High spatiotemporal variability in meiofaunal assemblages in Blanes Canyon (NW Mediterranean) subject to anthropogenic and natural disturbances

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1. ABSTRACT

We investigated the natural and anthropogenic drivers controlling the spatiotemporal distribution of the meiofauna in the submarine Blanes Canyon, and its adjacent western slope (NW Mediterranean margin of the Iberian Peninsula). We analyzed the relationships between the main sedimentary environmental variables (i.e. grain size, Chl-a, Chl-a:phaeopigments, CPE, organic carbon and total nitrogen) and the density and structure of the meiofaunal assemblages along a bathymetric gradient (from 500 to 2000 m depth) in spring and autumn of 2012 and 2013.

Twenty-one and 16 major taxa were identified for respectively the canyon and slope, where the assemblages were always dominated by nematodes. The gradual decreasing meiofaunal densities with increasing depth at the slope showed little variability among stations and corresponded with a uniform pattern of food availability. The canyon was environmentally much more variable and sediments contained greater amounts of food resources (Chl-a and CPE) throughout, leading not only to increased meiofaunal densities compared to the slope, but also different assemblages in terms of composition and structure. This variability in the canyon is only partly explained by seasonal food inputs. The high densities found at 900 m and 1200 m depth coincided with significant increases in food availability compared to shallower and deeper stations in the canyon. Our results suggest that the disruption in expected bathymetric decrease in densities at 900-1200m water depth coincided with noticeable changes in the environmental variables typical for disturbance and deposition events (e.g., higher sand content and CPE), evoking the hypothesis of an anthropogenic effect at these depths in the canyon. The increased downward particle fluxes at 900 to 1200 m depth caused by bottom trawling along canyon flanks, as reported in previous studies, support our hypothesis and allude to a substantial anthropogenic factor influencing benthic assemblages at these depths. The possible relationships of the observed patterns and some major natural environmental (e.g., surface productivity or dense shelf water cascading) and anthropogenic (e.g. the lateral advection and downward transport of food-enriched sediments resuspended by the daily canyon-flank trawling activities) drivers are discussed.

Keywords

Submarine canyon; Northwestern Mediterranean; Meiobenthos; deep-sea; response to food sources; anthropogenic activities; trawling.

2. INTRODUCTION

There is increasing evidence that submarine canyons play important ecological roles in the functioning of deep-sea ecosystems (Amaro et al., 2016; Thurber et al., 2014). Submarine canyons are important routes for the transport of organic matter from surface waters and continental shelf areas to the deep sea basins (Granata et al 1999; Durrieu de Madron et al., 2000; Palanques et al., 2005; Canals et al., 2006; Pasqual et al., 2010), and they contribute significantly to regional biodiversity and secondary production along continental margins (Gili et al., 1999, 2000; Sardá et al., 2009; Ingels et al., 2009; Vetter et al., 2010; De Leo et al., 2010;). Different oceanographic and geological processes are responsible for their role as organic matter supply routes, including slope instabilities, turbidity currents events caused by river floods or episodic storms, and dense shelf water cascading (De Stigter et al., 2007; Allen and Durrieu de Madron, 2009; Puig et al., 2014). Additionally, anthropogenic activities along canyon flanks such as bottom trawling can alter seafloor community structure and biodiversity through physical habitat disturbance and the re-suspension of sediments, which ultimately accumulate at greater depths inside the canyon axis (Palanques, et al., 2006; Martín et al., 2008, 2014; Puig et al., 2012, 2015a, b; Pusceddu et al., 2014; Wilson et al., 2015).

More than 500 large submarine canyons have been identified in the Mediterranean Sea (Harris and Whiteway, 2011) with several of them located along the Catalan margin (NW Mediterranean). Among those, Blanes Canyon has been intensively studied in the past decade (Zúñiga et al, 2009; Sánchez-Vidal et al., 2012; Canals et al., 2013; Lopez-Fernandez et al., 2013). It has been shown that the canyon axis experiences strong current intensifications coupled with high particle fluxes to the deepest parts of the canyon, which are linked to major events like storms and subsequent river discharges, as well as dense water formation during winter. These characteristics cause the off-shelf sediment transport through the Blanes Canyon axis to vary substantially over time. Moreover, the downward particle fluxes within the canyon can be affected by sediment resuspension caused by daily bottom trawling activities along the canyon flanks (Company et al., 2008, Sardà et al., 2009), with increased fluxes attributed to this

process observed mainly between 900 and 1200 m depth (Lopez-Fernandez et al., 2013). In general, the particulate matter fluxes in the canyon area and at the adjacent open slope have two defined seasonal periods (Zúñiga et al., 2009; Lopez-Fernandez et al., 2013). During autumn-winter mass fluxes increase in response to river flooding coupled with major coastal storms. During the spring-summer months the biological component of the particulate fluxes becomes more important as a response to the phytoplankton bloom. However, the open slope mass flux has been reported to be three orders of magnitude lower than inside the Blanes Canyon with sinking particles containing lower amounts of lithogenics and higher levels of organic carbon (OC) (Lopez-Fernandez et al., 2013).

Most, if not all, oceanographic and geological processes that drive the ecological function and processes in submarine canyons elicit a response from the canyon fauna (Amaro et al., 2016). Elevated and depressed faunal densities have been reported in canyons, compared to slope areas (Cartes et al., 1994, 2009, 2010; Vetter and Dayton, 1998; Garcia and Thomsen, 2008; Ingels et al., 2009, 2013; De Leo et al., 2010; Tecchio et al., 2013; Romano et al., 2013). Complex canyon hydrodynamics can lead to areas characterized by strong deposition next to areas typified by intense erosion processes, which are highly variable in time. These factors have been identified as driving marked temporal and spatial variability in benthic fauna standing stocks (De Bovée, 1990; Ingels et al., 2013; Romano et al., 2013; Tecchio et al., 2013). Despite the difficulties associated with sampling these deep-sea environments, the collection of benthic biological time-series is crucial in providing the necessary information to understand ecological processes and their importance in canyon systems.

The main forcing processes affecting canyons influence benthic organisms, and the meiofauna is no exception in this context (Giere et al., 2009). Metazoan meiofauna dominate the deep-sea benthos in terms of abundance and biomass (Vincx et al., 1994; Rex et al., 2006; Giere, 2009; Pape et al., 2013a; Pape et al., 2013b). Quantitative deep-sea meiofaunal studies in the Mediterranean, have mostly focused on slope and basin environments (De Bovée et al., 1990; Soetaert et al., 1991; Tselepides and Lampadariou, 2004; Bianchelli et al., 2008; Romano et al., 2013; Rumolo et al., 2015), while studies targeting wide bathymetric gradients along canyons axes are particularly rare (De Bovée, 1990; García et al., 2007; Bianchelli et al. 2010). Meiobenthic taxa, such as Nematoda, seem particularly resilient to both natural and anthropogenic physical disturbance compared to other benthic organisms such as the macrofauna

(Pusceddu et al., 2013). However, chronic deep-sea anthropogenic activities such as bottom trawling on canyon flanks can cause a reduction in meiofauna abundance and diversity through a decrease in OM content in the trawled sediments (Pusceddu et al., 2014).

The aim of the present work is to study the distribution patterns of the metazoan meiofauna along the Blanes Canyon axis compared with those from the adjacent open slope. Samples were collected covering a bathymetric range from 500 to 2000 m depth in two periods (i.e. spring and autumn) and over two successive years (2012 and 2013) to identify variations in the main meiofaunal descriptors (i.e., density, community composition and richness of taxa). Subsequently, their relationship with the main driving sediment variables (e.g. grain size, organic content), including those related with food input (e.g. Chlorophyll-*a* content), and environmental constraints (both natural and anthropogenic) were analyzed. Based on previous observations from submarine canyon systems we expect that Blanes Canyon will be characterized by high-density meiofauna communities, but also by high temporal community variability which is only partly explained by seasonal differences in food input.

3. MATERIAL AND METHODS

3.1. Sampling

Within the frame of the DosMares research project, sediment samples were collected in and around Blanes Canyon during four cruises (DM-I: early spring 2012, DM-II: autumn 2012, DM-III: spring 2013 and DM-IV: autumn 2013) on board of the R/V García del Cid (Fig. 1). Six stations were sampled along the canyon axis (BC500, BC900, BC1200, BC1500, BC1750 and BC2000) and five on the adjacent open slope (OS500, OS900, OS1500, OS1750 and OS2000). Despite a comprehensive sampling campaign, full temporal and water-depth coverage could not be obtained owing to technical and logistical reasons (see Table 1 for details).

