence of particular surface productivity regimes (Gambi et al., 2014, Rosli et al., 2016). Surface export of primary production to the seafloor is influenced by water column processes and hence the quantity and quality of food arriving to the seabed is in part dependent on the water depth. In this context, small-scale horizontal patchiness may be driven by variations in micro-topography, disturbance, and food availability (Gallucci et al., 2009), whereas vertical sediment profiles are likely determined either by gradients in biogeochemical conditions (e.g., food availability and oxygen concentration) (Jorissen et al., 1995; Soetaert et al. 2002), or by macrofauna activities (e.g., predation, bioturbation, competition for food sources) (Braeckman et al. 2011; Gorska et al., 2014). Nematode population descriptors and grain size are often highly correlated, suggesting that large differences in the nematode distribution can be explained by sediment structure and heterogeneity, especially in canyons where habitat heterogeneity is particularly enhanced compared to slope systems (e.g. Leduc et al., 2012b). The complex geology and hydrodynamic regimes associated with canyons may affect sediment and OM deposition and accumulation rates. In these circumstances, the vertical sediment profile acquires a pronounced structure, thereby enhancing the microhabitat's diversity.

The deepest canyon station has a nematode community closely resembling those of the nearby slope. As the area has also very limited topographic relief, we conclude that this deepest station (like the slope) does not experience any "canyon-effect". Conversely, at 1,500 and 1,750 m depth nematode communities and environmental characteristics were more heterogeneous, in parallel with the complex topography typically derived from enhanced transport, deposition and fluxes along the canyon axis and flanks. Accordingly, the high TN throughout the whole vertical profile at both depths suggests the occurrence of high sedimentation and burial events. There are multiple lines of evidence to explain what may have caused this, which we will explain in more detail in the next section.

4.3. Anthropogenically mediated effects around Blanes Canyon

Evident small-scale differences at community level may derive from the nematode responses to disturbance. In Blanes Canyon, sedimentary alteration may be associated with the impact of bottom trawling activities (Román et al., 2016, Paradis et al., 2018). This canyon, as other areas along the Catalan margin, supports considerable bottom trawling fishing grounds in its head and flanks, where the deep-sea red shrimp *Aristeus antennatus* is among the main target species (Sardà et al., 1994; Tudela et al., 2003). Fish trawling activities cause seafloor erosion resulting in increased sediment resuspension and deposition, as well as in sediment particle-size alteration in both the trawled and surrounding areas (Martin et al., 2014a,b; Puig et al., 2012; Puig et al., 2015a,b). Often, this leads to a decrease in OM in the trawled sediments (Martín et al., 2014b, Pusceddu et al., 2014). These processes may cause a reduction in meiofauna abundance and diversity (Pusceddu et al., 2014), or at least induce changes in the community structure in the directly affected areas. In addition, the generally steep topography of canyon habitats makes them prone to slope instability and turbidity following trawling events on the escarpments and interfluvial areas (Puig et al., 2012). These events may in turn remove organic-rich sediment down-slope to deeper parts of the canyon (Puig et al., 2012; Pusceddu et al., 2014), causing potential disturbance to deeper fauna, as well as supporting infaunal proliferations at locations deeper than expected.

The impact of surface sediment remobilization and relocation of the fauna has been recently assessed along the axes of the nearby canyons Arenys, Besòs and Morrás (Paradis et al., 2017), but also at Blanes Canyon (Paradis et al., 2018). These authors postulate bottom trawling (i.e., through enhanced sedimentation rates) as a major cause altering natural sedimentary environments, independently of the canyons' morphology. Trawl-induced resuspended particulate matter caused three- to fourfold increase in sedimentation rates in comparison with the natural accumulation.

The analysis of meiofauna communities along the Blanes Canyon axis, allowed to suggest that trawling impacts in its upper (900 m depth) and mid (1,200 m depth) regions gave rise to the formation of anthropogenic depocenters, subsequently causing increases in infaunal standing stocks (Román et al., 2016). The recent observations on deposition rates at the Blanes Canyon revealed that, although they tended to decrease down to 1,200 m depth, they increased again at 1,500 and 1,700 m depth. Natural sediment accumulation rates would be close to 0.21 and 0.18 cm·year⁻¹ at 1,500 and 1,700 m depth, respectively, but the actual observed rates were 0.88 and 0.65 cm·year⁻¹, respectively; and can be attributed with no doubts to trawling activities (Paradis et al., 2018). Down to the deepest canyon region, far away from the sources of anthropogenic disturbance (2,000 m depth), trawling-induced resuspension and deposition was reduced and the observed sedimentation rates did not differ

much from the natural ones (Paradis et al., 2018). It is therefore likely the reason explaining why both sediment characteristics and nematode community descriptors at BC2000 in our study more closely resembled those of the nearby slope.

Our results indicate that the ‘canyon effect’ affecting the nematode communities in our study may well be a combination of natural heterogeneity and anthropogenic impacts, which are likely driving benthic variability at various spatial scales at Blanes Canyon. The reported increases in sedimentation rates in our sampling sites, as reported by Paradis et al. (2018), are reflected in the sediment qualitative and quantitative characteristics, as well as in the altered vertical sediment profiles and, ultimately, in the nematode assemblages they contain.

5. ACKNOWLEDGEMENTS

The authors thank the RV García del Cid crew for logistic support during the campaigns. Thanks to Galderic Lastras for the elaboration of map. We are grateful to Dr Pere Puig and Dr Joan B. Company for their helpful discussions on the data on the environmental conditions in the canyon. This work is a contribution to the project DOS MARES (2010-21810-C03-03), funded by the Agencia Española de Investigación (AEI) and the European Funds for Regional Development (FEDER) and to the Consolidated Research Group on Marine Benthic Ecology of the Generalitat de Catalunya (2017SGR378). Sara Román was funded through “Formación de Personal Investigador” grant under the DOS MARES project. Chiara Romano received funding from the People Programme (Marie Curie Action) of the EU’s Seventh Framework Programme (FP7/2007-2013) under REA grant agreement N. PIOF-GA-2013-628146 (@DeepFall_Proj).

REFERENCES

- Amaro, T., Allcock, A. L., Aslam, T., Davies, J. S., De Stigter, H. C., Danovaro, R., De Stigter, H. C., Howell, K. L., Gambi, C., Gooday, A. J., Gunton, L. M., Hall, R., Howell, K. L., Ingels, J., Kiriakoulakis, K., Kershaw, C. E., Wilson, A. M., Robert, K., Stewart, H., Van Rooij, D., White, M., Wilson, A. M., 2016. The Whittard Canyon – A case study of submarine canyon processes. *Progress in oceanography* 146, 38-57.
- Anderson, M. J., Robinson, J., 2003. "Generalized discriminant analysis based on distances." *Australian & New Zealand Journal of Statistics* 45(3): 301-318.
- Anderson, M., Gorley, R. N., Clarke, R. K., 2008. *Permanova+ for Primer: Guide to Software and Statistical Methods*. Plymouth: PRIMER-E Ltd, 214.

