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1 **Meiofaunal biodiversity in submarine canyons of the Mediterranean Sea: a**
2 **meta-analysis**

3
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22 **Keywords:** Mediterranean Sea, canyons, meiofauna, deep-sea biodiversity, biodiversity hotspots,
23 habitat heterogeneity

24 **ABSTRACT**

25 Deep-sea canyons include highly heterogeneous habitats characterised by a large variability in
26 terms of geomorphological, oceanographic and ecological features. Despite the increasing efforts
27 conducted in the last decade to investigate deep-sea canyon ecology, patterns and drivers of their
28 biodiversity are still controversial. Here, we carried out a meta-analysis of meiofaunal abundance,
29 biomass, richness of higher taxa and taxonomic composition from 18 Mediterranean canyons,
30 located in the Western (Balearic, Catalan, Ligurian margins), Central (South Adriatic margin) and
31 Eastern (Cretan margin) basins. We also compared Mediterranean canyons with 3 canyons located
32 in the European margins of the Northern Atlantic Ocean at similar latitudes. Our results revealed the
33 presence of weak differences in terms of meiofaunal abundance and biomass among canyons and
34 adjacent slopes. However, their biodiversity (expressed as expected richness of higher meiofaunal
35 taxa) was typically similar or higher in canyons than in open slopes. High levels of dissimilarity
36 were also observed between canyons and slopes in terms of taxonomic composition. The variability
37 of meiofaunal assemblages in canyons appear linked to their geomorphological heterogeneity. The
38 results of the meta-analysis also indicate that the most important drivers of the observed patterns
39 were water depth, regional setting (i.e., differences among Mediterranean Western, Central and
40 Eastern sub-basins) and geomorphological characteristics of the canyons. We conclude that deep-
41 sea Mediterranean canyons contribute significantly to the deep-sea biodiversity at both regional and
42 whole-basin scale.

43

44

45 **1. Introduction**

46 **1.1 Deep Mediterranean Sea canyons**

47 The deep sea is the most extensive and remote ecosystem on Earth. The perception of the deep-sea
48 environment has dramatically changed in the last century; it was originally hypothesised as a
49 species-poor system, it is now recognised as one of the most important reservoirs of biodiversity on
50 Earth (Danovaro et al., 2014). An increasing amount of information has also demonstrated that this
51 vast domain contains an extraordinary number of habitats with high spatial complexity, which
52 sustain high levels of biodiversity (Snelgrove and Smith, 2002; Vanreusel et al., 2010; Ramirez-
53 Llodra et al., 2011; Danovaro et al., 2014; Zeppilli et al., 2016). Spatial heterogeneity in the deep
54 sea has been mostly investigated in terms of variations in sediment characteristics and gradients of
55 key environmental variables (including bathymetry, temperature, salinity, organic matter flux,
56 oxygen concentration, hydrodynamism; Levin et al., 2001; Vanreusel et al., 2010; Danovaro et al.,
57 2014; Zeppilli et al., 2016). In this regard, there is now a large consensus that habitat heterogeneity,
58 along with the quantity and quality of food resources, represents a key factor influencing the
59 distribution of deep-sea biodiversity, both at large and small spatial scales (Zeppilli et al., 2016).

60 Even though they are common on most continental margins, submarine canyons were
61 largely ignored until the 1970s. The interest in submarine canyons and related seafloor structures
62 has been driven by economic reasons (i.e. exploration for fossil energy resources, exploitation of
63 ancient deposits, laying cables and pipelines; Würtz, 2012a), particularly in the Mediterranean Sea,
64 where canyons support fisheries of high economic interest (Company et al., 2008; Fernandez-
65 Arcaya et al., 2017). More recently, the availability of innovative technologies (e.g., ROVs, swath
66 bathymetry, side-scan sonar, and definitive position-fixing systems; Canals et al., 2004; 2006;
67 Weaver et al., 2004; Würtz, 2012a) contributed largely to renewed scientific interest on the
68 exchanges between the continental shelf and the deep ocean, and on the biodiversity and
69 functioning of the benthic and pelagic compartments.