Samples for meiofauna and sediment variables were obtained using a 6-tube multicorer KC Denmark A/S (inner diameter 9.4 cm; length 60 cm), yielding samples with an intact sediment-water interface. Between 1 and 3 multicore deployments (replicates) were conducted at each sampling station depending on the cruise (Table 1). From each multicore deployment, one core was used for meiofaunal and three for sediment analyses, which were all carefully sub-sampled on board by means of a small

PVC tube (36 mm of diameter, 5 cm sediment depth) taken from the center of the core to maintain a consistent sample surface area for all replicates. Meiofauna samples were fixed in buffered 4% formaldehyde, while those for sediment variables were frozen and stored at -20°C until analysis in the laboratory.

3.2. Sediment variables

3.2.1. Grain size

Grain sizes were analyzed using a Master Sizer 2000 laser analyzer. Each sample was first defrosted and homogenized. Then, aliquots (~1 g) were treated with a 6% hydrogen peroxide solution for 48 h to remove organic matter and subsequently washed with distilled water to eliminate salts. Before each measurement 10 drops of distilled water with sodium hexametaphosphate (0.05 %) was added to disperse the sediment. Then samples were homogenized prior to running the analysis. Sediments were grouped into grain size fractions as follows: clay (<4 µm), silt (4–63 µm) and sand (63 µm–2 mm).

3.2.2. Geochemical analysis

Aliquots of 0.5 to 5 g of sediment from each sample were freeze-dried to analyze total carbon organic carbon (OC) and total nitrogen (TN) using an elemental analyzer Flash 1112 EA interfaced to a Delta C Finnigan MAT isotope ratio mass spectrometer at the “Centres Científics i Tecnològics de la Universitat de Barcelona”. Samples for OC were first de-carbonated using repeated additions of 25% HCl with 60°C drying steps in between until no effervescence was observed (Nieuwenhuize et al., 1994).

3.2.3. Pigment content

Sediment aliquots were freeze-dried and homogenized to extract pigments. About 1 g dry weight of sediment was mixed in 4 ml 90% acetone and the obtained extract was centrifuged (4 min at 3000 rpm, 4°C) and filtered through a Whatman Anodisc 25 (0.1 µm). Pigments were analyzed by Ultra Performance Liquid Chromatography. Chlorophyll-*a* (Chl-*a*) and chlorophyll degradation products were identified 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 (protocol modified of Buchaca and Catalan, 2008). Chloroplastic Pigments Equivalents (CPE: sum of Chl-*a* and phaeopigments, its degradation products)

was used to estimate OM produced by surface primary productivity. The ratio Chl-*a*: phaeopigments (Chl-*a*:phaeo) was used as a proxy to estimate the freshness of photosynthetically derived OM (Thiel, 1978).

3.3. *Meiofauna*

The fixed samples were rinsed through a 1000 µm mesh then sieved through a 32 µm mesh. The retained 32 µm fraction was washed and centrifuged three times using the colloidal silica polymer LUDOX HS40 (specific gravity 1.18) to achieve density gradient separation of the meiofauna (Heip et al. 1985). The supernatant of each washing cycle was again collected on a 32-µm sieve. After extraction, samples were kept in 4 % formaldehyde and stained with Rose Bengal. All metazoan meiobenthic organisms were classified at higher taxon level following Higgins and Thiel (1988) and counted under stereomicroscope (50 x magnification).

3.4. *Data analyses*

Both univariate and multivariate non-parametric permutational (PERMANOVA) analyses were performed to test differences in meiofauna density and assemblage composition, as well as sediment variables between sampled periods, locations and depths. Differences between locations (i.e. canyon vs slope) and water depths were tested with two different 2-way crossed designs, using Location (Lo: fixed) and Water Depth (WD: fixed) as factors, both for uni- and multivariate analysis (PERMANOVA Anderson, 2005; Anderson et al., 2008). In the first 2-way PERMANOVA analysis to assess overall differences between locations we pooled the data from the four sampling times and considered all the depths (6 levels: 500, 900, 1200, 1500, 1750, 2000 m). Subsequently, we considered data from each campaign separately and performed a 2-way PERMANOVA analysis for each campaign including only the sampled depths that were in common between canyon and slope (e.g. spring 2012: 1750 and 2000 m; autumn 2012: 1500, 1750, 2000 m; spring 2013: 500, 900, 1500, 1750, autumn 2013: 1750 m).

Considering that the sampling effort of this study was mainly focused on the canyon and for the slope a less complete data matrix was available, we also analyzed the data from each location separately by means of two-way crossed design using Time

(Tm: fixed) and WD (fixed) as factors. For the canyon data the factor WD had 6 levels (500-2000 m, see Table 1) and for the slope it had 3 levels (1500-2000 m).

Additional non-metric multidimensional scaling (MDS) visualization was used to show the spatial variations of meiofauna community structure based on Bray Curtis similarity values.

Differences in sediment variables over the terms Tm and WD were assessed by univariate PERMANOVA, except for the grain size content, where clay, silt and sand percentages were considered as multivariate variables. Additionally, Principal Component Analyses (PCA) based on sediment variables were performed to assess differences in spatial distribution between the canyon and slope samples and the temporal and spatial patterns in the canyon. Prior to calculating the Euclidean distance resemblance matrix, the full set of 11 available sediment variables was tested for collinearity (Draftsman plot and Spearman correlation) and variables with correlations (R^2) > 0.95 (redundant) were omitted from the analyses (i.e. Chl-*a*:OC and phaeopigments). The data were then checked for uniform distribution (Chl-*a*, CPE and Chl-*a*:phaeo were log (0.01+X) transformed) followed by normalization (subtracting the mean and dividing by the standard deviation, for each variable) to bring them to a common unit before analysis.

The univariate meiofaunal density data were square root transformed and Euclidean distance was used to calculate the resemblance matrix. Multivariate analyses of the meiofauna assemblage composition were done on a Bray-Curtis resemblance matrix based on fourth-root transformed data.

Additionally, regression analyses were performed to reveal the form, distribution and significance (null hypothesis rejected when the significance level was > 5%) of the functional relationships between each dependent variable (sediment variables and meiofauna density, using water depth as independent variable) and assess the differences between canyon and slope samples.

Spearman correlations were used to assess the strength of the relationship between the selected sediment variables and meiofauna density (based on the complete data set, including both canyon and slope samples). Finally, the relationships between meiofauna composition and sediment variables were investigated using the Distance based Linear Model routine (DISTLM) in PERMANOVA + (Anderson et al., 2008). The DISTLM assemblage was built using a step-wise selection procedure and adjusted R^2 was used as selection criterion.

All described analyses were performed using PRIMER v6 with PERMANOVA + add-on software (Clarke and Gorley, 2006; Anderson et al., 2008) and XLSTAT (Addinsoft) software.

3.5. Ancillary data

To assess the impact of bottom trawling fisheries in the Blanes canyon, positioning of fishing vessels was obtained from the Fishing Monitoring Centre of the Spanish General Secretariat of Maritime Fishing (SEGEMAR) as Vessel Monitoring System (VMS) data, a protocol established by the Common Fisheries Policy of the European Union (2011). Each vessel equipped with VMS provide its registered harbour, heading, speed and Global Positioning System coordinates with an error margin of 100 m, and transmits this information by Inmarsat-C to the Fishing Monitoring Centre in less than 10 min at 2-hour time intervals (Gerritsen et al., 2013). VMS positioning from bottom trawlers operating in the study area during 2006-2013 was subsequently converted to fishing effort (hours/km²), computed in grid cells of 0.5' latitude x 0.5' longitude as shown in Figure 1, following the method and the software tools described in Hitzen et al. (2012).

To assess the relative role of the various oceanographic processes contributing to the temporal variability of downward particle fluxes in the study area during the study period, surface primary production was obtained from satellite data of chlorophyll-a concentration at www.nasa.gov. Daily river discharge series measured at the nearest gauging station to Tordera River mouth was obtained from *Agència Catalana de l'Aigua* (ACA) and significant wave height was provided by *Puertos del Estado* (www.puertos.es).

4. RESULTS

4.1. Sediment characteristics

Canyon and slope sediments were predominantly muddy (2-63 µm) with high silt content (62% to 77%, respectively) over the whole bathymetric gradient (Table 2). Sediments were in general characterized by a high sand content in the canyon, except at BC2000 (pair-wise comparison Lo x WD, $p < 0.01$, Fig. 2, Table 2). Along the slope, sediments became progressively finer with increasing water depth ($R^2 = 0.79$ and 0.39

respectively for clay and sand, $p < 0.05$, Fig. 2; Table 2; PERMANOVA, $p < 0.05$, Table 4) whilst in the canyon there was no consistent bathymetric trend (Fig. 2). In general (slope and canyon samples pooled), grain size decreased until BC900, peaked at BC1200 and, then decreased again with depth (Table 2).