- Anderson, M. J., 2005. Permutational multivariate analysis of variance. Department of Statistics, University of Auckland, Auckland 26, 32-46.
- Andrassy, I., 1956. The determination of volume and weight of nematodes. *Acta Zoologica (Hungarian Academy of Science)* 2, 1-15.
- Austen, M. C., Warwick, R. M., & Ryan, K. P., 1993. *Astomonema southwardorum* sp. nov., a gutless nematode dominant in a methane seep area in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 73(3), 627-634.
- Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series* 215, 79-92.
- 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, 420-433.
- Bianchelli, S., Gambi, C., Mea, M., Pusceddu, A., Danovaro, R., 2013. Nematode diversity patterns at different spatial scales in bathyal sediments of the Mediterranean Sea. *Biogeosciences* 10, 5465-5479.
- Braeckman, U., Van Colen, C., Soetaert, K., Vincx, M., Vanaverbeke, J., 2011. Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment. *Marine Ecology Progress Series* 422, 179-191.
- Buchaca, T., Catalan, J., 2008. On the contribution of phytoplankton and benthic biofilms to the sediment record of marker pigments in high mountain lakes. *Journal of Paleolimnology* 40, 369-383.
- Canals, M., Puig, P., de Madron, X., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. *Nature* 444, 354-7.
- Clarke, K. R., Gorley, R. N., 2006. *PRIMER V6: user manual-tutorial*. Plymouth Marine Laboratory.
- Company, J. B., Puig, P., Sardà, F., Palanques, A., Latasa, M., Scharek, R., 2008. Climate Influence on Deep Sea Populations. *PLoS ONE* 3, e1431.
- Curdia, J., Carvalho, S., Ravara, A., Gage, J., Rodrigues, A., Quintino, V., 2004. Deep macrobenthic communities from Nazaré submarine canyon (NW Portugal). *Scientia Marina* 68, 171-180.
- Danovaro, R., Dinét, A., Duineveld, G., Tselepides, 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, 287-312.
- Danovaro R., Gambi C., Lampadariou N., Tselepides A., 2008. Deep-sea nematode biodiversity in the Mediterranean basin: testing for longitudinal, bathymetric and energetic gradients. *Ecography*, 1, 231–244.

Danovaro, R., Bianchelli, S., Gambi, C., Mea, M., Zeppilli, D., 2009. α -, β -, γ -, δ - and ϵ -diversity of deep-sea nematodes in canyons and open slopes of northeast Atlantic and Mediterranean margins. *Marine Ecology Progress Series* 396, 197-209.

deBovée F., Guidi, L.D., Soyer, J., 1990. Quantitative distribution of deep-sea meiobenthos in the northwestern Mediterranean (Gulf of Lions). *Continental Shelf Research*, 10, 1123-1145.

De Grisse, A. T., 1969. Redescription ou modifications de quelques technique utilis [a] es dan l'etude des n [a] ematodes phytoparasitaires. *Meded. Rijksfaculteit Landbouwwetenschappen Gent* 34, 351-369.

De Leo, F., Smith, C., Rowden, A., Bowden, D., Clark, M., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings - Royal Society. Biological sciences* 277, 2783-92.

De Leo, F., Vetter, E., Smith, C., Rowden, A., McGranaghan, M., 2014. Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands. *Deep Sea Research. Part II, Topical studies in oceanography* 104, 267-290.

De Leonardis, C., Sandulli, R., Vanaverbeke, J., Vicx, M., De Zio, S., 2008. Meiofauna and nematode diversity in some Mediterranean subtidal areas of the Adriatic and Ionian Sea. *Scientia Marina* 72, 5-13.

De Stigter, H., Boer, W., Jesus, C., Thomsen, L., 2007. Recent sediment transport and deposition in the Nazare Canyon, Portuguese continental margin. *Marine Geology* 246, 144-164.

Duineveld, G., Lavaleye, M., Berghuis, E., De Wilde, P., 2001. Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic). *Oceanologica Acta* 24, 69-83.

Duros, P., 2011. Live (stained) benthic foraminifera in the Whittard Canyon, Celtic margin (NE Atlantic). *Deep Sea Research. Part I, Oceanographic research papers* 58, 128-146.

Eckman, J. E., Thistle, D., 1988. Small-scale spatial pattern in meiobenthos in the San Diego Trough. *Deep Sea Research Part A. Oceanographic Research Papers* 35, 1565-1578.

Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A. L., Davies, J. S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V. A. I., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A. A., Sanchez, F., Van den Beld, I. M. J., 2017. Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review. *Frontiers in Marine Science* 4, doi:10.3389/fmars.2017.00005.

Flach, E., Muthumbi, A., Heip, C., 2002. Meiofauna and macrofauna community structure in relation to sediment composition at the Iberian margin compared to the Goban Spur (NE Atlantic). *Progress in Oceanography* 52, 433-457.

- Flexas, M. M., Boyer, D. L., Espino, M., Puigdefabregas, J., Rubio, A., 2008. Circulation over a submarine canyon in the NW Mediterranean. *Journal of Geophysical Research* 113 , C12002.
- Fonseca, G., Soltwedel, T., Vanreusel, A., Lindergerth, M., 2010. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic Deep seas. *Progress in Oceanography*, 84 (3), 174-184.
- Gage J.D., Lamont P.A., Kroeger K., 2000. Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland. *Hydrobiologia*, 440, 261–271.
- Gallucci, F., Moens, T., Fonseca, G., 2009. Small-scale spatial patterns of meiobenthos in the Arctic deep sea. *Marine Biodiversity* 39, 9-25.
- Gambi, C., Pusceddu, A., Benedetti Cecchi, L., Danovaro, R., 2014. Species richness, species turnover and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. *Global ecology and biogeography* 23, 24-39.
- Gambi, C., Danovaro, R., 2016. Biodiversity and life strategies of deep-sea meiofauna and nematode assemblages in the Whittard Canyon (Celtic margin, NE Atlantic Ocean). *Deep Sea Research. Part I, Oceanographic research papers* 108, 13-22.
- Garcia, R., Koho, K. A., De Stigter, H. C., Epping, E., Koning, E., Thomsen, L., 2007. Distribution of meiobenthos in the Nazaré canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *MARINE ECOLOGY PROGRESS SERIES* 340, 207-220.
- Giere, O., 2009. *Meiobenthology: the microscopic motile fauna of aquatic sediments*. Springer, Berlin, 1-527.
- Gorelli, G., Sardà, F., Company, J.B., 2016. Fishing effort increase and resource status of the deep-sea red shrimp *Aristeus antennatus* (Risso 1816) in the northwest Mediterranean Sea Since the 1950s. *Rev. Fish. Sci. Aquac.* 24, 192–202. <https://doi.org/10.1080/23308249.2015.1119799>.
- Grémare, A., Medernach, L., de Bovée, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Marine Ecology Progress Series*. 234, 85–94.
- Guilini, K., Bezerra, T.N., Deprez, T., Fonseca, G., Holovachov, O., Leduc, D., Miljutin, D., Moens, T., Sharma, J., Smol, N., Tchesunov, A., Mokievsky, V., Vanaverbeke, J., Vanreusel, A., Vincx, M., 2016. NeMys: World database of free-living marine nematodes. Accessed at <http://nemys.ugent.be> on 20.7.2016.
- Gunton, L. M., Gooday, A. J., Glover, A. G., Bett, B. J., 2015. Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500m; NE Atlantic). *Deep Sea Research Part I, Oceanographic Research Papers* 97, 29-39.

