1	High spatiotemporal variability in meiofaunal assemblages in Blanes Canyon (NW
2	Mediterranean) subject to anthropogenic and natural disturbances
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20 **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.

28 Twenty-one and 16 major taxa were identified for respectively the canyon and slope, 29 where the assemblages were always dominated by nematodes. The gradual decreasing 30 meiofaunal densities with increasing depth at the slope showed little variability among 31 stations and corresponded with a uniform pattern of food availability. The canyon was 32 environmentally much more variable and sediments contained greater amounts of food 33 resources (Chl-a and CPE) throughout, leading not only to increased meiofaunal 34 densities compared to the slope, but also different assemblages in terms of composition 35 and structure. This variability in the canyon is only partly explained by seasonal food 36 inputs. The high densities found at 900 m and 1200 m depth coincided with significant 37 increases in food availability compared to shallower and deeper stations in the canyon. 38 Our results suggest that the disruption in expected bathymetric decrease in densities at 39 900-1200m water depth coincided with noticeable changes in the environmental 40 variables typical for disturbance and deposition events (e.g., higher sand content and 41 CPE), evoking the hypothesis of an anthropogenic effect at these depths in the canyon. 42 The increased downward particle fluxes at 900 to 1200 m depth caused by bottom 43 trawling along canyon flanks, as reported in previous studies, support our hypothesis 44 and allude to a substantial anthropogenic factor influencing benthic assemblages at 45 these depths. The possible relationships of the observed patterns and some major natural 46 environmental (e.g., surface productivity or dense shelf water cascading) and 47 anthropogenic (e.g. the lateral advection and downward transport of food-enriched 48 sediments resuspended by the daily canyon-flank trawling activities) drivers are 49 discussed.

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52 Keywords

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

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56 2. INTRODUCTION

57 There is increasing evidence that submarine canyons play important ecological roles 58 in the functioning of deep-sea ecosystems (Amaro et al., 2016; Thurber et al., 2014) 59 Submarine canyons are important routes for the transport of organic matter from surface 60 waters and continental shelf areas to the deep sea basins (Granata et al 1999; Durrieu de 61 Madron et al., 2000; Palanques et al., 2005; Canals et al., 2006; Pasqual et al., 2010), 62 and they contribute significantly to regional biodiversity and secondary production 63 along continental margins (Gili et al., 1999, 2000; Sardá et al., 2009; Ingels et al., 2009; 64 Vetter et al., 2010; De Leo et al., 2010;). Different oceanographic and geological 65 processes are responsible for their role as organic matter supply routes, including slope 66 instabilities, turbidity currents events caused by river floods or episodic storms, and 67 dense shelf water cascading (De Stigter et al., 2007; Allen and Durrieu de Madron, 68 2009; Puig et al., 2014). Additionally, anthropogenic activities along canyon flanks such 69 as bottom trawling can alter seafloor community structure and biodiversity through 70 physical habitat disturbance and the re-suspension of sediments, which ultimately 71 accumulate at greater depths inside the canyon axis (Palanques, et al., 2006; Martín et 72 al., 2008, 2014; Puig et al., 2012, 2015a, b; Pusceddu et al., 2014; Wilson et al., 2015).

73 More than 500 large submarine canyons have been identified in the Mediterranean 74 Sea (Harris and Whiteway, 2011) with several of them located along the Catalan margin 75 (NW Mediterranean). Among those, Blanes Canyon has been intensively studied in the 76 past decade (Zúñiga et al, 2009; Sánchez-Vidal et al., 2012; Canals et al., 2013; Lopez-77 Fernandez et al., 2013). It has been shown that the canyon axis experiences strong 78 current intensifications coupled with high particle fluxes to the deepest parts of the 79 canyon, which are linked to major events like storms and subsequent river discharges, 80 as well as dense water formation during winter. These characteristics cause the off-shelf 81 sediment transport through the Blanes Canyon axis to vary substantially over time. 82 Moreover, the downward particle fluxes within the canyon can be affected by sediment 83 resuspension caused by daily bottom trawling activities along the canyon flanks 84 (Company et al., 2008, Sardà et al., 2009), with increased fluxes attributed to this 85 process observed mainly between 900 and 1200 m depth (Lopez-Fernandez et al., 86 2013). In general, the particulate matter fluxes in the canyon area and at the adjacent 87 open slope have two defined seasonal periods (Zúñiga et al., 2009; Lopez-Fernandez et 88 al., 2013). During autumn-winter mass fluxes increase in response to river flooding 89 coupled with major coastal storms. During the spring-summer months the biological 90 component of the particulate fluxes becomes more important as a response to the 91 phytoplankton bloom. However, the open slope mass flux has been reported to be three 92 orders of magnitude lower than inside the Blanes Canyon with sinking particles 93 containing lower amounts of lithogenics and higher levels of organic carbon (OC) 94 (Lopez-Fernandez et al., 2013).

95 Most, if not all, oceanographic and geological processes that drive the ecological 96 function and processes in submarine canyons elicit a response from the canyon fauna 97 (Amaro et al., 2016). Elevated and depressed faunal densities have been reported in 98 canyons, compared to slope areas (Cartes et al., 1994, 2009, 2010; Vetter and Dayton, 99 1998; Garcia and Thomsen, 2008; Ingels et al., 2009, 2013; De Leo et al., 2010; 100 Tecchio et al., 2013; Romano et al., 2013). Complex canyon hydrodynamics can lead to 101 areas characterized by strong deposition next to areas typified by intense erosion 102 processes, which are highly variable in time. These factors have been identified as 103 driving marked temporal and spatial variability in benthic fauna standing stocks (De 104 Bovée, 1990; Ingels et al., 2013; Romano et al., 2013; Tecchio et al., 2013). Despite the 105 difficulties associated with sampling these deep-sea environments, the collection of 106 benthic biological time-series is crucial in providing the necessary information to 107 understand ecological processes and their importance in canyon systems.