Sedimentary Chl-*a* and CPE content were higher in the canyon than at the slope, except for Chl-*a* at BC500 in spring 2013 (Fig. 2, Table, Table 3). Slope samples exhibited decreasing Chl-*a* and CPE with increasing water depth ($R^2=0.58$ and 0.65 respectively, $p < 0.05$, Table 4; Fig. 2). Sedimentary Chl-*a* content was different between sampling periods (Tm x WD interaction, pairwise comparisons, $p < 0.01$, Table 4), particularly at OS1750 between spring and autumn 2012 ($p < 0.05$, Table 2). CPE did not differ between sampling periods (Table 4). Along the canyon axis, Chl-*a* decreased with increasing water depth (Fig. 2, $R^2=0.26$) but the high variability at BC1200 (autumn 2012 and spring 2013) and BC1500 (spring 2012) obscured this general pattern (Table 2). Chl-*a* differed significantly between sampling periods and water depths (PERMANOVA, $p < 0.01$, Table 4). As for Chl-*a*, CPE decreased with increasing water depth along the canyon axis, except for the peaks observed at BC1200 (autumn 2012 and spring 2013) and BC1500 (spring 2012) (Table 2, PERMANOVA, $p < 0.01$, Table 4).

The “freshness” (Chl-*a*: phaeo ratio) of OM did not differ significantly between the canyon and slope (PERMANOVA, $p > 0.05$, Table 3). At the slope, the freshness of OM did not show a clear decrease with increasing water depth (Fig. 2F) and differences between sampling periods were not significant (PERMANOVA, $p > 0.05$, Table 4). In the canyon, the freshness differed significantly between sampling periods and water depths, but a clear decrease with increasing depth occurred only in spring 2012 (Table 2; PERMANOVA, $p < 0.01$, Table 4). There were also significant differences between spring and autumn 2012 for BC500, BC900 and BC1500 and between autumn 2012 and 2013 at BC1750 and BC2000 (Tm x WD interaction, pairwise comparisons, $p < 0.01$, Table 4).

Sedimentary OC and TN differed significantly between the canyon and slope (PERMANOVA, $p < 0.05$, Table 3), with the main differences occurring at 500 m depth and the 1500-2000 m stations for OC and at 500 m and 1750 m depth for TN (pair-wise comparison, $p < 0.05$, see Fig. 2). At the slope, OC and TN differed significantly between sampling periods (Table 4), particularly between autumn 2012 and spring 2013 ($p < 0.05$, see Table 2). Also TN and OC differed significantly between water depths

(Table 4) but only TN decreased with increasing depth ($R^2 = 0.27$; Fig. 2). Along the canyon axis, OC and TN differed significantly between sampling periods and water depths (PERMANOVA, $p < 0.01$, Table 4), with a pronounced decrease with increasing water depth in spring 2013 (Table 2). OC and TN were significantly higher in spring 2013 and autumn 2012 (Table 2). TN also differed significantly between 2012 and 2013, particularly at BC1500 and BC1750 (Tm x WD interaction pairwise comparisons, $p < 0.01$, Table 2, 4).

Sedimentary C:N ratios did not differ significantly between canyon and slope (PERMANOVA, $p > 0.05$, Table 2, 3, Fig. 2). Along the canyon axis, C:N differed significantly between sampling periods (PERMANOVA, $p < 0.01$, Table 4), particularly between the years 2012 and 2013 (Table 2).

Canyon and slope samples separated in the PCA (Fig. 3A). Furthermore, slope samples were less variable in terms of environmental variables, except for OS500. The first two PC axes explained a 69.6% of the variation. The main contributors were Chl-*a* (-0.443), CPE (-0.388), Chl-*a*:phaeo (-0.374) and clay (0.367) for the axis PC1 and silt (-0.562), TN (-0.468), sand (0.450) and OC (-0.396) for the axis PC2 (numbers in parenthesis represent eigenvector values).

When the Canyon axis samples were analyzed separately, the first two axes of the PCA explained 65.4% of the variation (41.5% and 23.9% for PC1 and PC2, respectively; Fig 3B). The main contributors were sand (0.427), Silt (-0.392), Chl-*a* (0.379) and TN (-0.357) for PC1 and OC (0.596), Chl-*a* (0.376), sand (-0.388) and CPE (0.310) for PC2 (numbers in parenthesis represent eigenvectors). Sampling periods were clearly distinguishable in the PCA plot (Fig. 3B), particularly autumn 2012 and spring 2013, in accordance with the PERMANOVA analyses (Table 4). In particular spring 2013 samples were characterized by having greater pigments concentrations (Table 2) as suggested by the PCA. No consistent bathymetric differences could be observed in the PCA plot.

4.2. *Meiofauna density*

In general, total meiofauna densities were significantly higher inside the canyon than on the slope (Table 5; $p < 0.01$, Table 7, Fig. 4), particularly during spring 2012 and autumn 2012 (Table 5) at 1750 and 2000 m depth (pair-wise comparison, $p < 0.05$, data not shown, see Fig. 4).

At the slope, there were significant differences between depths (PERMANOVA, $p < 0.01$, Table 6), and a density decrease with increasing water depth ($R^2=0.84$, $p < 0.005$, Fig. 4) was observed. There was little between-replicate variability in density at each station along the slope, in contrast to the high variability observed in the canyon (Table 6). The minimum slope density recorded was 209 ± 44 ind. 10 cm^{-2} at OS2000 in autumn 2012 and the maximum was 1027 ± 72 ind. 10 cm^{-2} at 500 m depth in spring 2013 (Table 7, Fig. 5B).

Along the canyon axis, the densities did not show a clear bathymetric pattern, and they were characterized by high variability over the different sampling periods within and between depths (Fig. 4, 5 A). The minimum density recorded was 378 ± 69 ind. 10 cm^{-2} at BC900 in spring 2012 and the maximum was 1763 ± 245 ind. 10 cm^{-2} at BC500 in autumn 2012 (Table 7, Fig. 5 A). The highest variability was observed at BC900 and BC1200 (Fig. 5 A). There was a significant influence of water depth at each sampling period, except in spring 2013 (PERMANOVA, $p < 0.05$, Table 6). In fact, the observed differences were caused by the densities at BC500, which were significantly higher than those at the deepest stations (BC1500, except in spring 2012, BC1750 and BC2000) (Table S1, pair-wise comparison within Tm x WD; Fig 5 A).

Regarding the temporal variability, at the slope stations, meiofauna densities did not exhibit significant differences at any sampling depth (PERMANOVA, $p > 0.05$, Table 6; Fig. 5B). In contrast, densities inside the canyon differed significantly between sampling periods (Fig. 5A, Table 6), but no clear seasonal patterns were observed. In 2012, densities were higher in autumn than in spring, (except at BC1500) while the trend was the opposite in 2013 (except at BC900) (Fig. 5A). Significant intra-annual differences occurred in 2012 at BC1750, with higher densities in autumn compared to spring. Significant inter-annual variability mainly occurred between autumn periods at BC500 and BC1750, where densities were higher in 2012 than 2013, and at BC900, where the opposite was observed (Table S1, pair-wise comparisons). There were no temporal differences detected at stations BC1200, BC1500 and BC2000 (Table S1, pair-wise comparison; Fig 5A).

4.3. Meiofauna community composition

The meiofauna composition in the canyon and the slope was comparable to what is usually observed in the deep sea, with nematodes being dominant (79.2-97.6 %), followed by copepods (0.68-5.14%, mainly harpacticoids), nauplii larvae (0.65-4.9%) and polychaetes (0.51-3.12%) (Table 7). Other taxa (such as tardigrades and kinorhynchs) were regularly found but in low densities (less than 2%). A total of 21 major taxa were identified in the canyon, while only 16 taxa were collected at the open slope. Aplacophora, Amphipoda, Nemertea, Cumacea and Sipunculida were only present in the canyon samples (Table 7). Relative nematode abundance was slightly higher in all canyon samples compared to slope samples, except at the 900 m and 1750 m stations in spring 2013 and autumn 2013, respectively.

Considering all samples, meiofauna composition differed significantly between the canyon and the slope (Table 6, $p < 0.05$), except at the 900 m stations (Lo x WD, pairwise comparison, $p < 0.05$). For each sampling period, differences between locations were also evident, especially in spring and autumn 2012 (Table 6). At the slope, meiofauna composition varied between water depths (Table 6). The maximum of 13 taxa was found at OS1500 in autumn 2012 and the minimum number of 5 taxa was found at OS1750 in autumn 2013. Despite of the reduced number of slope samples, the number of taxa decreased with increasing water depth in autumn 2012 and spring 2013 (Table 7). In the canyon, the meiofauna community structure also differed among water depths (Table 6), except for the BC500-BC1200, BC900-BC1200, BC1500-BC1750 and BC1750-BC2000 pairwise comparisons (Table S2). However, the MDS ordination showed that there were no clear relationships between meiofauna community structure and bathymetry, except in autumn 2013 (Fig. 6). The maximum number of taxa (14) was found at BC900 in autumn 2012 and spring 2013 and the minimum (6) at BC2000 in autumn 2013 (Table S1). The reduced dominance of nematodes at BC900 is countered by a relative increase of copepod and nauplii densities (Table 7).