- Harris, P., Whiteway, T., 2011. Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. *Marine Geology* 285, 69-86.
- Heip, C., Vinx, M., Vranken, G., 1985. The Ecology of Marine Nematode. *Oceanography. Mar. Biology Annual Review* 23, 399-489.
- Higgins, R. P., Thiel, H., 1988. Introduction to the study of meiofauna. Smithsonian Institution Press.
- Huvenne, V. A., Tyler, P. A., Masson, D. G., Fisher, E. H., Hauton, C., Hühnerbach, V., Le Bas, T. P., Wolff, G. A., 2011. A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. *PloS one* 6, e28755.
- Ingels, J., Kiriakoulakis, K., Wolff, G., Vanreusel, A., 2009. Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazare Canyon, Western Iberian Margin. *Deep Sea Research. Part I, Oceanographic research papers* 56, 1521-1539.
- 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., Tchesunov, AV, Vanreusel, A., 2011b. Meiofauna in the Gollum Channels and the Whittard Canyon, Celtic Margin—How Local Environmental Conditions Shape Nematode Structure and Function. *PLOS ONE* 6, 15.
- Ingels, J., Vanreusel, A., 2013a. The importance of different spatial scales in determining structure and function of deep-sea infauna communities. *Biogeosciences*. 10, 195-232.
- Ingels J., Vanreusel A., Romano C., Coenjaerts J., Flexas M. M., Zúñiga D., Martín D. 2013b. Spatial and temporal infaunal dynamics of the Blanes submarine canyon-slope system - productivity and disturbance effects on nematode standing stocks, feeding types and gender-life stage ratios. *Progress in Oceanography* 118: 159-174.
- Ingels, J., Allcock, A.L., Bourque, J.R., Demopoulos, A., Kiriakoulakis, K., Lins, L., Martín, D., Robertson, C.M., Román, S., Rüggeberg, A., Vanreusel, A., Wolff, G.A., 2015. The curious tale of *Astomonema* in the deep sea – a chemosynthetic worm feeling at home in submarine canyons. 14th Deep-sea Biology Symposium, Aveiro (Portugal).
- Ismail, K., Huvenne, V. and Robert, K., 2018. Quantifying spatial heterogeneity in submarine canyons. *Progress in Oceanography* 169, 181-198.
<https://doi.org/10.1016/j.pocean.2018.03.006>
- Jensen, P., 1984. MEASURING CARBON CONTENT IN NEMATODES. *Helgoländer Meeresuntersuchungen* 38, 83-86.
- Jorissen, F. J., de Stigter, H. C., Widmark, J. G., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Marine micropaleontology* 26, 3-15.

- Lastras, G., Canals, M., Amblas, D., Lavoie, C., Church, I., 2011. Understanding sediment dynamics of two large submarine valleys from seafloor data: Blanes and La Fonera canyons, northwestern Mediterranean Sea. *Marine Geology* 280, 20-39.
- Leduc, D., Rowden, A., Bowden, D., Nodder, S., Probert, P. K., Pilditch, C. A., Duineveld, G. C. A., Witbaard, R., 2012a. Nematode beta diversity on the continental slope of New Zealand: spatial patterns and environmental drivers. *Marine ecology progress series* 454, 37-52.
- Leduc, D., Rowden, A., Probert, K.P., Pilditch, C. A., Nodder, S.D., Vanreusel, A., Duineveld G.C., Witbaard, R., 2012b. Further evidence for the effect of particle-size diversity on deep-sea benthic biodiversity. *Deep-Sea Research Part I, Oceanographic research papers* 63, 164-169.
- Leduc, D., Rowden, A. A., Nodder, S. D., Berkenbusch, K., Probert, P. K., Hadfield, M. G., 2014. Unusually high food availability in Kaikoura Canyon linked to distinct deep-sea nematode community. *Deep Sea Research Part II, Topical Studies in Oceanography* 104, 310-318.
- Leduc, D., Nodder, S., Berkenbusch, K., Rowden, A., 2015. Effect of core surface area and sediment depth on estimates of deep-sea nematode genus richness and community structure. *Marine Biodiversity* 45, 349-356.
- Lee, H., Vanhove, S., Peck, L. S., Vincx, M., 2001. Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biology* 24, 918-925.
- Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. R., Pawson, D., 2001. Environmental Influences on Regional Deep-Sea Species Diversity 1. *Annual Review of Ecology and Systematics* 32, 51-93.
- Levin, L. A., Dayton, P. K., 2009. Ecological theory and continental margins: where shallow meets deep. *Trends in ecology & evolution* 24, 606-617.
- Levin, L., Sibuet, M., 2012. Understanding Continental Margin Biodiversity: A New Imperative. *Annual Review of Marine Science* 4, 72-112.
- Levin, L. A., Sibuet, M., Gooday, A. J., Smith, C. R., Vanreusel, A., 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. *Marine Ecology* 31, 1-5.
- Lins, L., Vanreusel, A., van Campenhout, J., Ingels, J., 2013. Selective settlement of deep-sea canyon nematodes after resuspension - an experimental approach. *Journal of Experimental Biology and Ecology*, 410, 110-116.
- Lins, L., Guilini, K., Veit-Köhler, G., Hauquier, F., Alves, R. M. d. S., Esteves, A., Vanreusel, A., 2014. The link between meiofauna and surface productivity in the Southern Ocean. *Deep Sea Research Part II, Topical Studies in Oceanography* 108, 60-68.
- López-Fernández, P., Calafat, A., Sanchez Vidal, A., Canals, M., Flexas, M. M., Mar Flexas, M., Cateura, J., Company, J., 2013. Multiple drivers of particle fluxes in the Blanes submarine canyon and southern open slope: Results of a year round experiment. *Progress in Oceanography* 118, 95-107.

- Martín, J., Puig, P., Palanques, A., Masqué, P., García-Orellana, J., 2008. Effect of commercial trawling on the deep sedimentation in a Mediterranean submarine canyon. *Marine Geology* 252, 150-155.
- Martín, J., Puig, P., Palanques, A., Ribó, M., 2014a. Trawling-induced daily sediment resuspension in the flank of a Mediterranean submarine canyon. *Deep Sea Research Part II: Topical Studies in Oceanography* 104, 174-183.
- Martín, J., Puig, P., Masqué, P., Palanques, A., Sánchez-Gómez, A., 2014b. Impact of bottom trawling on deep-sea sediment properties along the flanks of a submarine canyon. *PloS one* 9, e104536.
- Maurer, D., Robertson, G., Gerlinger, T., 1994. Comparison of Community Structure of Soft-Bottom Macrobenthos of the Newport Submarine Canyon, California and the Adjoining Shelf. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 79, 591-603.
- Millot, C., 1999. Circulation in the western Mediterranean Sea. *Journal of Marine Systems* 20, 423-442.
- Moens, T., Braeckman, U., Derycke, S., Fonseca, G., Gallucci, F., Gingold, R., Guilini, K., Ingels, J., Leduc, D., Vanaverbeke, J., 2013. Ecology of free-living marine nematodes. *Nematoda* 2, 109-152.
- Musat, N., Giere, O., Gieseke, A., Thiermann, F., Amann, R., & Dubilier, N., 2007. Molecular and morphological characterization of the association between bacterial endosymbionts and the marine nematode *Astomonema* sp. from the Bahamas. *Environmental microbiology*, 9(5), 1345-1353. <https://doi.org/10.1111/j.1462-2920.2006.01232.x>
- Muthumbi, A., Vanreusel, A., Duineveld, G., Soetaert, K., Vincx, M., 2004. Nematode Community Structure along the Continental Slope off the Kenyan Coast, Western Indian Ocean. *International review of hydrobiology* 89, 188-205.
- Nieuwenhuize, J., Maas, Y. E., Middelburg, J. J., 1994. Rapid analysis of organic carbon and nitrogen in particulate materials. *Marine Chemistry* 45, 217-224.
- Ott, J., Bright, M., and Bulgheresi, S., 2004. Symbioses between marine nematodes and sulfur-oxidizing chemoautotrophic bacteria. *Symbiosis* 36: 103–126.
- Palanques, A., de Madron, X., Puig, P., Fabres, J., Guillen, J., 2006a. Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. *Marine Geology* 234, 43-61.
- Palanques, A., Martín, J., Puig, P., Guillén, J., Company, J., Sardà, F., 2006b. Evidence of sediment gravity flows induced by trawling in the Palamós (Fonera) submarine canyon (northwestern Mediterranean). *Deep Sea Research Part I: Oceanographic Research Papers* 53, 201-214.
- Palanques, A., Masqué, P., Puig, P., Sanchez-Cabeza, J. A., Frignani, M., Alvisi, F., 2008. Anthropogenic trace metals in the sedimentary record of the Llobregat continental shelf and

adjacent Foix Submarine Canyon (northwestern Mediterranean). *Marine Geology* 248, 213-227.