108 The main forcing processes affecting canyons influence benthic organisms, and the 109 meiofauna is no exception in this context (Giere et al., 2009). Metazoan meiofauna 110 dominate the deep-sea benthos in terms of abundance and biomass (Vincx et al., 1994; 111 Rex et al., 2006; Giere, 2009; Pape et al., 2013a; Pape et al., 2013b). Quantitative deep-112 sea meiofaunal studies in the Mediterranean, have mostly focused on slope and basin 113 environments (De Bovée et al., 1990; Soetaert et al., 1991; Tselepides and 114 Lampadariou, 2004; Bianchelli et al., 2008; Romano et al., 2013; Rumolo et al., 2015), 115 while studies targeting wide bathymetric gradients along canyons axes are particularly 116 rare (De Bovée, 1990; García et al., 2007; Bianchelli et al 2010). Meiobenthic taxa, 117 such as Nematoda, seem particularly resilient to both natural and anthropogenic 118 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).

123 The aim of the present work is to study the distribution patterns of the metazoan 124 meiofauna along the Blanes Canyon axis compared with those from the adjacent open 125 slope. Samples were collected covering a bathymetric range from 500 to 2000 m depth 126 in two periods (i.e. spring and autumn) and over two successive years (2012 and 2013) 127 to identify variations in the main meiofaunal descriptors (i.e., density, community composition and richness of taxa). Subsequently, their relationship with the main 128 129 driving sediment variables (e.g. grain size, organic content), including those related with 130 food input (e.g. Chlorophyll-a content), and environmental constraints (both natural and 131 anthropogenic) were analyzed. Based on previous observations from submarine canyon 132 systems we expect that Blanes Canyon will be characterized by high-density meiofauna 133 communities, but also by high temporal community variability which is only partly 134 explained by seasonal differences in food input.

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136 **3. MATERIAL AND METHODS**

3.1. Sampling

138 Within the frame of the DosMares research project, sediment samples were 139 collected in and around Blanes Canyon during four cruises (DM-I: early spring 2012, 140 DM-II: autumn 2012, DM-III: spring 2013 and DM-IV: autumn 2013) on board of the 141 R/V García del Cid (Fig. 1). Six stations were sampled along the canyon axis (BC500, 142 BC900, BC1200, BC1500, BC1750 and BC2000) and five on the adjacent open slope 143 (OS500, OS900, OS1500, OS1750 and OS2000). Despite a comprehensive sampling 144 campaign, full temporal and water-depth coverage could not be obtained owing to 145 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 152 PVC tube (36 mm of diameter, 5 cm sediment depth) taken from the center of the core 153 to maintain a consistent sample surface area for all replicates. Meiofauna samples were 154 fixed in buffered 4% formaldehyde, while those for sediment variables were frozen and 155 stored at -20°C until analysis in the laboratory.

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157 3.2. Sediment variables

158 *3.2.1. Grain size*

159 Grain sizes were analyzed using a Master Sizer 2000 laser analyzer. Each sample 160 was first defrosted and homogenized. Then, aliquots (~1 g) were treated with a 6% 161 hydrogen peroxide solution for 48 h to remove organic matter and subsequently washed 162 with distilled water to eliminate salts. Before each measurement 10 drops of distilled 163 water with sodium hexametaphosphate (0.05 %) was added to disperse the sediment. 164 Then samples were homogenized prior to running the analysis. Sediments were grouped 165 into grain size fractions as follows: clay (<4 μ m), silt (4–63 μ m) and sand (63 μ m–2 166 mm).

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168 *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).

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176 *3.2.3. Pigment content*

177 Sediment aliquots were freeze-dried and homogenized to extract pigments. About 1 178 g dry weight of sediment was mixed in 4 ml 90% acetone and the obtained extract was 179 centrifuged (4 min at 3000 rpm, 4°C) and filtered through a Whatman Anodisc 25 (0.1 180 µm). Pigments were analyzed by Ultra Performance Liquid Chromatography. 181 Chlorophyll-a (Chl-a) and chlorophyll degradation products were identified by 182 checking the retention times and the absorption spectra against a library based on 183 commercial standard mixtures (DHI, PPS-MiX-1) and extracts from pure cultures of 184 algae and bacteria (protocol modified of Buchaca and Catalan, 2008). Chloroplastic 185 Pigments Equivalents (CPE: sum of Chl-a and phaeopigments, its degradation products) 186 was used to estimate OM produced by surface primary productivity. The ratio Chl-*a*:
187 phaeopigments (Chl-*a*:phaeo) was used as a proxy to estimate the freshness of
188 photosynthetically derived OM (Thiel, 1978).

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190 *3.3. Meiofauna*

191 The fixed samples were rinsed through a 1000 µm mesh then sieved through a 192 32 µm mesh. The retained 32 µm fraction was washed and centrifuged three times using 193 the colloidal silica polymer LUDOX HS40 (specific gravity 1.18) to achieve density 194 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 195 196 kept in 4 % formaldehyde and stained with Rose Bengal. All metazoan meiobenthic 197 organisms were classified at higher taxon level following Higgins and Thiel (1988) and 198 counted under stereomicroscope (50 x magnification).

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200 *3.4. Data analyses*

201 Both univariate and multivariate non-parametric permutational (PERMANOVA) 202 analyses were performed to test differences in meiofauna density and assemblage 203 composition, as well as sediment variables between sampled periods, locations and 204 depths. Differences between locations (i.e. canyon vs slope) and water depths were 205 tested with two different 2-way crossed designs, using Location (Lo: fixed) and Water 206 Depth (WD: fixed) as factors, both for uni- and multivariate analysis (PERMANOVA 207 Anderson, 2005; Anderson et al., 2008). In the first 2-way PERMANOVA analysis to 208 assess overall differences between locations we pooled the data from the four sampling 209 times and considered all the depths (6 levels: 500, 900, 1200, 1500, 1750, 2000 m). 210 Subsequently, we considered data from each campaign separately and performed a 2-211 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; 212 213 autumn 2012: 1500, 1750, 2000 m; spring 2013: 500, 900, 1500, 1750, autumn 2013: 214 1750 m).

215 Considering that the sampling effort of this study was mainly focused on the 216 canyon and for the slope a less complete data matrix was available, we also analyzed the 217 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.