The structure of the slope assemblages did not differ between sampling periods (Table 6), despite there was an increase in number of taxa from spring to autumn 2012 (Table 7). In the canyon, there were clearly significant time differences (Table 6), with the most significant variations occurring both in 2012 (intra-annual) and between the two autumn periods (inter-annual, 2012-2013) (Table 6, Table S2, pair-wise

comparison). These differences were mainly owing to the increase in number of taxa from spring to autumn 2012 at all sampling stations (except at BC2000) (Table 7).

4.4. Relationship between meiofauna and environmental variables

Meiofaunal densities showed significant, positive correlations with the variables representing food inputs (i.e. CPE, Chl-*a*, and OC) both in the canyon and at the slope, but correlations were higher for the slope than in the canyon (Spearman correlation, Table 8). At the slope, negative correlations between meiofauna densities and TN and Clay were found, while a positive correlation with Sand occurred along the canyon axis.

Environmental variables all together explained 43% and 18% of the observed variation in meiofauna community structure in the slope and in the canyon, respectively (Table S3, S4, DISTLM), with the main contributor being Chl-*a*, (24% and 9%, respectively). Other variables significantly contributing were Clay, Silt, OC, C:N and CPE at the slope, and Clay, Sand, TN, CPE and Chl-*a*: phaeo in the canyon.

5. DISCUSSION

The Mediterranean is considered to be an oligotrophic sea, a characteristic which is often used to explain its typically low deep-sea meiofauna densities compared to similar depths in other oceans (Soltwedel, 2010; Bianchelli et al., 2010; Pape et al., 2013b). Mediterranean meiofauna densities range between 4 and 1497 ind. 10 cm⁻², with a clear decrease from west to east (Soltwedel, 2000; Bianchelli et al., 2010) which has been linked to the W-E gradient of increasing oligotrophy (Danovaro et al., 1999; Gambi and Danovaro, 2006; Danovaro et al., 2008). Similar low density ranges have only been reported in the Southern Pacific Ocean, Southern Atlantic Ocean and Arctic Ocean (see Bianchelli et al., 2010 for a review).

The maximum densities in the Blanes Canyon axis were higher than those observed in other Mediterranean canyons (Table 9). Minimum densities were equivalent to those of Cape of Creus Canyon, but about 5 to 8 times higher than in the remaining canyons, even when compared to previous data from Blanes Canyon (Romano et al., 2013) (Table 9). The study by Romano et al. (2013) included only a few canyon stations and a limited depth range, with samples from the eastern and western canyons flanks (900 m depth), from the canyon axis (1600 m depth), and from the eastern open slope (1600 m depth). In the present study, a much more comprehensive range of samples were obtained, including different seasons and years, and covering the canyon axis over

a wide bathymetric gradient, whilst also including stations from the adjacent western open slope, allowing a broader temporal and spatial assessment of the meiofauna in the Blanes Canyon system.

5.1. Spatial and temporal distribution of the meiofauna in the Blanes Canyon system

Contrary to the traditional perception that the whole of the deep-sea is a stable environment (e.g. Sanders, 1968), marked temporal variations of meiofaunal organisms have been observed in submarine canyons (De Boveé et al., 1990; Romano et al., 2013; Ramahlo et al., 2014; Rumolo et al., 2015) and slope systems (e.g., Hoste et al., 2007; Romano et al., 2013; Guidi-Guilvard et al., 2014). Such variations generally suggest contrasting scenarios between spring-summer and autumn-winter, with the former causing higher densities. Traditionally, this variability has often been associated to the seasonal trends in phytodetrital food availability, but it could also be associated with specific particulate matter transport mechanisms, particularly in submarine canyon environments (Pusceddu et al., 2013; Ramalho et al., 2014).

Previous studies in the Blanes Canyon have revealed high variability in particle fluxes, driven by a variety of causes: storms, dense water formation (by dense shelf water cascading and open sea convection), dust inputs, phytoplankton blooms, and bottom trawling (Lopez-Fernandez et al., 2013). The concatenation of such events influences sedimentary dynamics and ultimately meiofauna communities by altering sediment characteristics and food availability. Physical disturbances occurring in submarine canyons sediments are known to drive the composition of meiobenthic communities (Aller, 1997; Garcia et al., 2007; Ingels et al., 2009; Levin et al., 2012; Romano et al., 2013).

During the study period, temporal differences in meiofauna density and community composition have been observed mainly in the Blanes Canyon axis, with slope sediments showing much lower meiofaunal variability. Despite the potential bias caused by the reduced number of slope samples in our study, our results are consistent with observations by Romano et al. (2013). In their study, meiofaunal densities at 800 and 1600 m depth on the eastern slope reflected a less dynamic environment compared to canyon stations between spring and autumn at those depths. Additionally, in our study, meiofauna densities and composition also differed between sampling years inside the canyon (Table 6). These differences seemed to be related to the observed increase of

primary productivity in spring 2013 (Fig. 7A), which occurred on the slope, but was particularly reflected in the canyon sediments, where the sedimentary Chl-*a* content in 2013 was much higher than in 2012. Significant positive correlations between meiofaunal densities and Chl-*a* support this observation (Table 8). The C:N ratios showed a similar pattern, with increased values in 2013 compared to 2012 (Table 2), which is likely related to greater terrestrial runoff from the rivers in 2013 (Fig. 7B) combined with the resuspension caused by the high waves registered during spring 2013 (Fig. 7C). However, the responses of the meiofaunal assemblages were not homogeneous along the studied bathymetric range; likely an indication of other factors that can alter food availability in the canyon-slope sediments and ultimately meiofauna densities and community composition.

For instance, the food signals detected in the sediments (in terms of CPE and Chl-*a*, see Table 2), together with the sand content (Table 2), were highly heterogeneous in the upper canyon region and tended to be higher at BC1200. In this area, canyon flank tributaries (see Lastras et al., 2011) connect the canyon axis with some of the most frequently trawled grounds along the canyon rims (Fig. 1). As previously mentioned, Blanes Canyon and its adjacent open slopes comprise fishing grounds that have been subjected to persistent bottom trawling down to 800 m depth (Company et al., 2008; Sardà et al., 2009; Ramirez-Llodra et al., 2010). The main effort concentrates along the northern open slope from late winter to early summer and over the eastern canyon rim from late summer to mid-winter (Company et al., 2008; Sardà et al., 2009; Ramirez-Llodra et al., 2010). Data from moored sediment trap data in Blanes Canyon, recorded increase in particle fluxes (mostly lithogenic) recorded at 900 and 1200 m depth in the canyon axis (mainly in summer) that was attributed to the formation of sediment resuspension clouds by bottom trawling activities (Lopez-Fernandez et al., 2013). Our results show major differences in sediment composition (coarser) and meiofaunal densities (higher) at BC900 and, particularly, at BC1200 (Table 2; Fig 5A), which interrupts the expected distribution patterns under normal slope conditions. Altogether, these observations indicate the possible presence of an anthropogenic depocenter (i.e. a preferential area of sediment accumulation by trawling) at these depths in the Blanes Canyon axis in a similar way to the ones previously reported in the nearby La Fonera Canyon, Arenys and Besòs submarine canyons (Martín et al., 2008; Puig et al., 2015a,b; Fig. 1). Therefore, we suggest that the processes involved in the formation of sedimentary deposits caused by bottom trawling activities may be an important driver

for meiofaunal assemblages in canyon axes environments. Contrary to the negative direct effects of trawling over fishing grounds in canyon flanks (Pusceddu et al., 2014), the increased levels of OM around sedimentary depocenters are likely beneficial to the organisms living in the canyon axis, including the meiofauna. For instance, in La Fonera Canyon the burrowing echinoid *Brissopsis lyrifera* (Forbes, 1841) colonized and proliferated in the lower canyon axis (Mecho et al., 2014) following the formation of an anthropogenic deposit of fine-grained material (Puig et al. 2015a).

The relatively low densities detected at BC500, BC900 and BC1200 in the canyon axis in spring 2012 (Fig. 5A), however, seem to correspond to effects of a major (i.e. deep) dense shelf water cascading event at the NW Mediterranean margin in winter 2012 (see Durrieu de Madron et al., 2013). Such oceanographic process might have generated strong down-slope currents causing mechanical removing or burying of resident organisms. Consequently, this may lead to massive dispersal, growth inhibition, or even mortality of the meiofaunal component as has been previously reported in the Cap de Creus Canyon during the major deep cascading event in 2005 (Pusceddu et al., 2013). After the cascading event, the densities and number of taxa in autumn 2012 were much higher than in the previous spring, and also than those in autumn 2013, as dense shelf water cascading was less intense in 2013 and had almost no impact in Blanes Canyon (Anna Sanchez-Vidal, personal communication).