Paradis, S., Puig, P., Masqué, P., Juan-Díaz, X., Martín, J., Palanques, A., 2017. Bottom-trawling along submarine canyons impacts deep sedimentary regimes. *Scientific Reports* 7: 43332.

Paradis, S., Puig, P., Sánchez-Vidal, A., Masqué, P., García-Orellana, J., Calafat, A., Canals, M., 2018. Spatial distribution of sedimentation-rate increases in Blanes Canyon caused by technification of bottom trawling fleet. *Progress in Oceanography*, 169, 241-252 <https://doi.org/10.1016/j.pocean.2018.07.001>.

Pedrosa-Pàmies, R., Sanchez-Vidal, A., Calafat, A., Canals, M., Durán, R., 2013. Impact of storm-induced remobilization on grain size distribution and organic carbon content in sediments from the Blanes Canyon area, NW Mediterranean Sea. *Progress in Oceanography* 118, 122-136.

Platt, H., Warwick, R., 1988. Freelifving marine nematodes: Part II. British Chromadorida. *Synopses of the British Fauna* No. 38. EJ Brill, Dr. W. Backhuys for the Linnean Society of London and the Estuarine and Brackish-water Sciences Associatio.

Plante-Cuny, M.-R., Boday, A., 1987. Biomasse et production primaire du phytoplancton et du microphytobenthos de deux biotopes sableux (Golfe de Fos, France). *Oceanologica acta* 10, 223-237.

Puig, P., Canals, M., Company, J., Martin, J., Amblas, D., Martín, J., Lastras, G., Palanques, A., Calafat, A., 2012. Ploughing the deep sea floor. *Nature* 489, 286-289.

Puig, P., Palanques, A., Martín, J., 2014. Contemporary sediment-transport processes in submarine canyons. *Annual review of marine science* 6, 53-77.

Puig, P., Martín, J., Masqué, P., Palanques, A., 2015a. Increasing sediment accumulation rates in La Fonera (Palamós) submarine canyon axis and their relationship with bottom trawling activities. *Geophysical Research Letters* 42, 8106-8113.

Puig, P., Masqué, P., Martín, J., Paradis Vilar, S., Juan Díaz, X., Toro, M., Palanques, A., 2015b. Changes in sediment accumulation rates within NW Mediterranean submarine canyons caused by bottom trawling activities. In: Briand, F. (Ed.), *CIESM Workshop Monographs N° 47 "Submarine canyon dynamics in the Mediterranean and tributary seas – An integrated geological, oceanographic and biological perspective"*. CIESM Publisher, Monaco, 71–78.

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 shelf water cascading event on deep-sea benthic trophic conditions and meiofaunal biodiversity. *Biogeosciences* 10, 2659-2670.

Pusceddu, A., Bianchelli, S., Martin, J., Puig, P., Palanques, A., Martín, J., Masqué, P., Danovaro, R., Masque, P., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences of the United States of America* 111, 8861-8866.

- Ramalho, S. P., Adão, H., Kiriakoulakis, K., Wolff, G. A., Vanreusel, A., & Ingels, J., 2014. Temporal and spatial variation in the Nazaré Canyon (Western Iberian margin): Inter-annual and canyon heterogeneity effects on meiofauna biomass and diversity. *Deep Sea Research Part I: Oceanographic Research Papers*, 83, 102-114. <http://dx.doi.org/10.1016/j.dsr.2013.09.010>.
- Ramirez Llodra, E., Baptista Company, J., Sarda, F., Rotllant, G., 2010a. Megabenthic diversity patterns and community structure of the Blanes submarine canyon and adjacent slope in the Northwestern Mediterranean: a human overprint? *Marine Ecology* 31, 167-182.
- Rex, M. A., Etter, R. J., 2010. Deep-sea biodiversity: pattern and scale. Harvard University Press.
- Román, S., Vanreusel, A., Romano, C., Ingels, J., Puig, P., Company, J. B., Martin, D., 2016. High spatiotemporal variability in meiofaunal assemblages in Blanes Canyon (NW Mediterranean) subject to anthropogenic and natural disturbances. *Deep Sea Research Part I: Oceanographic Research Papers* 117, 70-83. <http://dx.doi.org/10.1016/j.dsr.2016.10.004>
- Román, S., Vanreusel, A., Ingels, J., Martin, D., 2018. Nematode community zonation in response to environmental drivers in Blanes Canyon (NW Mediterranean). *Journal of Experimental Marine Biology and Ecology*. <http://dx.doi.org/10.1016/j.jembe.2017.08.010>
- Romano, C., Voight, J., Company, J. B., Plyuscheva, M., Martin, D., 2013a. Submarine canyons as the preferred habitat for wood-boring species of *Xylophaga* (Mollusca, Bivalvia). *Progress in Oceanography* 118, 175-187.
- Romano, C., Coenjaerts, J., Flexas, M. M., Zúñiga, D., Vanreusel, A., Company, J. B., Martin, D., 2013b. Spatial and temporal variability of meiobenthic density in the Blanes submarine canyon (NW Mediterranean). *Progress in Oceanography* 118, 144-158.
- Romano C., M.M. Flexas, M. Segura, Román, S., N. Bahamon, J.M. Gili, D. Martin. 2017. Canyon effect and seasonal variability of deep-sea organisms in the NW Mediterranean: synchronous, year-long captures of "swimmers" from near-bottom sediment traps in a submarine canyon and its adjacent open slope. *Deep-Sea Research Part I: Oceanographic Research Papers* 129, 99-115
- Rosli, N., Leduc, D., Rowden, A., Clark, M., Probert, P. K., Berkenbusch, K., Neira, C., 2016. Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance. *PeerJ* 4, e2154-e2154.
- Rosli, N., Leduc, D., Rowden, A. A., Probert, P. K., 2017. Review of recent trends in ecological studies of deep-sea meiofauna, with focus on patterns and processes at small to regional spatial scales. *Marine Biodiversity*, 1-22.
- Rowe, G. T., Polloni, P. T., Haedrich, R. L., 1982. The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep Sea Research Part I. Oceanographic Research Papers* 29, 257-278.
- Sardà, F., Cartes, J., Norbis, W., 1994. Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean. *Fishery Bulletin* 92, 599-607.