223 Differences in sediment variables over the terms Tm and WD were assessed by 224 univariate PERMANOVA, except for the grain size content, where clay, silt and sand 225 percentages were considered as multivariate variables. Additionally, Principal 226 Component Analyses (PCA) based on sediment variables were performed to assess 227 differences in spatial distribution between the canyon and slope samples and the 228 temporal and spatial patterns in the canyon. Prior to calculating the Euclidean distance 229 resemblance matrix, the full set of 11 available sediment variables was tested for 230 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 231 232 phaeopigments). The data were then checked for uniform distribution (Chl-a, CPE and 233 Chl-a:phaeo were log (0.01+X) transformed) followed by normalization (subtracting the 234 mean and dividing by the standard deviation, for each variable) to bring them to a 235 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.

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256 3.5. Ancillary data

257 To assess the impact of bottom trawling fisheries in the Blanes canyon, positioning 258 of fishing vessels was obtained from the Fishing Monitoring Centre of the Spanish 259 General Secretariat of Maritime Fishing (SEGEMAR) as Vessel Monitoring System 260 (VMS) data, a protocol established by the Common Fisheries Policy of the European 261 Union (2011). Each vessel equipped with VMS provide its registered harbour, heading, 262 speed and Global Positioning System coordinates with an error margin of 100 m, and 263 transmits this information by Inmarsat-C to the Fishing Monitoring Centre in less than 264 10 min at 2-hour time intervals (Gerritsen et al., 2013). VMS positioning from bottom 265 trawlers operating in the study area during 2006-2013 was subsequently converted to fishing effort (hours/km²), computed in grid cells of 0.5^{-1} latitude x 0.5^{-1} longitude as 266 267 shown in Figure 1, following the method and the software tools described in Hitzen et 268 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 <u>www.nasa.gov</u>. 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* (<u>www.puertos.es</u>).

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278 **4. RESULTS**

279 4.1. Sediment characteristics

Canyon and slope sediments were predominantly muddy (2-63 μ m) 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 (R² =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).

289 Sedimentary Chl-a and CPE content were higher in the canyon than at the slope, 290 except for Chl-a at BC500 in spring 2013 (Fig. 2, Table, Table 3). Slope samples 291 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 292 293 between sampling periods (Tm x WD interaction, pairwise comparisons, p < 0.01, Table 294 4), particularly at OS1750 between spring and autumn 2012 (p < 0.05, Table 2). CPE did 295 not differ between sampling periods (Table 4). Along the canyon axis, Chl-a decreased 296 with increasing water depth (Fig. 2, $R^2=0.26$) but the high variability at BC1200 297 (autumn 2012 and spring 2013) and BC1500 (spring 2012) obscured this general pattern 298 (Table 2). Chl-a differed significantly between sampling periods and water depths 299 (PERMANOVA, p < 0.01, Table 4). As for Chl-*a*, CPE decreased with increasing water 300 depth along the canyon axis, except for the peaks observed at BC1200 (autumn 2012 301 and spring 2013) and BC1500 (spring 2012) (Table 2, PERMANOVA, p < 0.01, Table 302 4).

303 The "freshness" (Chl-a: phaeo ratio) of OM did not differ significantly between the 304 canyon and slope (PERMANOVA, p > 0.05, Table 3). At the slope, the freshness of 305 OM did not show a clear decrease with increasing water depth (Fig. 2F) and differences 306 between sampling periods were not significant (PERMANOVA, p > 0.05, Table 4). In 307 the canyon, the freshness differed significantly between sampling periods and water 308 depths, but a clear decrease with increasing depth occurred only in spring 2012 (Table 309 2; PERMANOVA, p < 0.01, Table 4). There were also significant differences between 310 spring and autumn 2012 for BC500, BC900 and BC1500 and between autumn 2012 and 311 2013 at BC1750 and BC2000 (Tm x WD interaction, pairwise comparisons, p < 0.01, 312 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 319 (Table 4) but only TN decreased with increasing depth (R^2 = 0.27; Fig. 2). Along the 320 canyon axis, OC and TN differed significantly between sampling periods and water 321 depths (PERMANOVA, p < 0.01, Table 4), with a pronounced decrease with increasing 322 water depth in spring 2013 (Table 2). OC and TN were significantly higher in spring 323 2013 and autumn 2012 (Table 2). TN also differed significantly between 2012 and 324 2013, particularly at BC1500 and BC1750 (Tm x WD interaction pairwise comparisons, 325 p < 0.01, Table 2, 4).

326 Sedimentary C:N ratios did not differ significantly between canyon and slope 327 (PERMANOVA, p > 0.05, Table 2, 3, Fig. 2). Along the canyon axis, C:N differed 328 significantly between sampling periods (PERMANOVA, p < 0.01, Table 4), particularly 329 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).

336 When the Canyon axis samples were analyzed separately, the first two axes of the 337 PCA explained 65.4% of the variation (41.5% and 23.9% for PC1 and PC2, 338 respectively; Fig 3B). The main contributors were sand (0.427), Silt (-0.392), Chl-a 339 (0.379) and TN (-0.357) for PC1 and OC (0.596), Chl-a (0.376), sand (-0.388) and CPE 340 (0.310) for PC2 (numbers in parenthesis represent eigenvectors). Sampling periods were 341 clearly distinguishable in the PCA plot (Fig. 3B), particularly autumn 2012 and spring 342 2013, in accordance with the PERMANOVA analyses (Table 4). In particular spring 343 2013 samples were characterized by having greater pigments concentrations (Table 2) as suggested by the PCA. No consistent bathymetric differences could be observed in 344 345 the PCA plot.

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347 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).

359 Along the canyon axis, the densities did not show a clear bathymetric pattern, 360 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 ± 69 361 ind. 10 cm⁻² at BC900 in spring 2012 and the maximum was 1763 ± 245 ind. 10 cm⁻² at 362 363 BC500 in autumn 2012 (Table 7, Fig. 5 A). The highest variability was observed at 364 BC900 and BC1200 (Fig.5 A). There was a significant influence of water depth at each 365 sampling period, except in spring 2013 (PERMANOVA, p < 0.05, Table 6). In fact, the 366 observed differences were caused by the densities at BC500, which were significantly 367 higher than those at the deepest stations (BC1500, except in spring 2012, BC1750 and 368 BC2000) (Table S1, pair-wise comparison within Tm x WD; Fig 5 A).