The meiofaunal communities in the deeper areas of the canyon, particularly at BC1500 and BC2000 seemed to be more stable over time (Fig. 5 A) where the effects of the anthropogenic (i.e. trawling) and natural (i.e. cascading) disturbances are likely to be much reduced. Conversely, we could not find a straightforward explanation for the relatively high variability observed at BC1750, highlighting the complexity of the biological, chemical and physical interactions driving the spatial and temporal variability within the meiofaunal assemblages in submarine canyon environments (Ingels et al., 2013; Ramalho et al., 2014).

5.2. Slope v.s Canyon

Decreasing meiobenthic densities with increasing water depth has been postulated as a basic principle in deep-sea ecology (e.g., Thiel, 1983; Tietjen, 1992), and has been linked to the bathymetric decrease in organic matter supply (POC flux) and the increasing distance from land (e.g. Soetaert et al., 1991; Danovaro et al., 1995;

Gooday et al., 1996; Fabiano and Danovaro, 1999; Soltwedel, 2000; García et al., 2007, García and Thomsen, 2008). However, as previously mentioned, such a depth-density relation may be modified by the presence of submarine canyons owing to their topographical and hydrographic heterogeneity. Canyons induce modifications in the hydrodynamic and biogeochemical processes of channeling organic matter towards the deep basin. Food availability and meiofauna density in canyons are generally higher compared to canyon interfluvial areas at similar depths (De Bovée, 1990; Soetaert et al., 1991; García and Thomsen, 2008; Koho et al., 2008; Ingels et al., 2009; Gambi and Danovaro, 2016; Amaro et al., 2016; Ingels et al., 2011) and Blanes Canyon is no exception in this context.

Mediterranean canyon and slope habitats seem to lack consistent bathymetric patterns, especially in the western basin (Bianchelli et al., 2010; Pusceddu et al., 2010). In Blanes Canyon, significant decreases in meiofaunal densities with depth were reported during autumn, while the spring trends were markedly more fluctuant (Romano et al., 2013). This bathymetric pattern, however, was not uniform as it was not clearly observed at the eastern open slope adjacent to the canyon.

Our results revealed a bathymetric decrease of meiofaunal density at the slope, but not in the canyon (Fig. 4). For instance, in the canyon axis, meiofauna was less abundant at BC900 than at the deeper stations (BC1500, BC1750 and BC2000) in spring 2012, but it was higher in autumn 2013 (Fig. 5A), likely as a result of the combined canyon heterogeneity and the oceanographic and anthropogenic drivers favoring a higher variability along the axis (see section 5.1). It was clear that densities inside the canyon were higher than those at the western slope, and this was particularly evident for the deepest stations (BC1500, BC1750 and BC2000). However, the deep canyon stations exhibited high temporal meiofauna density variability, almost double the variability observed for the slope (i.e. 31% vs. 16.6% on average, respectively). These results provide further evidence that a heterogeneous canyon environment can lead to meiofaunal assemblages with highly variable distributional patterns in space and time, whilst slope environments tend to be more stable as evidenced by the uniformity of meiofauna density and community structure at the western (present study) and eastern slope (Romano et al., 2013).

We observed a decrease in sedimentary food sources (e.g. phytopigments) with increasing depth along the slope; a pattern which agrees with previous findings (Soetaert et al., 1991; Koho et al., 2008; Ingels et al., 2009; among others) and is likely

related to the dynamics of the particle fluxes in Blanes Canyon (Zúñiga et al., 2009; Lopez-Fernandez et al., 2013). Moreover, sedimentary phytopigment values were much lower at the slope than in the canyon, which supports the view of canyons playing important roles in catching and channeling organic inputs (Fig. 2). A similar depth-related pattern was observed for meiofauna density and composition (Table 7), which show low temporal variation and positive correlations with food sources (Chl-*a*, CPE, Chl-*a*:phaeo), suggesting a causal relationship.

In the canyon, the high variability within and between depths along the axis, both in terms of meiofauna density and sediment variables (Table 2; Fig. 5 A) prevent us from finding a clear relationship. This is likely an indication that meiofaunal distribution can only be partly explained by the variability in food availability under canyon settings. The observed variability can, in turn, be traced back to hydrodynamic forcing, the topographic heterogeneity and/or physical anthropogenic impacts driving the canyon system (Levin et al., 2012; Gambi et al., 2010. Pusceddu et al., 2014).

Sediment grain size is known to be a key actor in driving meiofauna distributions (Giere et al., 2009). In the slope, sample sediments tend to be coarser in the shallow parts compared to the deeper parts, and meiofauna showed a strong negative correlation with clay content (Fig. 2). An increase in the fine sediment fractions leads to more compacted sediments, causing a reduction in the interstitial space available for meiofaunal organisms. In the canyon, sand content was positively related with meiofauna density (Table 8). All canyon axis samples (except the shallowest one at BC500) contained coarser sediments than those at the slope presumably caused by the local sedimentological and hydrological conditions and was reflected in the higher meiofauna densities. Grain size trends illustrate the physical dynamism and variable conditions along the axis in the Blanes Canyon, except at BC2000, where the conditions appear to be similar to those in the slope.

Slope and canyon systems clearly differ in meiofaunal composition (Table 5) with more rare taxa (i.e., other than nematodes, copepods, nauplii and polychaetes), and generally in greater numbers in the canyon than at the slope. This stands in contrast to the study by Gambi et al. (2010) but supports several other studies that claim submarine canyons to be *hotspots* of benthic biodiversity and biomass in the deep-sea at least in terms of rare meiofaunal taxa (e.g. Danovaro et al., 1999; Gili et al. 2000; De Leo et al., 2010; Ramírez- Llodra., et al., 2010; Vetter et al., 2010).

Conclusions

The sedimentary environments within and nearby the Blanes submarine canyon are subjected to numerous and heterogeneous processes occurring with distinct frequencies and intensities over time, and, leading to cyclic episodes of deposition, resuspension and transport. In addition to this natural variability, the influence of anthropogenic activities, particularly intensive bottom trawling fisheries, reveals to be a key factor affecting both geological and biological processes.

Our results confirm that Blanes Canyon compared to its adjacent open slope, exhibits (1) larger sediment properties variability, (2) higher meiofaunal densities, and (3) more diverse meiofauna communities.

Densities show a clear bathymetric gradient at the western open slope, a gradient that appears disrupted along the canyon axis. The lateral advection and accumulation of food-enriched shallow-water sediments resulting from bottom trawling activities along the canyon rims seems to be the cause of an increase in meiofauna density and diversity at BC900 and, particularly, at BC1200.

The temporal variability observed in the canyon meiofauna is only partly explained by the seasonal patterns of food input. Major oceanographic processes such as recurrent dense shelf water cascading events seem to play a key role.

Nematodes dominate in all studied environments, and are therefore major contributors to the observed meiofaunal patterns. It is expected that further studies based on high-resolution taxonomic identification of this group, as well as the usage of other descriptors such as biomass or stage/sex-ratio distributions, will contribute to clarify the observed meiofaunal patterns and the extent of their bathymetric and seasonal responses to the environmental changes driving the functioning of Blanes Canyon.

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Table 1. Sampling stations, geographical position, depth range (minimum – maximum) and sampling intensity. BC: Blanes canyon, OS: open slope.

Station	Latitude	Longitude	Water Depth (m)	Sampling intensity			
				Spring 2012	Autumn 2012	Spring 2013	Autumn 2013
BC500	41°38'66''N	02°52'75''E	462-484	2	2	1	3
BC900	41°34'28''N	02°50'95''E	835-903	2	3	3	1
BC1200	41°30'93''N	02°51'07''E	1194-1258	2	2	3	–
BC1500	41°27'37''N	02°52'93''E	1457-1520	2	3	3	3
BC1750	41°21'51''N	02°52'07''E	1726-1785	2	3	3	3
BC2000	41°14'90''N	02°52'97''E	1943-1980	2	3	–	3
OS500	41°19'10''N	02°46'75''E	493-509	–	–	3	–
OS900	41°16'29''N	02°48'96''E	887	–	–	1	1
OS1500	41°08'28''N	02°53'75''E	1451-1480	–	3	3	–
OS1750	41°06'79''N	02°57'02''E	1731-1751	2	3	3	1
OS2000	41°02'65''N	03°01'22''E	1975-1998	2	3	–	–

Table 2. Mean $\pm$ standard deviation values of environmental variables for each year at each station, BC: Blanes canyon; OS: Open slope, Spr: Spring; Aut: Autumn; Clay, Silt, Sand: volume percent clay, silt and sand content; TN: total nitrogen concentration; C:N: molar carbon/nitrogen ratio; OC: organic carbon concentration; Chl-a: chlorophyll a; CPE: chloroplastic pigment equivalents; Chl-a:phaeo: chlorophyll a divided by its degradation products (phaeopigments) indicating “freshness” of the phytodetrital OM.