- Sardà, F., Company, J. B., Bahamón, N., Rotllant, G., Flexas, M. M., Sánchez, J. D., Zúñiga, D., Coenjaerts, J., Orellana, D., Jordà, G., Puigdefàbregas, J., Sánchez-Vidal, A., Calafat, A., Martín, D., Espino, M., 2009. Relationship between environment and the occurrence of the deep-water rose shrimp *Aristeus antennatus* (Risso, 1816) in the Blanes submarine canyon (NW Mediterranean). *Progress In Oceanography* 52, 227-238. doi:10.1016/j.pocean.2009.07.001.
- Schlacher, T. A., Williams, A., Althaus, F., Schlacher-Hoenlinger, M. A., 2010. High-resolution seabed imagery as a tool for biodiversity conservation planning on continental margins. *Marine Ecology* 31, 200-221.
- Schratzberger, M., Jennings, S., 2002. Impacts of chronic trawling disturbance on meiofaunal communities. *Marine biology* 141, 991-1000.
- Shannon, C., 1948. A mathematical theory of communication, *bell System technical Journal* 27: 379-423 and 623-656. *Mathematical Reviews (MathSciNet)*: MR10, 133e.
- 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., Vincx, M., Heip, C., 1995. Nematode community structure along a Mediterranean shelf-slope gradient. *Marine Ecology* 16, 189-206.
- Soetaert, K., Muthumbi, A., Heip, C., 2002. Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. *Marine ecology progress series* 242, 179-193.
- Soltwedel, T., 2000. Metazoan meiobenthos along continental margins: a review. *Progress in Oceanography* 46, 59-84.
- Soltwedel, T., Hasemann, C., Quéric, N.-V., 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 1. Oceanographic research papers* 52, 815-835.
- Tchesunov, A., Ingels, J., Popova, E., 2012. Marine free-living nematodes associated with symbiotic bacteria in deep-sea canyons of north-east Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom* 92, 1257-1271.
- Thiel, H., 1978. Benthos in upwelling regions. *Upwelling ecosystems*. Springer, 124-138.
- Thiel, H., 1983. Meiobenthos and nanobenthos of the deep sea. *The sea* 8, 167-230.
- Tietjen J.H., 1976. Distribution and species diversity of deep sea nematodes off North Carolina. *Deep-Sea Research*, 23, 755-768.
- Tietjen, J. H., 1992. Abundance and biomass of metazoan meiobenthos in the deep-sea, deep-sea food chains and the global carbon cycle. *NATO ASI series. Series C, Mathematical and physical sciences* 360, 45-62.

- Tubau, X., Canals, M., Lastras, G., Rayo, X., Rivera, J., Amblas, D., 2015. Marine litter on the floor of deep submarine canyons of the Northwestern Mediterranean Sea: The role of hydrodynamic processes. *Progress in oceanography* 134, 379-403.
- Tudela, S., Sardà, F., Maynou, F., Demestre, M., 2003. Influence of submarine canyons on the distribution of the deep-water shrimp, *Aristeus antennatus* (Risso, 1816) in the NW Mediterranean. *Crustaceana* 76, 217-225.
- Van Gaever, S., Galeron, 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, 2259-2269.
- Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). *Marine ecology progress series* 181, 237-256.
- Vanreusel, A., Vanden Bossche, I., Thiermann, F., 1997. Free-living marine nematodes from hydrothermal sediments: similarities with communities from diverse reduced habitats. *Marine Ecology Progress Series* 157, 207-219.
- Vanreusel, A., Fonseca, G., Danovaro, R., da Silva, M.C., Esteves, A.M., Ferrero, T., Gad, G., Galtsova, V., Gambi, C., Genevois, V.D., Ingels, J., Ingole, B., Lampadariou, N., Merckx, B., Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D., Radziejewska, T., Raes, M., Tchesunov, A., Vanaverbeke, J., Van Gaever, S., Venekey, V., Bezerra, T.N., Flint, H., Copley, J., Pape, E., Zeppilli, D., Martinez, P.A., Galeron, J., 2010. The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. *Marine Ecology Evolutionary Perspective* 31, 6–20.
- Vetter, E., Dayton, P., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep Sea Research Part II: Topical Studies in Oceanography* 45, 25-54.
- Vetter, E., Dayton, P., 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Marine Ecology Progress Series* 186, 137-148.
- Vetter, E., Smith, C., De Leo, F., 2010. Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. *Marine ecology* 31, 183-199.
- Vivier, M. H., 1978. Influence d'un deversement industriel profond sur la nematofaune (Canyon de Cassidaigne, Mediterranee). *Téthys* 8, 307-321.
- Weaver, P. P., Billett, D. S., Boetius, A., Danovaro, R., Freiwald, A., Sibuet, M., 2004. Hotspot ecosystem research on Europe's deep-ocean margins. *Oceanography* 17, 132-143.
- Wieser, W., 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden: *Arkiv För Zoologi* 2, 439-484.

Wilson, A. M., Kiriakoulakis, K., Raine, R., Gerritsen, H. D., Blackbird, S., Allcock, A. L., White, M., 2015. Anthropogenic influence on sediment transport in the Whittard Canyon, NE Atlantic. *Marine pollution bulletin* 101, 320-329.

Zeppilli, D., Pusceddu, A., Trincardi, F., Danovaro, R., 2016. Seafloor heterogeneity influences the biodiversity–ecosystem functioning relationships in the deep sea. *Scientific Reports*, 6:26352.

Zeppilli, D., Leduc, D., Fontanier, C., Fontaneto, D., Fuchs, S., Gooday, A. J., ... & Neves, R. C., 2018. Characteristics of meiofauna in extreme marine ecosystems: a review. *Marine Biodiversity*, 48(1), 35-71. <https://doi.org/10.1007/s12526-017-0815-z>.

Zúñiga, D., Flexas, M. M., Sanchez-Vidal, A., Coenjaerts, J., Calafat, A. i., Jordà, G., García-Orellana, J., Puigdefàbregas, J., Canals, M., Espino, M., Sardà, F., Company, J. B., 2009. Particle fluxes dynamics in Blanes submarine canyon (Northwestern Mediterranean). *Progress In Oceanography* 82, 239-251.

Table 1. Sampling details from each sampled ecosystem. BC= Blanes canyon; OS= western open slope. Each deployment code refers to one replicate (three replicates per station in total).

Habitat	Station	Date	Deployment code	Depth (m)	Latitude N	Longitude E
BC	BC1500	08/10/2012	MC16	1450,2	41°27'31''	02°52'57''
BC	BC1500	08/10/2012	MC17	1463	41°27'38''	02°52'46''
BC	BC1500	08/10/2012	MC18	1457	41°27'29''	02°52'58''
BC	BC1750	11/10/2012	MC27	1745,9	41°21'16''	02°52'13''
BC	BC1750	11/10/2012	MC29	1751	41°21'20''	02°52'13''
BC	BC1750	11/10/2012	MC30	1726,5	41°21'38''	02°52'15''
BC	BC2000	11/10/2012	MC31	1943	41°14'53''	02°52'60''
BC	BC2000	11/10/2012	MC32	1969,2	41°15'5''	02°53'5''
BC	BC2000	11/10/2012	MC33	1980	41°14'56''	02°53'25''
OS	OS1500	12/10/2012	MC42	1454	41°08'42''	02°53'33''
OS	OS1500	12/10/2012	MC43	1451	41°08'37''	02°53'32''
OS	OS1500	12/10/2012	MC44	1480	41°08'30,7''	02°53'48,1''
OS	OS1750	11/10/2012	MC39	1742,1	41°06'42''	02°57'02''
OS	OS1750	11/10/2012	MC40	1731	41°07'01''	02°57'7''
OS	OS1750	12/10/2012	MC41	1751	41°06'84''	02°57'34''
OS	OS2000	11/10/2012	MC34	1979	41°02'26''	03°01'15''
OS	OS2000	11/10/2012	MC35	1998	41°02'11''	03°01'26''
OS	OS2000	11/10/2012	MC36	1994	41°02'5''	03°01'39''

Table 2. Results from univariate PERMANOVA four-way analyses for differences in sedimentary variables. Test for Ecosystems (*Ec*: Canyon and Slope); water depth (*WD*: 1,500, 1,750 and 2,000 m), Sediment layer (*SL*: 0-1, 1-2, 2-5 cm) and Corer (*Co*, nested in *Ha* and *WD*). Clay, Silt, Sand: volume percent clay, silt, sand content; TN: total nitrogen concentration; OC: organic carbon concentration; Chl *a*: chlorophyll *a*; CPE: chloroplastic pigment equivalents; Chl*a*:phaeo: chlorophyll *a*: phaeopigments ratio. Data were normalised and resemblance was calculated using Euclidean distance. Bold values indicate significant differences at $p < 0.05$, bold italic values indicate significant differences at $p < 0.01$.