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370 Regarding the temporal variability, at the slope stations, meiofauna densities did 371 not exhibit significant differences at any sampling depth (PERMANOVA, p > 0.05, 372 Table 6; Fig. 5B). In contrast, densities inside the canyon differed significantly between 373 sampling periods (Fig. 5A, Table 6), but no clear seasonal patterns were observed. In 374 2012, densities were higher in autumn than in spring, (except at BC1500) while the 375 trend was the opposite in 2013 (except at BC900) (Fig. 5A). Significant intra-annual 376 differences occurred in 2012 at BC1750, with higher densities in autumn compared to 377 spring. Significant inter-annual variability mainly occurred between autumn periods at 378 BC500 and BC1750, where densities were higher in 2012 than 2013, and at BC900, 379 where the opposite was observed (Table S1, pair-wise comparisons). There were no 380 temporal differences detected at stations BC1200, BC1500 and BC2000 (Table S1, pair-381 wise comparison; Fig 5A).

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386 *4.3. Meiofauna community composition*

387 The meiofauna composition in the canyon and the slope was comparable to what is 388 usually observed in the deep sea, with nematodes being dominant (79.2-97.6 %), 389 followed by copepods (0.68-5.14%, mainly harpacticoids), nauplii larvae (0.65-4.9%) 390 and polychaetes (0.51-3.12%) (Table 7). Other taxa (such as tardigrades and 391 kinorhynchs) were regularly found but in low densities (less than 2%). A total of 21 392 major taxa were identified in the canyon, while only 16 taxa were collected at the open 393 slope. Aplacophora, Amphipoda, Nemertea, Cumacea and Sipunculida were only 394 present in the canyon samples (Table 7). Relative nematode abundance was slightly 395 higher in all canyon samples compared to slope samples, except at the 900 m and 1750 396 m stations in spring 2013 and autumn 2013, respectively.

397 Considering all samples, meiofauna composition differed significantly between the 398 canyon and the slope (Table 6, p< 0.05), except at the 900 m stations (Lo x WD, pair-399 wise comparison, p < 0.05). For each sampling period, differences between locations 400 were also evident, especially in spring and autumn 2012 (Table 6). At the slope, 401 meiofauna composition varied between water depths (Table 6). The maximum of 13 402 taxa was found at OS1500 in autumn 2012 and the minimum number of 5 taxa was 403 found at OS1750 in autumn 2013, Despite of the reduced number of slope samples, the 404 number of taxa decreased with increasing water depth in autumn 2012 and spring 2013 405 (Table 7). In the canyon, the meiofauna community structure also differed among water 406 depths (Table 6), except for the BC500-BC1200, BC900-BC1200, BC1500-BC1750 407 and BC1750-BC2000 pairwise comparisons (Table S2). However, the MDS ordination 408 showed that there were no clear relationships between meiofauna community structure 409 and bathymetry, except in autumn 2013 (Fig. 6). The maximum number of taxa (14) 410 was found at BC900 in autumn 2012 and spring 2013 and the minimum (6) at BC2000 411 in autumn 2013 (Table S1). The reduced dominance of nematodes at BC900 is 412 countered by a relative increase of copepod and nauplii densities (Table 7).

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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 419 comparison). These differences were mainly owing to the increase in number of taxa420 from spring to autumn 2012 at all sampling stations (except at BC2000) (Table 7).

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22 4.4. Relationship between meiofauna and environmental variables

423 Meiofaunal densities showed significant, positive correlations with the variables 424 representing food inputs (i.e. CPE, Chl-*a*, and OC) both in the canyon and at the slope, 425 but correlations were higher for the slope than in the canyon (Spearman correlation, 426 Table 8). At the slope, negative correlations between meiofauna densities and TN and 427 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.

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434 **5. DISCUSSION**

435 The Mediterranean is considered to be an oligotrophic sea, a characteristic which 436 is often used to explain its typically low deep-sea meiofauna densities compared to 437 similar depths in other oceans (Soltwedel, 2010; Bianchelli et al., 2010; Pape et al., 438 2013b). Mediterranean meiofauna densities range between 4 and 1497 ind. 10 cm⁻², with 439 a clear decrease from west to east (Soltwedel, 2000; Bianchelli et al., 2010) which has 440 been linked to the W-E gradient of increasing oligotrophy (Danovaro et al., 1999; 441 Gambi and Danovaro, 2006; Danovaro et al., 2008). Similar low density ranges have 442 only been reported in the Southern Pacific Ocean, Southern Atlantic Ocean and Artic 443 Ocean (see Bianchelli et al., 2010 for a review).

444 The maximum densities in the Blanes Canyon axis were higher than those 445 observed in other Mediterranean canyons (Table 9). Minimum densities were equivalent 446 to those of Cape of Creus Canyon, but about 5 to 8 times higher than in the remaining 447 canyons, even when compared to previous data from Blanes Canyon (Romano et al., 448 2013) (Table 9). The study by Romano et al. (2013) included only a few canyon stations 449 and a limited depth range, with samples from the eastern and western canyons flanks 450 (900 m depth), from the canyon axis (1600 m depth), and from the eastern open slope 451 (1600 m depth). In the present study, a much more comprehensive range of samples 452 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.

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

458 Contrary to the traditional perception that the whole of the deep-sea is a stable 459 environment (e.g. Sanders, 1968), marked temporal variations of meiofaunal organisms 460 have been observed in submarine canyons (De Boveé et al., 1990; Romano et al., 2013; 461 Ramahlo et al., 2014; Rumolo et al., 2015) and slope systems (e.g., Hoste et al., 2007; 462 Romano et al., 2013; Guidi-Guilvard et al., 2014). Such variations generally suggest 463 contrasting scenarios between spring-summer and autumn-winter, with the former 464 causing higher densities. Traditionally, this variability has often been associated to the 465 seasonal trends in phytodetrital food availability, but it could also be associated with 466 specific particulate matter transport mechanisms, particularly in submarine canyon 467 environments (Pusceddu et al., 2013; Ramalho et al., 2014).