Station	Sampling period	Clay		Silt		Sand		CPE		Chl-a	
		(%)	SD	(%)	SD	(%)	SD	($\mu\text{g/g}$)	SD	($\mu\text{g/g}$)	SD
BC500	Spr-12	19.75	1.5	66.14	8.1	14.11	9.53	2.71	0.85	0.17	0.045
	Aut-12	19.28	0.5	73.16	0.8	7.555	0.29	4.07	1.28	0.13	0.018
	Spr-13	20.29	0	65.51	0	14.2	0	3.98	0	0.46	0
	Aut-13	21.22	0.4	71.01	0.6	7.768	0.92	2.9	0.06	0.26	0.029
BC900	Spr-12	21.72	0.7	70.86	3.2	7.422	3.97	2.23	1.29	0.07	0.014
	Aut-12	18.23	1.9	73.11	0.9	8.658	1.75	3.45	1.11	0.07	0.034
	Spr-13	17.8	0.8	71.12	1.5	11.08	2.25	3.19	1.49	0.15	0.113
	Aut-13	18.58	1.9	72.99	2.5	8.427	3.44	3.98	2.73	0.18	0.072
BC1200	Spr-12	16.02	3.9	62.37	5.6	21.6	9.55	1.3	1.43	0.07	0.055
	Aut-12	18.7	1.6	68.89	3.3	12.51	4.87	4.7	0.11	0.1	0.007
	Spr-13	16.9	1	67.2	2.4	15.9	3.45	5.71	1.5	0.29	0.162
	Aut-13	–	–	–	–	–	–	–	–	–	–
BC1500	Spr-12	17.68	1.5	71.8	8.2	10.52	9.71	3.96	1.39	0.18	0.099
	Aut-12	18.48	0.9	77.07	0.5	4.448	1.39	2.02	0.83	0.03	0.009
	Spr-13	16.18	2	65.09	3.6	18.73	5.53	1.94	0.47	0.12	0.082
	Aut-13	16.54	1.4	70.62	3.9	12.85	5.22	2.23	0.87	0.09	0.02
BC1750	Spr-12	20.43	1	74.99	0.3	4.585	0.73	2.16	0.46	0.07	0.008
	Aut-12	19.32	0.3	75.85	1.2	4.831	1.08	1.27	0.4	0.04	0.015
	Spr-13	17.22	1.2	71.55	2.8	11.23	2.53	2.62	0.77	0.12	0.021
	Aut-13	19.49	0.5	75.47	0.8	5.042	0.94	3.35	1.57	0.1	0.045
BC2000	Spr-12	18.86	0.2	74.85	0.7	6.282	0.53	0.78	0.12	0.02	0.011
	Aut-12	21.33	0.7	73.47	0.7	5.202	0.82	0.87	0.31	0.02	0.008
	Spr-13	–	–	–	–	–	–	–	–	–	–
	Aut-13	19.18	1.5	72.93	1.3	7.882	2.82	1.2	0.3	0.07	0.023
OS500	Spr-13	14.35	0	62.88	4.9	22.76	2.13	2.49	0	0.23	0.17
OS900	Spr-13	17.57	0	80.3	0	2.13	0	2.65	0	0.07	0
OS1500	Aut-12	23.57	0.3	71.96	0.3	4.46	0.16	0.38	0.18	0.01	0.005
	Spr-12	21.74	0.8	73.47	0.5	4.79	0.54	1.36	0.55	0.03	0.016
OS1750	Spr-12	23.82	1.4	69.78	6	6.5	0.98	0.53	0.3	0.02	0.003
	Aut-12	24.38	0.9	70.1	0.8	5.52	0.2	0.29	0.27	0	0
	Spr-13	24.66	0	71.81	0	3.53	0	0.35	0	0.01	0
	Aut-13	24.24	0	71.91	0	3.85	0	0.31	0	0.02	0
OS2000	Spr-12	21.65	6.9	65.95	2.3	12.4	8.62	0.28	0.3	0	0
	Aut-12	24.38	1.2	70.1	0.8	5.52	0.12	0.67	0.26	0.01	0.006

Table 2: *continued*

Station	Sampling period	Chl- <i>a</i> :phaeo		OC		TN		C:N	
		(µg/g)	SD	(%)	SD	(%)	SD		SD
BC500	Spr-12	1.074	0.3	0.773	0.1	0.1	0.01	7.71	0.47
	Aut-12	0.054	0.1	0.897	0	0.113	0	7.92	0.1
	Spr-13	0.024	0	1.12	0	0.097	0	11.6	0
	Aut-13	0.248	0.1	1.092	0.1	0.094	0.01	11.7	2.07
BC900	Spr-12	0.222	0.1	0.785	0.1	0.098	0.01	7.99	0.41
	Aut-12	0.066	0	0.734	0.1	0.093	0.01	7.87	0.12
	Spr-13	0.193	0	0.871	0	0.081	0	10.7	0.57
	Aut-13	0.259	0.1	0.883	0.1	0.083	0	10.6	0.32
BC1200	Spr-12	0.271	0.2	0.56	0.3	0.075	0.03	7.34	0.83
	Aut-12	0.063	0	0.753	0	0.093	0.01	7.74	0.16
	Spr-13	0.102	0	0.886	0	0.078	0	11.4	0.2
	Aut-13	—	—	—	—	—	—	—	—
BC1500	Spr-12	0.136	0	0.755	0	0.103	0	7.36	0.08
	Aut-12	0.053	0	0.758	0	0.106	0.01	7.2	0.32
	Spr-13	0.191	0	0.798	0.1	0.069	0	11.6	1.74
	Aut-13	0.195	0.1	0.772	0.1	0.068	0.01	12	1.65
BC1750	Spr-12	0.084	0	0.735	0	0.107	0	6.9	0.06
	Aut-12	0.054	0	0.783	0.1	0.111	0.01	7.22	1.55
	Spr-13	0.109	0	0.861	0	0.072	0	12.1	0.72
	Aut-13	0.129	0	0.829	0	0.087	0	9.71	0.36
BC2000	Spr-12	0.063	0.1	0.672	0	0.1	0	6.73	0.21
	Aut-12	0.057	0	0.836	0.1	0.092	0	9.06	1.18
	Spr-13	—	—	—	—	—	—	—	—
	Aut-13	0.262	0.2	0.765	0	0.082	0	9.4	0.2
OS500	Spr-13	0.094	0.1	0.66	0	0.07	0	9.88	0.85
OS900	Spr-13	0.023	0	0.9	0	0.09	0	9.58	0
OS1500	Aut-12	0.01	0	0.62	0	0.09	0	7.15	0.09
	Spr-12	0.027	0	0.77	0	0.07	0	10.5	0.18
OS1750	Spr-12	0.271	0.4	0.59	0	0.09	0	6.87	0.01
	Aut-12	0	0	0.61	0	0.09	0	7.23	0.3
	Spr-13	0.025	0	0.7	0	0.07	0	10.1	0
	Aut-13	0.066	0	0.66	0	0.08	0	8.6	0
OS2000	Spr-12	0	0	0.653	0.1	0.09	0.01	6.73	1.46
	Aut-12	0.016	0	0.61	0.4	0.09	0	6.88	0.32

Table 3. Results from univariate and multivariate PERMANOVA two-way analyses for differences in sedimentary abiotic variables. Test for locations (Lo: Canyon and Slope); water depth (WD) and interaction term. TN: total nitrogen concentration; C:N: molar carbon/nitrogen ratio; OC: organic carbon concentration; Chl-*a*: chlorophyll *a*; CPE: chloroplastic pigment equivalents; Chl-*a*:phaeo: chlorophyll *a*: phaeopigments ratio. Data was normalised; 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	Mean grain size	TN	C:N	OC	CPE	Chl-a	Chl-a: phaeo
Lo	1	0.3014	0.0245	0.794	0.0001	0.0022	0.0416	0.7895
WD	4	0.004	0.4368	0.4526	0.005	0.0002	0.0001	0.4589
Lo x WD	4	0.0008	0.0269	0.4067	0.0096	0.0347	0.5768	0.4216
Res	66							
Total	76							

Table 4. Univariate and multivariate PERMANOVA two-way analyses for environmental data in the slope and canyon systems, Test for sampling periods (Tm: Spring 2012, autumn 2012, spring 2013 and autumn 2013); water depth (WD) and interaction terms, TN: total nitrogen concentration; C:N: molar carbon/nitrogen ratio; OC: organic carbon concentration; Chl-*a*: chlorophyll *a*; CPE: chloroplastic pigment equivalents; Chl-*a*:phaeo: chlorophyll *a* divided by its degradation products (phaeopygments) indicating “freshness” of the phytodetrital OM, Data was normalised; 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	Mean grain size	TN	OC	C:N	CPE	Chl- <i>a</i>	Chl- <i>a</i> : phaeo
Slope								
Tm	3	0.1409	0.0146	0.0018	0.0003	0.589	0.0645	0.1085
WD	3	0.0149	0.0262	0.0408	0.9999	0.0446	0.0417	0.7311
Tm x WD	2	0.1184	0.4582	0.7418	0.5727	0.2603	0.015	0.6779
Res	10							
Total	17							
Canyon								
Tm	3	0.001	0.0001	0.0001	0.0001	0.4549	0.0002	0.0001
WD	5	0.0003	0.0028	0.0006	0.2479	0.0162	0.001	0.0001
Tm x WD	13	0.0844	0.0099	0.1304	0.0938	0.1099	0.3101	0.0001
Res	35							
Total	56							

Table 5. Results of PERMANOVA two-way analyses for differences in univariate (density) and multivariate (composition) meiofauna descriptors among locations (Lo: canyon and slope), water depth (WD) and interaction item, ECV: estimated component of variation. Noted that the numbers of collected samples were not equal in each location, resulting different degrees of freedom (df) for interaction terms, Information about missing samples is reported in Table 1. *: Monte Carlo inferred values (PERMANOVA permutations <100).