Source	df	Clay	Silt	Sand	OC	TN	Chl <i>a</i>	CPE	Chl <i>a</i> :phaeo
<i>Ec</i>	1	0.0002	0.0001	0.2668	0.0002	0.0002	0.0002	0.0009	0.2032
<i>WD</i>	2	0.1144	0.1716	0.5709	0.2815	0.1167	0.1177	0.0265	0.7769
<i>SL</i>	2	0.0001	0.0001	0.0291	0.0115	0.0076	0.5103	0.1015	0.5068
<i>Ec</i> x <i>WD</i>	2	0.0059	0.0004	0.1464	0.5908	0.0077	0.0394	0.2687	0.1646
<i>Ec</i> x <i>SL</i>	2	0.0508	0.0407	0.5373	0.4223	0.79	0.6769	0.6133	0.325
<i>WD</i> x <i>SL</i>	4	0.6318	0.8572	0.4728	0.2223	0.1017	0.4681	0.4687	0.521
<i>Co</i> (<i>Ec</i> x <i>WD</i>)	12	0.7945	0.7895	0.1043	0.0697	0.0923	0.9862	0.8071	0.528
<i>Ec</i> x <i>WD</i> x <i>SL</i>	4	0.2334	0.3282	0.5049	0.8489	0.7369	0.6246	0.5728	0.8808
Res	24								
Total	53								

Table 3. Results of two-way PERMANOVA analyses for differences in nematode descriptors using Ecosystem (*Ec*) and water depth (*WD*) as factors. Bold: $p < 0.05$; bold italic: $p < 0.01$.

Source	df	SS	MS	Pseudo-F	P(perms)	Perms
Density						
Ec	1	482.03	482.03	35.823	0.0001	9827
WD	2	153.54	76.77	5.7053	0.0194	9954
Ec x WD	2	224.33	112.17	8.3359	0.0073	9959
Res	12	161.47	13.456			
Total	17	1021.4				
Biomass						
Ec	1	19.757	19.757	11.448	0.0085	9847
WD	2	4.5913	2.2956	1.3302	0.3055	9949
Ec x WD	2	4.4388	2.2194	1.286	0.334	9957
Res	12	15.533	1.7258			
Total	17	41.973				
Genus richness						
Ec	1	206.72	206.72	27.36	0.0003	9730
WD	2	103.44	51.722	6.8456	0.0113	9943
Ec x WD	2	290.11	145.06	19.199	0.0004	9957
Res	12	90.667	7.5556			
Total	17	690.94				
EG(51)						
Ec	1	22.809	22.809	6.9543	0.022	9989
WD	2	16.24	8.1199	2.4757	0.12	9979
Ec x WD	2	25.694	12.847	3.9169	0.063	9958
Res	12	39.359	3.2799			
Total	17	104.1				
Shannon diversity						
Ec	1	0.27411	0.27411	26.81	0.0009	9834
WD	2	0.13399	6.70E-02	6.5523	0.0121	9945
Ec x WD	2	1.37E-02	6.84E-03	0.66856	0.5293	9949
Res	12	0.12269	1.02E-02			
Total	17	0.54446				
Community structure						
Ec	1	2950.8	2950.8	4.4459	0.0006	9942
WD	2	2637.1	1318.6	1.9866	0.0062	9910
Ec x WD	2	3756.2	1878.1	2.8296	0.0002	9911
Res	12	7964.7	663.72			
Total	17	17309				

Table 4. Structural diversity indices per sediment layer and station (0-5 cm, bold values).

Station	Layer (cm)	Genus richness	EG(51)	Shannon diversity
BC1500	0-1	53	20.61	3.08
	1-2	38	17.13	2.70
	2-5	22	11.63	1.87
	0-5	65	25.03	3.24
BC1750	0-1	53	20.41	3.06
	1-2	29	16.30	2.51
	2-5	19	8.56	1.51
	0-5	64	25.95	3.20
BC2000	0-1	46	18.20	2.81
	1-2	50	17.81	2.66
	2-5	35	8.39	1.74
	0-5	68	25.51	3.08
OS1500	0-1	46	21.64	2.95
	1-2	29	15.59	2.12
	2-5	13	12.26	2.07
	0-5	60	22.18	2.96
OS1750	0-1	44	19.79	2.92
	1-2	34	18.77	2.61
	2-5	24	13.55	2.15
	0-5	59	23.83	3.03
OS2000	0-1	32	17.85	2.74
	1-2	13	7.85	1.52
	2-5	14	8.88	1.98
	0-5	40	19.85	2.75

Table 5. Relative abundance of the dominant (> 2%) nematode genera per station (0-5 cm, all replicates included).

BC1500	%	BC1750	%	BC2000	%	OS1500	%	OS1750	%	OS2000	%
	14	<i>Molgolaim</i>	9.		20		22		18		22
<i>Sabatieria</i>	.6	<i>us</i>	6	<i>Sabatieria</i>	.2	<i>Sabatieria</i>	.2	<i>Sabatieria</i>	.5	<i>Sabatieria</i>	.9
<i>Halalaimu</i>	8.		9.	<i>Acantholai</i>	9.	<i>Acantholai</i>	10	<i>Acantholai</i>	9.	<i>Acantholai</i>	8.
<i>s</i>	6	<i>Halalaimus</i>	1	<i>mus</i>	7	<i>mus</i>	.4	<i>mus</i>	7	<i>mus</i>	3
<i>Sphaerolai</i>	8.	<i>Acantholai</i>	8.		6.		6.		6.		7.
<i>mus</i>	0	<i>mus</i>	4	<i>Tricoma</i>	5	<i>Tricoma</i>	7	<i>Halalaimus</i>	9	<i>Halalaimus</i>	8
<i>Pomponema</i>	4.		7.		6.		5.	<i>Monhystrel</i>	5.		5.
	6	<i>Sabatieria</i>	6	<i>Halalaimus</i>	4	<i>Halalaimus</i>	7	<i>la</i>	2	<i>Diplopeltula</i>	4
<i>Diplopeltula</i>	4.		6.	<i>Molgolaim</i>	4.	<i>Amphimon</i>	3.	<i>Chromador</i>	4.	<i>Metasphaer</i>	4.
	4	<i>Tricoma</i>	6	<i>us</i>	2	<i>hystrella</i>	9	<i>ella</i>	3	<i>olaimus</i>	6
<i>Oxystomina</i>	4.	<i>Amphimon</i>	4.	<i>Chromador</i>	3.	<i>Daptonema</i>	3.		4.	<i>Sphaerolai</i>	4.
<i>a</i>	1	<i>hystrella</i>	5	<i>ella</i>	5	<i>a</i>	8	<i>Tricoma</i>	2	<i>mus</i>	0
<i>Acantholaimus</i>	3.	<i>Metasphaerolaimus</i>	4.	<i>Metasphaerolaimus</i>	3.		3.	<i>Syringolaim</i>	4.		3.
	9		0		0	<i>Pselionema</i>	1	<i>mus</i>	0	<i>Pselionema</i>	3
<i>Cervonema</i>	3.	<i>Sphaerolaimus</i>	3.	<i>Diplopeltula</i>	2.	<i>Monhystrel</i>	2.	<i>Desmoscol</i>	2.	<i>Amphimon</i>	3.
<i>a</i>	6	<i>mus</i>	7	<i>a</i>	7	<i>la</i>	6	<i>ex</i>	8	<i>ystrella</i>	0
<i>Daptonema</i>	3.		3.		2.	<i>Chromador</i>	2.	<i>Amphimon</i>	2.	<i>Syringolaim</i>	2.
<i>a</i>	3	<i>Cervonema</i>	6	<i>Oxystomina</i>	6	<i>ella</i>	0	<i>hystrella</i>	7	<i>us</i>	9
	3.		2.	<i>Monhystrell</i>	2.				2.	<i>Monhystrell</i>	2.
<i>Tricoma</i>	0	<i>Pselionema</i>	9	<i>a</i>	1			<i>Pselionema</i>	6	<i>a</i>	8
<i>Disconema</i>	3.		2.	<i>Syringolaim</i>	2.			<i>Sphaerolaimus</i>	2.		2.
<i>a</i>	0	<i>Marylynnia</i>	8	<i>us</i>	1				3	<i>Vasostoma</i>	7
<i>Actinonema</i>	2.		2.	<i>Amphimon</i>	2.						2.
<i>ma</i>	9	<i>Daptonema</i>	4	<i>hystrella</i>	0					<i>Oxystomina</i>	5
<i>Halichoan</i>	2.	<i>Monhystrell</i>	2.							<i>Symplocost</i>	2.
<i>olaimus</i>	9	<i>a</i>	1							<i>oma</i>	0
<i>Pselionema</i>	2.									<i>Thalassomo</i>	2.
<i>a</i>	3									<i>nhystera</i>	0
<i>Molgolaimus</i>	2.										
<i>Marylynnia</i>	2.										
<i>a</i>	0										