468 Previous studies in the Blanes Canyon have revealed high variability in particle 469 fluxes, driven by a variety of causes: storms, dense water formation (by dense shelf 470 water cascading and open sea convection), dust inputs, phytoplankton blooms, and 471 bottom trawling (Lopez-Fernandez et al., 2013). The concatenation of such events 472 influences sedimentary dynamics and ultimately meiofauna communities by altering 473 sediment characteristics and food availability. Physical disturbances occurring in 474 submarine canyons sediments are known to drive the composition of meiobenthic 475 communities (Aller, 1997; Garcia et al., 2007; Ingels et al; 2009; Levin et al., 2012; 476 Romano et al., 2013).

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478 During the study period, temporal differences in meiofauna density and 479 community composition have been observed mainly in the Blanes Canyon axis, with 480 slope sediments showing much lower meiofaunal variability. Despite the potential bias 481 caused by the reduced number of slope samples in our study, our results are consistent 482 with observations by Romano et al. (2013). In their study, meiofaunal densities at 800 483 and 1600 m depth on the eastern slope reflected a less dynamic environment compared 484 to canyon stations between spring and autumn at those depths. Additionally, in our 485 study, meiofauna densities and composition also differed between sampling years inside 486 the canyon (Table 6). These differences seemed to be related to the observed increase of

487 primary productivity in spring 2013 (Fig. 7A), which occurred on the slope, but was 488 particularly reflected in the canyon sediments, where the sedimentary Chl-a content in 489 2013 was much higher than in 2012. Significant positive correlations between 490 meiofaunal densities and Chl-a support this observation (Table 8). The C:N ratios 491 showed a similar pattern, with increased values in 2013 compared to 2012 (Table 2), 492 which is likely related to greater terrestrial runoff from the rivers in 2013 (Fig. 7B) 493 combined with the resuspension caused by the high waves registered during spring 2013 494 (Fig. 7C). However, the responses of the meiofaunal assemblages were not 495 homogeneous along the studied bathymetric range; likely an indication of other factors 496 that can alter food availability in the canyon-slope sediments and ultimately meiofauna 497 densities and community composition.

498 For instance, the food signals detected in the sediments (in terms of CPE and 499 Chl-a, see Table 2), together with the sand content (Table 2), were highly heterogeneous 500 in the upper canyon region and tended to be higher at BC1200. In this area, canyon 501 flank tributaries (see Lastras et al., 2011) connect the canyon axis with some of the most 502 frequently trawled grounds along the canyon rims (Fig. 1). As previously mentioned, 503 Blanes Canyon and its adjacent open slopes comprise fishing grounds that have been 504 subjected to persistent bottom trawling down to 800 m depth (Company et al., 2008; 505 Sardà et al., 2009; Ramirez-Llodra et al., 2010). The main effort concentrates along the 506 northern open slope from late winter to early summer and over the eastern canyon rim 507 from late summer to mid-winter (Company et al., 2008; Sardà et al., 2009; Ramirez-508 Llodrà et al., 2010). Data from moored sediment trap data in Blanes Canyon, recorded 509 increase in particle fluxes (mostly lithogenic) recorded at 900 and 1200 m depth in the 510 canyon axis (mainly in summer) that was attributed to the formation of sediment 511 resuspension clouds by bottom trawling activities (Lopez-Fernandez et al., 2013). Our 512 results show major differences in sediment composition (coarser) and meiofaunal 513 densities (higher) at BC900 and, particularly, at BC1200 (Table 2; Fig 5A), which 514 interrupts the expected distribution patterns under normal slope conditions. Altogether, 515 these observations indicate the possible presence of an anthropogenic depocenter (i.e. a 516 preferential area of sediment accumulation by trawling) at these depths in the Blanes 517 Canyon axis in a similar way to the ones previously reported in the nearby La Fonera 518 Canyon, Arenys and Besòs submarine canyons (Martín et al., 2008; Puig et al., 2015a,b; 519 Fig. 1). Therefore, we suggest that the processes involved in the formation of 520 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).

528 The relatively low densities detected at BC500, BC900 and BC1200 in the 529 canyon axis in spring 2012 (Fig. 5A), however, seem to correspond to effects of a major 530 (i.e. deep) dense shelf water cascading event at the NW Mediterranean margin in winter 531 2012 (see Durrieu de Madron et al., 2013). Such oceanographic process might have 532 generated strong down-slope currents causing mechanical removing or burying of 533 resident organisms. Consequently, this may lead to massive dispersal, growth inhibition, 534 or even mortality of the meiofaunal component as has been previously reported in the 535 Cap de Creus Canyon during the major deep cascading event in 2005 (Pusceddu et al., 536 2013). After the cascading event, the densities and number of taxa in autumn 2012 were 537 much higher than in the previous spring, and also than those in autumn 2013, as dense 538 shelf water cascading was less intense in 2013 and had almost no impact in Blanes 539 Canyon (Anna Sanchez-Vidal, personal communication).

540 The meiofaunal communities in the deeper areas of the canyon, particularly at 541 BC1500 and BC2000 seemed to be more stable over time (Fig. 5 A) where the effects of 542 the anthropogenic (i.e. trawling) and natural (i.e. cascading) disturbances are likely to be 543 much reduced. Conversely, we could not find a straightforward explanation for the 544 relatively high variability observed at BC1750, highlighting the complexity of the 545 biological, chemical and physical interactions driving the spatial and temporal 546 variability within the meiofaunal assemblages in submarine canyon environments 547 (Ingels et al., 2013; Ramalho et al., 2014).