TOTAL		Density			Community		
Source	df	P(perm)	perms	ECV	P(perm)	perms	ECV
Lo	1	0.0048	9816	14186	0.0015	9950	44.254
WD	5	0.0002	9952	19683	0.0001	9903	76.817
LoxWD	4	0.2167	9960	3203	0.0263	9902	34.775
Res	66			37.75			228.71
Total	76						
Spring 2012							
Lo	1	0.0301	257	30374	0.0395	270	203.41
WD	1	0.2523	269	0.1619	0.1971	270	22.417
LoxWD	1	0.056	269	3.32	0.7886	270	47.525
Res	4			0.74108			151.7
Total	7						
Autumn 2012							
Lo	1	0.0001	9833	51798	0.0082	9965	65.749
WD	2	0.0165	9964	12271	0.0125	9942	66.353
LoxWD	2	0.0056	9966	35035	0.1453	9948	52.148
Res	12			13829			224.41
Total	17						
Spring 2013							
Lo	1	0.1099	9945	13076	0.0551	9949	48.16
WD	3	0.476	9941	-1,0705	0.1405	9932	33.898
LoxWD	3	0.9418	9961	-4.5482	0.4453	9913	3.5567
Res	10			6.4624			224.88
Total	17						
Autumn 2012							
Lo	1	0.722	4*	-28.614	0.6623	4*	-28.614
Res	2			44.914			44.914
Total	3						

Table 6. Univariate and multivariate PERMANOVA two-way analyses for meiofauna density and composition data in the slope and Blanes canyon, Test for sampling periods (Tm: Spring 2012, autumn 2012, spring 2013 and autumn 2013); water depth (WD) and interaction terms, Bold values indicate significant differences at $p < 0.05$, bold italic values indicate significant differences at $p < 0.01$

Slope		Density			Community		1144
Source	df	P(perm)	perms	ECV	P(perm)	perms	1145
Time	3	0.2364	9949	0.58963	0.0617	9919	1146
WD	2	0.0006	9949	14.902	0.003	9937	1147
Tm x WD	2	0.0602	9959	49.737	0.2846	9933	1148
Res	10			40.131			1148
Total	17						1149
Canyon		Density			Community		1150
Source	df	P(perm)	perms	ECV	P(perm)	perms	1151
Time	3	0.0234	9957	66.955	0.0119	9918	1151
WD	5	0.0271	9951	609712	0.0001	9994	1152
Tm x WD	13	0.0203	9938	18.078	0.0602	9894	1153
Res	33			31.739			1154
Total	54						1154

Table 7. Relative abundance of meiofaunal taxa and total density per sampling period and station. BC: Blanes canyon, OS: open slope; Std: standard deviation; S: number of taxa.

Time	Spring 2012							
Station	BC500	BC900	BC1200	BC1500	BC1750	BC2000	OS1750	OS2000
<i>Relative abundance (%)</i>								
Amphipoda	-	-	-	-	-	-	-	-
Aplacophora	-	-	-	-	-	-	-	-
Bivalvia	-	-	0.21	0.09	0.15	0.37	-	-
Cnidaria	-	-	-	-	-	-	-	-
Cumacea	-	-	-	-	-	-	-	-
Gastrotrycha	-	-	-	-	0.15	0.09	-	-
Halacaroida	-	0.13	0.05	-	-	-	0.19	0.16
Holoturoidea	-	-	-	-	-	-	-	-
Copepoda	1.77	11.39	3.92	1.96	4.50	4.32	6.56	4.06
Isopoda	0.12	0.13	-	0.04	0.45	0.28	0.19	-
Kinorhynca	0.50	0.79	0.21	0.14	0.22	0.18	-	-
Loricifera	-	-	-	-	-	0.01	-	-
Nauplii	1.73	4.9	2.88	1.62	2.78	3.85	5.79	3.89
Nematoda	93.94	79.21	89.51	94.42	90.55	88.53	84.94	89.49
Nemertea	-	-	-	-	-	-	-	-
Oligochaeta	-	-	-	-	-	-	-	-
Ostracoda	0.04	-	0.27	0.09	-	-	-	-
Polychaeta	1.86	3.31	2.77	1.38	1.05	1.03	1.73	1.86
Rotifera	0.04	-	-	0.23	0.15	-	0.57	0.16
Sipunculida	-	-	-	-	-	-	-	-
Tanaidacea	-	-	-	-	-	-	-	-
Tardigrada	-	0.13	0.16	-	-	1.22	-	0.33
Total (ind. 10 cm⁻²)	1212.5	377.5	919.5	1048	666.5	532	259	295
Std	122.4	69.2	52.1	111.9	166.4	104.3	35.3	32.2
S	8	8	9	9	9	10	7	7

Table 7: continued

Time	Autumn 2012								
Station	BC500	BC900	BC1200	BC1500	BC1750	BC2000	OS1500	OS1750	OS2000
<i>Relative abundance (%)</i>									
Amphipoda	0.02	-	-	-	-	-	-	-	-
Aplacophora	-	-	-	-	-	-	-	-	-
Bivalvia	0.19	0.47	0.26	0.53	0.05	0.09	0.14	0.18	0.13
Cnidaria	-	0.03	-	-	-	-	0.04	-	-
Cumacea	-	0.07	-	-	-	-	-	-	-
Gastrotrycha	-	-	-	-	-	-	-	0.08	-
Halacaroidea	-	0.03	0.03	0.09	0.05	-	0.04	-	-
Holoturoidea	-	-	-	-	-	-	-	-	-
Copepoda	1.99	4.99	2.12	1.62	2.86	2.32	3.54	5.57	3.25
Isopoda	0.05	-	-	0.04	0.09	-	0.09	0.04	-
Kinorrhynca	0.13	0.74	0.93	0.17	0.09	-	0.09	0.08	0.13
Loricifera	-	-	-	-	-	-	-	-	-
Nauplii	2.69	3.73	1.21	0.9	2.47	1.2	2.22	3.41	2.07
Nematoda	91.55	87.44	93.03	94.96	92.49	95.07	93.49	89.67	93.22
Nemertea	0.05	-	-	-	-	-	-	-	-
Oligochaeta	-	-	0.07	-	-	-	0.04	-	0.26
Ostracoda	0.08	0.07	0.07	0.04	0.09	0.09	0.28	0.08	0.88
Polychaeta	1.9	1.78	1.99	1.35	0.84	0.51	0.56	0.9	0.15
Rotifera	0.11	0.07	0.20	0.17	0.21	0.38	0.18	0.35	0.57
Sipunculida	-	0.15	-	-	-	-	-	-	-
Tanaidiacea	-	0.03	0.07	0.04	-	-	-	0.04	-
Tardigrada	-	0.30	-	0.04	0.07	0.33	0.18	0.61	0.88
Total (ind. 10 cm⁻²)	1763	841	990.3	741.3	1389.3	777.3	704.6	371.3	225.3
Std	244.6	280.8	831.5	132.6	64.7	461.9	68.2	107.6	66.5
S	11	14	11	12	11	8	13	12	10