Table 6. SIMPER analyses results showing nematode genera accounting for community dissimilarity at Depth scale in the canyon and slope ecosystems (cut-off applied at 90% contribution). > and < symbols indicate the direction of the higher Average abundance of each genus between water depth comparisons.

Dissimilarity within Ecosystems (4 > %)											
1500 vs. 1750				1500 vs. 2000				1750 vs. 2000			
49				39				47			
.0				52.2				.0			
Canyon	4	Slope	.8	Canyon	9	Slope	6	Canyon	8	Slope	5
Molgolai	7.	Sabatieri	9.	Sabatieri	0	Sabati	8.	Sabati	14	Sabatieri	76
mus	83	< a	08	a	9	< eria	59	eria	.3	< a	<
Sabatieri	6.	Chromad	5.	Sphaerol	3	Diplop	6.	Molg	5.	Diplopelt	77
a	42	> orella	49	aimus	5	> eltula	58	olaim	21	> ula	<
Tricoma	5.	Syringola	5.	Acanthol	2	Tricom	5.	Trico	4.	Metasph	4.
	41	< imus	2	aimus	8	< a	18	ma	0	aerolaim	3
Acanthol	5.		5.		4.	Acanth					4.
aimus	19	< Tricoma	02	Tricoma	6	< s	59			Acanthol	12
										aimus	>
											4.
						Desmo	4.				07
						scolex	04			Tricoma	>
										Chromad	4.
										orella	01
											>
Dissimilarity between Ecosystems (4 > %)											
BC1500				BC1750				BC2000			
vs. 52				vs. .0				vs. 45.0			
OS1500				OS1750				OS2000			
.1				9				1			
Sabatieri	9.	Sabatieri		Sabatieri	7.			Sabatieri	7.		
a	44	< a	14	a	6	<		a	6	<	
Acanthol	7.	Molgolai	8.	Molgolai	5.			Molgolai	5.		
aimus	52	< mus	19	mus	3	>		mus	3	>	
Sphaerol	5.	Syringola	5.	Metasph	4.			Metasph	4.		
aimus	17	> imus	23	aerolaim	4			aerolaim	4		
			4.	us	9	<		us	9	<	
		Tricoma	04	Tricoma	4	>		Tricoma	4	>	
					4.				4.		
				Sphaerol	1			Sphaerol	1		
				aimus	3	<		aimus	3	<	

Table 7. Summary of the results of 4-way PERMANOVA analyses for differences in all nematode descriptors using Ecosystem (*Ec*), water depth (*WD*), sediment layer (*SL*) and Core (*Co*) as factors. The * symbol denotes significant differences.

Descriptors	Ec	WD	SL	Ec x WD	Ec x SL	WD x SL	Co	Ec x WD x SL
Density	*	*	*		*			*
Biomass	*				*		*	*
Genus richness	*	*	*	*				*
Shannon diversity	*	*	*	*	*			
Comm. Structure	*	*	*	*	*			*

Table 8. SIMPER analyses results showing nematode genera accounting for community dissimilarity at sediment layer scale in the canyon and slope Ecosystems (cut-off applied at 90% contribution). > and < symbols indicate the direction of the higher Average abundance of each genus between sediment layer comparisons.

Dissimilarity within Ecosystems (4 > %)											
0-1 vs. 1-2 cm				0-1 vs. 2-5 cm				1-2 vs. 2-5 cm			
	69.3		66.		86.0		78.1		57.7		54.9
Canyon	3	Slope	75	Canyon	5	Slope	4	Canyon	8	Slope	6
			27.								
Sabatier	18.0	Sabatier	84		28.0	Sabatier	18.7	Sabatier	21.1	Sabatier	15.4
ria	4 <	ia	<	Sabatier	1 <	ria	1 <	ria	4 <	ria	2 >
Acantholaimus	6.67	Acantholaimus	6.1	Acantholaimus	6.34	Acantholaimus	8.27	Sphaerolaimus	5.29	Acantholaimus	5.83
	>		>		>		>		>		>
			5.1								
Molgolaimus	4.9		3		4.99		4.88	Cervone	4.65	Hopperia	5.55
	>	Tricoma	>	Halalaimus	>	Tricoma	>	ma	>	a	<
	4.52			Molgolaimus	4.21	Halalaimus	4.37	Halalaimus	4.31	Halalaimus	4.72
Tricoma	>			s	>	mus	>	mus	>	mus	>
Sphaerolaimus	4.16				4.06	Hopperia	4.3			Syringolaimus	4.68
	<			Tricoma	>	a	<			aimus	<
										Chromadorea	4.42
										dorella	>
										Monhystrella	4.34
										trella	<
										Oxystomina	4.28
										mina	<
Dissimilarity between Ecosystems (4 > %)											
0-1 vs. 53.6				1-2 vs. 57.				2-5 vs. 2-5 55.9			
0-1 cm 7				1-2 cm 09				cm 1			
Molgolaimus	6.38	Sabatier	20.		14.5						
	>	ia	1 <	Sabatier	>						
Acantholaimus	5.83	Sphaerolaimus	5.2		5.61						
	<	laimus	1 >	Hopperia	<						
	5.32	Acantholaimus	5.1	Syringolaimus	5.31						
Tricoma	>	laimus	5 <	us	<						
Sabatier	5.3	Cervone	4.8	Amphimonhystrella	4.57						
ria	<	ma	2 >	Monhystrella	4.48						
				a	<						
				Paramphimonhystrella	4.41						
					>						
					4.4						
				Diplopeltula	<						

Table 9. Spearman correlation coefficients between univariate nematode descriptors and sediment environmental variables at water depth (N=9) and sediment layer (SL) (N=27) - scales in the canyon and on the slope. Bold values indicate significant differences at $p < 0.05$.