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550 5.2. Slope v.s Canyon

551 Decreasing meiobenthic densities with increasing water depth has been 552 postulated as a basic principle in deep-sea ecology (e.g., Thiel, 1983; Tietjen, 1992), 553 and has been linked to the bathymetric decrease in organic matter supply (POC flux) 554 and the increasing distance from land (e.g. Soetaert et al., 1991; Danovaro et al., 1995; 555 Gooday et al., 1996; Fabiano and Danovaro, 1999; Soltwedel, 2000; García et al., 2007, 556 García and Thomsen, 2008). However, as previously mentioned, such a depth-density 557 relation may be modified by the presence of submarine canyons owing to their 558 topographical and hydrographic heterogeneity. Canyons induce modifications in the 559 hydrodynamic and biogeochemical processes of channeling organic matter towards the 560 deep basin. Food availability and meiofauna density in canyons are generally higher 561 compared to canyon interfluve areas at similar depths (De Bovée, 1990; Soetaert et al., 562 1991; García and Thomsen, 2008; Koho et al., 2008; Ingels et al., 2009; Gambi and 563 Danovaro, 2016; Amaro et al., 2016; Ingels et al., 2011) and Blanes Canyon is no 564 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.

571 Our results revealed a bathymetric decrease of meiofaunal density at the slope, 572 but not in the canyon (Fig. 4). For instance, in the canyon axis, meiofauna was less 573 abundant at BC900 than at the deeper stations (BC1500, BC1750 and BC2000) in 574 spring 2012, but it was higher in autumn 2013 (Fig. 5A), likely as a result of the 575 combined canyon heterogeneity and the oceanographic and anthropogenic drivers 576 favoring a higher variability along the axis (see section 5.1). It was clear that densities 577 inside the canyon were higher than those at the western slope, and this was particularly 578 evident for the deepest stations (BC1500, BC1750 and BC2000). However, the deep 579 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). 580 581 These results provide further evidence that a heterogeneous canyon environment can 582 lead to meiofaunal assemblages with highly variable distributional patterns in space and 583 time, whilst slope environments tend to be more stable as evidenced by the uniformity 584 of meiofauna density and community structure at the western (present study) and 585 eastern slope (Romano et al., 2013).

586 We observed a decrease in sedimentary food sources (e.g. phytopigments) with 587 increasing depth along the slope; a pattern which agrees with previous findings 588 (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 depthrelated 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).

603 Sediment grain size is known to be a key actor in driving meiofauna 604 distributions (Giere et al., 2009). In the slope, sample sediments tend to be coarser in the 605 shallow parts compared to the deeper parts, and meiofauna showed a strong negative 606 correlation with clay content (Fig. 2). An increase in the fine sediment fractions leads to 607 more compacted sediments, causing a reduction in the interstitial space available for 608 meiofaunal organisms. In the canyon, sand content was positively related with 609 meiofauna density (Table 8). All canyon axis samples (except the shallowest one at 610 BC500) contained coarser sediments than those at the slope presumably caused by the 611 local sedimentological and hydrological conditions and was reflected in the higher 612 meiofauna densities. Grain size trends illustrate the physical dynamism and variable 613 conditions along the axis in the Blanes Canyon, except at BC2000, where the conditions 614 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).

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624 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.

631 Our results confirm that Blanes Canyon compared to its adjacent open slope,
632 exhibits (1) larger sediment properties variability, (2) higher meiofaunal densities, and
633 (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.

639 The temporal variability observed in the canyon meiofauna is only partly explained
640 by the seasonal patterns of food input. Major oceanographic processes such as recurrent
641 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.

	T - 494 J -		Water Depth		Sampling	, intensit	y 998
Station	Latitude	Longitude	(m)	Spring 2012	Autumn 2012	Spring 2013	Au 9999 n 2013
BC500	41°38′66′′N	02°52′75´′E	462-484	2	2	1	1090
BC900	41°34′28′′N	02°50′95´Έ	835-903	2	3	3	1001
BC1200	41°30′93´´N	02°51′07′′E	1194-1258	2	2	3	1002
BC1500	41°27′37′′N	02°52′93′′E	1457-1520	2	3	3	1002
BC1750	41°21′51′′N	02°52′07´Έ	1726-1785	2	3	3	1003
BC2000	41°14′90′′N	02°52′97′′E	1943-1980	2	3	_	1004
OS500	41°19′10′′N	02°46′75´′E	493-509	_	_	3	1007
OS900	41°16′29′′N	02°48′96´Έ	887	_	_	1	1005
OS1500	41°08′28′′N	02°53′75′′E	1451-1480	_	3	3	1006
OS1750	41°06′79´′N	02°57′02´Έ	1731-1751	2	3	3	1007
OS2000	41°02′65´´N	03°01′22′′E	1975-1998	2	3	-	-
							1008

Table 2. Mean ± 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 (phaeopygments) indicating "freshness" of the
phytodetrital OM.

E4 a4 ! am	Sampling	Clay		Silt		Sand		CPE		Chl-a	
Station	period	(%)	SD	(%)	SD	(%)	SD	(µg/g)	SD	(µg/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

1034	Table 2:	continued

	Sampling	Chl-a:	phaeo	OC		TN		C:N	1025
Station	period	(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
									1063

1068 Table 3. Results from univariate and multivariate PERMANOVA two-way 1069 analyses for differences in sedimentary abiotic variables. Test for locations (Lo: 1070 Canyon and Slope); water depth (WD) and interaction term. TN: total nitrogen 1071 concentration; C:N: molar carbon/nitrogen ratio; OC: organic carbon concentration; 1072 Chl-a: chlorophyll a; CPE: chloroplastic pigment equivalents; Chl-a:phaeo: chlorophyll 1073 a: phaeopigments ratio. Data was normalised; resemblance was calculated using 1074 Euclidean Distance. Bold values indicate significant differences at p < 0.05, bold italic 1075 values indicate significant differences at p < 0.01.