Table 7: *continued*

Time	Spring 2013								
Station	BC500	BC900	BC1200	BC1500	BC1750	OS500	OS900	OS1500	OS1750
<i>Relative abundance (%)</i>									
Amphipoda	-	0.02	-	-	-	-	-	-	-
Aplacophora	-	-	-	0.02	-	-	-	-	-
Bivalvia	0.07	0.23	0.12	0.12	0.25	0.16	0.42	0.04	-
Cnidaria	-	-	-	-	-	-	-	-	-
Cumacea	-	-	-	-	0.02	-	-	-	-
Gastrotricha	-	0.16	0.04	-	-	0.06	0.10	-	1
Halacaroida	-	0.09	0.01	-	0.02	0.06	-	0.04	-
Holoturoidea	-	-	-	-	-	-	-	-	-
Copepoda	1.16	5.14	1.58	0.68	2.05	2.43	1.27	2.77	4.59
Isopoda	-	0.05	-	0.02	0.21	-	-	0.04	-
Kinorhynca	0.46	0.79	0.55	0.02	0.12	0.41	0.73	0.19	0.36
Loricifera	-	-	-	-	-	-	-	-	-
Nauplii	1.09	4.73	2.46	0.78	1.59	5.48	3.79	3.36	4.39
Nematoda	94.88	86.07	93.71	97.65	94.32	89.25	91.35	92.38	88.22
Nemertea	-	-	-	-	-	-	-	-	-
Oligochaeta	-	-	0.04	-	0.02	-	-	-	-
Ostracoda	-	0.25	0.01	-	-	0.22	0.31	0.19	2
Polychaeta	2.17	1.78	1.34	0.59	0.90	1.19	0.94	0.74	0.99
Rotifera	0.15	0.07	0.01	0.02	0.09	0.19	0.21	0.10	0.79
Sipunculida	-	-	-	-	-	-	-	-	-
Tanaidiacea	-	0.02	0.04	-	-	0.12	0.31	-	-
Tardigrada	-	0.54	0.04	0.02	0.40	0.36	0.52	0.10	-
Total (ind. 10 cm⁻²)	1289	1387.6	1663.3	1022.7	1069	1027	948	674	501
Std	-	785.1	671.9	335.8	499.1	72	-	117.1	-
S	7	14	13	10	12	12	11	11	8

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Table 7: *continued*

Time	Autumn 2013					
Station	BC500	BC900	BC1500	BC1750	BC2000	OS1750
<i>Relative abundance (%)</i>						
Amphipoda	-	-	-	-	-	-
Aplacophora	-	-	-	-	-	-
Bivalvia	0.22	0.22	0.26	0.17	-	-
Cnidaria	-	-	-	-	-	-
Cumacea	0.07	-	-	-	-	-
Gastrotrycha	0.03	0.06	0.03	-	-	-
Halacaroida	-	-	-	-	-	-
Holoturoidea	-	-	-	-	-	-
Copepoda	4.41	3.99	1.39	2.00	2.01	4.54
Isopoda	0.19	0.04	0.03	0.17	-	-
Kinorhynca	0.94	0.70	0.03	0.05	-	-
Loricifera	-	-	-	-	-	-
Nauplii	0.65	3.00	0.87	1.59	1.80	2.47
Nematoda	89.85	90.19	96.35	94.32	95.19	90.09
Nemertea	-	-	-	-	-	-
Oligochaeta	-	-	-	-	-	-
Ostracoda	0.45	0.01	-	0.05	-	-
Polychaeta	3.12	1.34	0.82	0.90	0.53	1.03
Rotifera	-	-	0.03	0.11	-	-
Sipunculida	-	-	-	-	0.06	-
Tanaidiacea	-	-	-	-	-	-
Tardigrada	0.03	0.32	0.13	-	-	1.03
<i>Total (ind. 10 cm⁻²)</i>	877	1613.3	768	588	748	484
Std	25.5	487.6	195.6	318	9.8	-
S	11	10	10	10	4	5

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Table 8. Spearman correlation between environmental variables and meiofauna density for canyon and slope systems. Bold values indicate significant differences at $p < 0.05$, bold italic values indicate significant differences at $p < 0.01$.

Environmental variables	Meiofauna density	
	Canyon	Slope
CPE	0,438	0,569
Chl- <i>a</i>	0,474	0,541
Chl- <i>a</i> :phaeo	-0,059	0,474
OC	0,367	0,591
TN	0,013	-0,465
C:N	0,210	0,591
Clay	-0,253	-0,600
Silt	-0,201	0,147
Sand	0,297	-0,108

Table 9: Comparison of mean meiofaunal densities with depths in different submarine canyon areas (Iberian and Western Mediterranean coasts).

Location	Canyon	Depth-range (m)	Meiofauna (ind. 10 cm-2)	Source
NW Mediterranean	Cassidaigne	245-810	245-801	Vivier (1978)
NW Mediterranean	Gulf of Lions (several)	672-2300	36-1005	De Bovée (1990)
NW Mediterranean	Gulf of Lions (several)	830-1380	530-1290	Grémare et al. (2002)
NW Mediterranean	Lacaze-Duthiers	600-1300	836-1050	Danovaro et al. (1999)
NW Mediterranean	Lacaze-Duthiers	434-1497	205-1391	Bianchelli et al. (2010)
NW Mediterranean	Cap de Creus	960-1874	147-597	Bianchelli et al. (2010)
NW Mediterranean	Blanes	400-1600	25-1500	Romano et al. (2013)
NW Mediterranean	Blanes	500-2000	209-1763	Present study
Western Mediterranean	Buscarró	600-800	40-123	Rumolo et al. (2015)
Atlantic	Cascais	445-2100	492-900	Bianchelli et al. (2010)
Atlantic	Nazaré	332-1121	9.9-236.5	Garcia et al. (2007)
Atlantic	Nazaré	458-897	747-1484	Bianchelli et al. (2010)

CAPTION OF FIGURES

Figure 1. Map of the study area showing the sampling stations and the fishing effort (hours/km²). BC: Blanes canyon, OS: Western open slope.

Figure 2. Bathymetric patterns of each environmental variable selected. Continuous and dashed lines are the significant regression ($p < 0.05$) for canyon and slope samples respectively.

Figure 3. Principal component analysis (PCA) ordination based on 9 environmental variables selected. A) Canyon vs slope. B) Canyon.

Figure 4. Bathymetric scatter plot of meiofaunal densities. Dashed line represent significant regression ($p < 0.05$) for slope samples.

Figure 5. Temporal fluctuations of meiofaunal density within the A) Blanes canyon and B) Slope.

Figure 6. MDS based on meiofaunal community composition in the Blanes canyon and at the western slope for each sampling period (based on Bray Curtis similarity values of four-root transformed data). A) Spring 2012. B) Autumn 2012. C) Spring 2013. D) Autumn 2013.

Figure 7. Temporal variation of ancillary data in the study area. A) Chlorophyll-a concentration /surface productivity. B) Temporal variation of high waves in the study area. Lines indicate monthly average (blue), monthly max (red) and hourly data (green). C) Monthly discharge of the Tordera river measured at the gauging nearest station to river mouth (data from Agència Catalana de l'Aigua, ACA).

SUPPLEMENTARY MATERIAL

Table S1. Results of the two-way PERMANOVA pair-wise test (Factor “Time” with 4 levels (spring, autumn 2012, spring, autumn 2013), factor “WD “: Water Depth, with 6 levels (500, 900, 1200, 1500, 1750 and 2000 m)) for meiofauna density. Data was square-root transform and resemblance was calculated using Euclidean Distance prior to analysis, Bold values indicate significant differences at $p < 0.05$, bold italic indicate significant at $p < 0.01$.

Table S2. Results from pair-wise multivariate PERMANOVA analyses for differences in meiofauna composition. PERMANOVA pair-wise comparisons between Time and water depth (WD). Spr: spring; Aut: autumn. Data was fourth-root transform and resemblance was calculated using Bray Curtis prior to analysis. Bold values indicate significant differences at $p < 0.05$ and bold italic indicate significant at $p < 0.01$.

Table S3. Distance-based linear model (DISTLM) for meiofauna assemblages and selected environmental variables for the western open slope. Variables: Selected environmental variables used to calculate the optimum model. Marginal tests: explanation of variation for each variable taken separately. Sequential tests: conditional tests of individual variables in constructing the model. Each test examines whether adding the variable contributes significantly to the explained variation. Selection procedure: step-wise, selection criterion: adjusted R^2 . Prop.: % variation explained. Cumul.: cumulative variation explained. Chl-a: chlorophyll a, CPE: chloroplastic pigment equivalents, Chl-a:phaeo: chlorophyll a divided by its degradation products indicating ‘freshness’ of the phytodetrital OM, TN: total nitrogen content, OC: organic carbon content, C:N: molar carbon-nitrogen ratio.

Table S4. Distance-based linear model (DISTLM) for meiofauna assemblages and selected environmental variables for the Blanes Canyon. Variables: Selected environmental variables used to calculate the optimum model. Marginal tests: explanation of variation for each variable taken separately. Sequential tests: conditional tests of individual variables in constructing the model. Each test examines whether adding the variable contributes significantly to the explained variation. Selection procedure: step-wise, selection criterion: adjusted R^2 . Prop.: % variation explained.

1348 Cumul.: cumulative variation explained. Chl-a: chlorophyll a, CPE: chloroplastic
1349 pigment equivalents, Chl-a:phaeo: chlorophyll a divided by its degradation products
1350 indicating ‘freshness’ of the phytodetrital OM, TN: total nitrogen content, OC: organic
1351 carbon content, C:N: molar carbon-nitrogen ratio.

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