Canyon	Chl α	CPE	Chl α : phaeo	OC	TN	Clay	Silt	Sand
Density								
Water depth	0.133	-0.133	0.400	0.067	0.447	-0.183	0.183	-0.117
SL	-0.036	-0.119	-0.324	0.011	0.205	-0.721	0.592	0.155
Biomass								
Water depth	0.533	0.350	0.000	-0.017	0.464	-0.450	0.250	0.167
SL	0.083	-0.018	-0.075	-0.079	0.408	-0.626	0.596	-0.119
Genus richness								
Water depth	-0.695	-0.812	0.117	0.160	-0.258	0.653	-0.460	-0.167
SL	-0.042	-0.127	-0.290	0.016	0.121	-0.561	0.537	0.032
EG (51)								
Water depth	0.200	0.183	0.217	0.184	-0.371	0.250	0.083	-0.100
SL	0.075	0.002	-0.246	-0.015	0.145	-0.665	0.584	0.120
Shannon diversity								
Water depth	0.633	0.750	0.300	0.084	0.473	-0.683	0.900	-0.483
SL	0.083	0.020	-0.233	-0.027	0.206	-0.719	0.641	0.175
Slope	Chl α	CPE	Chlα: phaeo	OC	TN	Clay	Silt	Sand
Density								
Water depth	0.338	-0.200	0.338	0.429	0.353	-0.714	0.600	-0.429
SL	0.070	0.413	0.082	0.217	0.182	-0.440	0.259	0.421
Biomass								
Water depth	0.101	-0.543	0.101	0.314	0.177	-0.771	0.714	-0.600
SL	-0.361	-0.189	-0.354	-0.363	-0.225	-0.077	-0.018	0.090
Genus richness								
Water depth	-0.304	-0.257	-0.304	-0.086	-0.177	-0.371	0.086	-0.086
SL	-0.599	-0.276	-0.577	-0.538	-0.674	0.015	-0.148	0.235
EG (51)								
Water depth	0.507	0.543	0.507	0.200	0.441	-0.086	-0.029	0.086
SL	-0.335	0.307	-0.322	0.010	-0.152	-0.52	0.348	0.327
Shannon diversity								
Water depth	0.270	0.429	0.270	0.257	0.000	-0.029	-0.143	0.486
SL	-0.448	-0.315	-0.410	-0.473	-0.6	0.054	-0.100	0.113

Figure 1. Overview (up right) and detailed map of the location of sampling stations. BC: Blanes Canyon, OS: open slope. Colour maps are redrawn from bathymetric map of GRC of Marine Geosciences of University of Barcelona.

Figure 2. Environmental variables used in this study for canyon (BC) and slope (OS) stations: TN (total nitrogen), Chl *a* (Chlorophyll *a*), CPE (Chloroplastic Pigment Equivalents), Chl *α*: phaeo (Chlorophyll *α*: phaeopigments) and OC (organic carbon). Black lines represent the median and lower box indicates the first quartile and upper box the third quartile. Upper line on the boxes shows the maximum value and lower line the minimum value.

Figure 3. Principal component analysis (PCA) ordination based on selected environmental variables at the studied stations. Fill symbols represent canyon samples.

Figure 4 . Average nematode densities (ind/10cm²) in the studied stations. Superimposed are: average nematode biomass (μgC/10 cm²). Scales were made uniform for better comparison. Error bars are standard deviations.

Figure 5. Principal coordinates analysis (PCO) plot on standardized nematode genera relative abundance data and Bray-Curtis similarity measurement at the study stations. BC: Blanes canyon; OS: open slope. Fill symbols represent canyon samples.

Figure 6. Average nematode densities (ind/10cm²) along the sediment profile in the studied stations. Superimposed are: average nematode biomass (μgC/10 cm²). Scales were made uniform for better comparison. Error bars denote standard deviations.

Figure 7. Vertical profile of nematode relative abundances for each station. Only genera with abundance > 6% in one of the layers were included, the others were grouped as “rest”.

Figure 8. Distance-based redundancy (dbRDA) plots illustrating the DISTLM model based on the nematode genera assemblages and the fitted environmental variables as vectors for the sediment layers **A)** 1-2 cm and **B)** 2-5 cm.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7

Figure 8.

SUPPLEMENTARY MATERIAL

Figure S1. Average values for selected sedimentary parameters along the vertical sediment profile. Chl *a*: chlorophyll *a*; CPE: chloroplastic pigment equivalents; Chl-*a*:phaeo: chlorophyll *a* divided by its degradation products (phaeophytines) indicating 'freshness' of the phytodetrital OM; OC: organic carbon concentration; TN: total nitrogen concentration; Clay, Silt, Sand: volume percent clay, silt, sand content. BC= Blanes Canyon; OS=open slope. Values averaged over replicates.

Table S1. 4- factor PERMANOVA pair-wise test results for significant sediment layer (SL) water depth (WD) and double interactions (Ec x WD and Ec x SL) based on sediment variables: A) Clay; B) Silt C) Sand; D) TN: total nitrogen concentration; E) OC: organic carbon concentration; F) Chl *a*: chlorophyll *a*; G) CPE: chloroplastic pigment equivalents; perms: possible permutations; P (MC): Monte-Carlo p-values. Bold P(MC) values: $p < 0.05$; bold italic values: $p < 0.01$. BC: Blanes Canyon; OS: Open slope.

Table S2. 2- factor PERMANOVA pair-wise test results for significant water depth (WD) and double interactions (Ec x WD) based on nematode descriptors: A) Density; B) Genus richness; C) Shannon diversity; D) Community structure. Ec: Ecosystem and WD: water depth; perms: possible permutations; P (MC): Monte-Carlo p-values. Bold P(MC) values: $p < 0.05$; bold italic values: $p < 0.01$. BC: Blanes Canyon; OS: Open slope.

Table S3. List of identified genera and families in the study stations, with trophic group (FT) classification according to the definitions of Wieser (1953): 1A: selective deposit feeder, 1B: non-selective deposit feeder, 2A: epistratum feeder, 2B: predator/scavenger. And 3: chemosynthetic, symbiosis with sulphur oxidising endosymbiotic bacteria in the gut.

Table S4. Results of 4-way PERMANOVA analyses for differences in nematode descriptors using Ecosystem (Ec), water depth (WD), sediment layer (SL) and Core (Co, nested in Ha x WD) as factors. Bold: $p < 0.05$; bold italic: $p < 0.01$. ECV: Estimated Component of Variation (ECV) showed as percentage.

Table S5. Summary of pair-wise comparisons for the triple interaction terms (Ec x WD x SL). The * symbol denotes significant differences at $p < 0.05$. **A.** Within WD x SL, Comparisons BC, OS. **B.** Within Ec x SL, Comparisons WD. **C.** Within Ec x WD, Comparisons SL.

Table S6. Pair-wise comparisons for Shannon diversity. (Ec x WD) (Ec x SL). The * symbol denotes significant differences at $p < 0.05$.

Table S7. Distance-based linear model (DISTLM) for nematode community structure and selected environmental variables at regional scale for **A)** 1-2 and **B)** 2-5 sediment layers.

Highlights

- Nematode community (standing stocks, diversity and community structure) differed between canyon and slope.
- Blanes Canyon harbours more spatially heterogeneous and diverse nematode communities than its adjacent open slope.
- Vertical sediment profile distribution was one of the most important sources of variability affecting the community structure and structural diversity, both in canyon and slope environments.

Accepted manuscript