	Source	df	Mean g e df		grain TN	C·N	C:N OC		Chl-a	Chl-a:
	bource	ui	size	111	0.11	00	CIL	Cini-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								
1076										
1077										
1078										
1079										
1080										
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1095	Table 4. Univariate and multivariate PERMANOVA two-way analyses for
1096	environmental data in the slope and canyon systems, Test for sampling periods (Tm:
1097	Spring 2012, autumn 2012, spring 2013 and autumn 2013); water depth (WD) and
1098	interaction terms, TN: total nitrogen concentration; C:N: molar carbon/nitrogen ratio;
1099	OC: organic carbon concentration; Chl-a: chlorophyll a; CPE: chloroplastic pigment
1100	equivalents; Chl-a:phaeo: chlorophyll a divided by its degradation products
1101	(phaeopygments) indicating "freshness" of the phytodetrital OM, Data was normalised;
1102	resemblance was calculated using Euclidean Distance, Bold values indicate significant
1103	differences at p < 0.05, bold italic values indicate significant differences at p < 0.01

								1105
Source	df	Mean grain size	TN	OC	C:N	CPE	Chl-a	Chi-a: phateo
Slope								1107
Tm	3	0.1409	0.0146	0.0018	0.0003	0.589	0.0645	b1;0;85
WD	3	0.0149	0.0262	0.0408	0.9999	0.0446	0.0417	P17391
Tm x WD	2	0.1184	0.4582	0.7418	0.5727	0.2603	0.015	0.6779
Res	10							1110
Total	17							1111
Canyon								1112
Tm	3	0.001	0.0001	0.0001	0.0001	0.4549	0.0002	b10b301
WD	5	0.0003	0.0028	0.0006	0.2479	0.0162	0.001	P_0PQ1
Tm x WD	13	0.0844	0.0099	0.1304	0.0938	0.1099	0.3101	0.0001
Res	35							1115
Total	56							1116

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			Communit	У	
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						

1136

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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

1143	p < 0.05, bold itali	c values indicate significant	differences at $p < 0.01$
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Slope		Density			Community		1144
Source	df	P(perm)	perms	ECV	P(perm)	perms	ECV
Time	3	0.2364	9949	0.58963	0.0617	9919	B446 2
WD	2	0.0006	9949	14.902	0.003	9937	P 8 47
Tm x WD	2	0.0602	9959	49.737	0.2846	9933	17.488
Res	10			40.131			1148
Total	17						1149
Canyon		Density			Community		1150
Canyon Source	df	Density P(perm)	perms	ECV	Community P(perm)	perms	1150 ECV
Canyon Source Time	df 3	Density P(perm) 0.0234	perms 9957	ECV 66.955	Community P(perm) 0.0119	perms 9918	1150 ECV 1151 18.466
Canyon Source Time WD	df 3 5	Density P(perm) 0.0234 0.0271	perms 9957 9951	ECV 66.955 609712	Community P(perm) 0.0119 0.0001	perms 9918 9994	1150 ECV 1151 18.466 17.5238
Canyon Source Time WD Tm x WD	df 3 5 13	Density P(perm) 0.0234 0.0271 0.0203	perms 9957 9951 9938	ECV 66.955 609712 18.078	Community P(perm) 0.0119 0.0001 0.0602	perms 9918 9994 9894	1150 ECV 1151 18:466 17:5238 B2:535
Canyon Source Time WD Tm x WD Res	df 3 5 13 33	Density P(perm) 0.0234 0.0271 0.0203	perms 9957 9951 9938	ECV 66.955 609712 18.078 31.739	Community P(perm) 0.0119 0.0001 0.0602	perms 9918 9994 9894	1150 ECV 18:466 77528 B25355 192.63

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1173 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:

1175 number of taxa.

Time	Spring 201	12						
Station	BC500	BC900	BC1200	BC1500	BC1750	BC2000	OS1750	OS2000
Relative abundanc	e (%)							
Amphipoda	-	-	-	-	-	-	-	-
Aplacophora	-	-	-	-	-	-	-	-
Bivalvia	-	-	0.21	0.09	0.15	0.37	-	-
Cnidaria	-	-	-	-	-	-	-	-
Cumacea	-	-	-	-	-	-	-	-
Gastrotrycha	-	-	-	-	0.15	0.09	-	-
Halacaroidea	-	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	-
Kinorrhynca	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	-	-	-	-	-	-	-	-
Tanaidiacea	-	-	-	-	-	-	-	-
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

- 11/2

Time	Autumn 2	012							
Station	BC500	BC900	BC1200	BC1500	BC1750	BC2000	OS1500	OS1750	OS2000
Relative abundanc	e (%)								
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
a	11	14	11	12	11	8	13	12	10

Table 7: *continued*

Station Relative abundance Amphipoda Aplacophora	BC500								
Relative abundance Amphipoda Aplacophora	$\langle 0 \rangle$	BC900	BC1200	BC1500	BC1750	OS500	OS900	OS1500	OS1750
Amphipoda Aplacophora	(%)								
Aplacophora	-	0.02	-	-	-	-	-	-	-
	-	-	-	0.02	-	-	-	-	-
Bivalvia	0.07	0.23	0.12	0.12	0.25	0.16	0.42	0.04	-
Cnidaria	-	-	-	-	-	-	-	-	-
Cumacea	-	-	-	-	0.02	-	-	-	-
Gastrotrycha	-	0.16	0.04	-	-	0.06	0.10	-	1
Halacaroidea	-	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
lsopoda	-	0.05		0.02	0.21	-	-	0.04	-
Kinorrhynca	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	-	-	-	-	-	-	-	-	-
Fanaidiacea	-	0.02	0.04	-	-	0.12	0.31	-	-
Fardigrada	-	0.54	0.04	0.02	0.40	0.36	0.52	0.10	-
<i>Total (ind. 10 cm⁻²)</i>	1289	1387.6	1663.3	1022.7	1069	1027	948	674	501
Std	-	785.1	671.9	335.8	499.1	72	-	117.1	-
5	7	14	13	10	12	12	11	11	8

 Table 7: continued

Table 7: continued

Time	Autumn 2	013				
Station	BC500	BC900	BC1500	BC1750	BC2000	OS1750
Relative abundance	e (%)					
Amphipoda	-	-	-	-	-	-
Aplacophora	-	-	-	-	-	-
Bivalvia	0.22	0.22	0.26	0.17	-	-
Cnidaria	-	-	-	-	-	-
Cumacea	0.07	-	-	-	-	
Gastrotrycha	0.03	0.06	0.03	-	-	-
Halacaroidea	-	-	-	-	-	-
Holoturoidea	-	-	-	-	-	-
Copepoda	4.41	3.99	1.39	2.00	2.01	4.54
Isopoda	0.19	0.04	0.03	0.17	-	-
Kinorrhynca	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
Total (ind. 10 cm ⁻²) 877	1613.3	768	588	748	484
Std	25.5	487.6	195.6	318	9.8	-
S	11	10	10	10	4	5

- 1225 Table 8. Spearman correlation between environmental variables and meiofauna
- 1226 density for canyon and slope systems. Bold values indicate significant differences at p

Environmental	Meiofauna density ¹²²⁸		
variables	Canyon	Slope ¹²²⁹	
CPE	0,438	0,569230	
Chl-a	0,474	0,54 1231	
Chl-a:phaeo	-0,059	0,47#232	
OC	0,367	<i>0,59</i> µ233	
TN	0,013	-0,465 34	
C:N	0,210	$^{0,591}_{1235}$	
Clay	-0,253	-0,600	
Silt	-0,201	0,147	
Sand	0,297	-0,108	
		1238	

< 0.05, bold italic values indicate significant differences at p < 0.01.

Table 9: Comparison of mean meiofaunal densities with depths in different submarine

1260 canyon areas (Iberian and Western Mediterranean coasts).

NW Mediterranean Ca NW Mediterranean Gu	assidaigne	245-810		
NW Mediterranean Gu	-1f -f I : (1)		245-801	Vivier (1978)
	in of Lions (several)	672-2300	36-1005	De Bovée (1990)
NW Mediterranean Gu	ulf of Lions (several)	830-1380	530-1290	Grémare et al. (2002)
NW Mediterranean La	caze-Duthiers	600-1300	836-1050	Danovaro et al. (1999)
NW Mediterranean La	caze-Duthiers	434-1497	205-1391	Bianchelli et al. (2010)
NW Mediterranean Ca	ap de Creus	960-1874	147-597	Bianchelli et al. (2010)
NW Mediterranean Bl	anes	400-1600	25-1500	Romano et al. (2013)
NW Mediterranean Bl	anes	500-2000	209-1763	Present study
Western Bu Mediterranean	ıscarró	600-800	40-123	Rumolo et al. (2015)
Atlantic Ca	ascais	445-2100	492-900	Bianchelli et al. (2010)
Atlantic Na	azaré	332-1121	9.9-236.5	Garcia et al. (2007)
Atlantic Na	azaré	458-897	747-1484	Bianchelli et al. (2010)

1280	CAPTION OF FIGURES
1281	Figure 1. Map of the study area showing the sampling stations and the fishing effort
1282	(hours/km ²). BC: Blanes canyon, OS: Western open slope.
1283	
1284	Figure 2. Bathymetric patterns of each environmental variable selected. Continuous and
1285	dashed lines are the significant regression (p< 0.05) for canyon and slope samples
1286	respectively.
1287	
1288	Figure 3. Principal component analysis (PCA) ordination based on 9 environmental
1289	variables selected. A) Canyon vs slope. B) Canyon.
1290	
1291	Figure 4. Bathymetric scatter plot of meiofaunal densities. Dashed line represent
1292	significant regression (p<0.05) for slope samples.
1293	
1294	Figure 5. Temporal fluctuations of meiofaunal density within the A) Blanes canyon and
1295	B) Slope.
1296	
1297	Figure 6. MDS based on meiofaunal community composition in the Blanes canyon and
1298	at the western slope for each sampling period (based on Bray Curtis similarity values of
1299	four-root transformed data). A) Spring 2012. B) Autumn 2012. C) Spring 2013. D)
1300	Autumn 2013.
1301	
1302	Figure 7. Temporal variation of ancillary data in the study area. A) Chlorophyll-a
1303	concentration /surface productivity. B) Temporal variation of high waves in the study
1304	area. Lines indicate monthly average (blue), monthly max (red) and hourly data (green).
1305	C) Monthly discharge of the Tordera river measured at the gauging nearest station to
1306	river mouth (data from Agència Catalana de l'Aigua, ACA).
1307	
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1314 SUPPLEMENTARY MATERIAL

1315**Table S1.** Results of the two-way PERMANOVA pair-wise test (Factor "Time" with 41316levels (spring, autumn 2012, spring, autumn 2013), factor "WD ": Water Depth, with 61317levels (500, 900, 1200, 1500, 1750 and 2000 m)) for meiofauna density. Data was1318square-root transform and resemblance was calculated using Euclidean Distance prior to1319analysis, Bold values indicate significant differences at p < 0.05, bold italic indicate</td>1320significant at p < 0.01.</td>

1321

1322Table S2. Results from pair-wise multivariate PERMANOVA analyses for1323differences in meiofauna composition. PERMANOVA pair-wise comparisons1324between Time and water depth (WD). Spr: spring; Aut: autumn. Data was fourth-root1325transform and resemblance was calculated using Bray Curtis prior to analysis. Bold1326values indicate significant differences at p < 0.05 and bold italic indicate significant at p</td>1327< 0.01.</td>

1328

1329 Table S3. Distance-based linear model (DISTLM) for meiofauna assemblages and 1330 selected environmental variables for the western open slope. Variables: Selected 1331 environmental variables used to calculate the optimum model. Marginal tests: 1332 explanation of variation for each variable taken separately. Sequential tests: conditional 1333 tests of individual variables in constructing the model. Each test examines whether 1334 adding the variable contributes significantly to the explained variation. Selection 1335 procedure: step-wise, selection criterion: adjusted R². Prop.: % variation explained. 1336 Cumul.: cumulative variation explained. Chl-a: chlorophyll a, CPE: chloroplastic 1337 pigment equivalents, Chl-a:phaeo: chlorophyll a divided by its degradation products 1338 indicating 'freshness' of the phytodetrital OM, TN: total nitrogen content, OC: organic 1339 carbon content, C:N: molar carbon-nitrogen ratio.

1340

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 R². 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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