70 So far, in the Mediterranean Sea, more than 500 large submarine canyons have been
71 documented (Canals et al., 2004; Weaver et al., 2004; Harris and Whiteway, 2011; Würtz, 2012a).
72 Recent worldwide studies indicate that the Mediterranean canyons are typically different from any
73 other marine region (Harris and Whiteway, 2011), since they are: i) more closely spaced (14.9 km
74 vs 33.0 km on global worldwide average), ii) more dendritic (12.9 limbs vs 4.8 limbs per 100,000
75 km²), iii) shorter (mean length of 26.5 km vs 43.4 km), iv) steeper (mean slope of 6.5° vs 5.1°) and
76 v) smaller in depth range (mean depth: 1613 m vs 1992 m) than canyons occurring in all other
77 oceans.

78

79 **1.2 Biodiversity in Mediterranean deep canyons**

80 Information about the biology of submarine canyon fauna is still scarce and fragmented, but
81 morphologic and oceanographic features are generally assumed to influence faunal characteristics
82 (Ramirez-Llodra et al., 2009; Danovaro et al., 2010). Mediterranean canyons play an important role
83 even in structuring the populations and life cycles of fauna and influence fishery resources
84 (Stefanescu et al., 1994; Sardà et al., 2009), thus providing important ecosystem goods and services
85 (Fernandez-Arcaya et al., 2017). Moreover, unique benthic ecosystems are associated with
86 submarine canyons, particularly in the heads of shelf-incising canyons, characterised by steep
87 bedrock exposures upon which highly diversified communities may occur, as those dominated by
88 cold-water corals (Orejas et al., 2009; Würtz, 2012a; Angeletti et al., 2014; D’Onghia et al., 2017;
89 Taviani et al., 2017). Due to their prominent topographic features, submarine canyons facilitate the
90 shelf-slope exchanges of water and organic-inorganic matter, so that canyons are considered “fast-
91 track corridors” or “super highways” for transported material (Hickey et al., 1997; Monaco et al.,
92 1999; Weaver et al., 2004; Canals et al., 2006; Puig et al., 2008). Canyon-driven upwellings
93 enhance the local primary productivity that increases the amount food resources available to
94 euphausiids, mesopelagic fishes, shrimps and squids, which in turn attracts a variety of top pelagic
95 and benthic-pelagic predators (as tunas, sword fishes, sharks, turtles, birds and cetaceans; Würtz,

2012a). Submarine canyons are important conduits of organic matter and promote pelago-benthic coupling, which provides nourishment to the deep-sea sediments and feeds diversified benthic macro- and megafauna assemblages and bento-nekton species of commercial interest (Garcia et al., 2008; Würtz, 2012a). As a result, the pelagic food chain is extended and intensive pelagic and demersal fisheries are commonly located at the heads of submarine canyons, down to 800 m depth (Hooker et al., 1999; Aïssi et al., 2012; David and Di-Méglio, 2012; Pace et al., 2012).

102

103 **1.3 Aim of the study**

104 Despite the general idea that abundance, biomass and biodiversity of faunal assemblages inside
105 canyons are markedly higher from that on the adjacent open slopes and of the surrounding areas
106 (the so-called “canyon effect”; Vetter and Dayton, 1998; Ramirez-Llodra et al., 2009), available
107 information has provided conflicting results so far, which leave us with the idea that each canyon is
108 a system apart, with specific biological and ecological drivers and features (Grémare et al., 2002;
109 Soltwedel et al., 2005; Garcia et al. 2007; Bianchelli et al., 2010; Ingels et al., 2011a; 2011b; 2013;
110 Romano et al., 2013; Ramalho et al., 2014; Rumolo et al., 2015; Román et al., 2016; Thistle et al.,
111 2017). In this paper, we conducted a meta-analysis of the existing data on meiofaunal assemblages,
112 in terms of abundance, biomass and higher-taxa diversity in the Mediterranean deep canyons and
113 adjacent open slopes at different spatial scales. We used meiofaunal assemblages as a model to
114 perform the meta-analysis, since: i) they dominate multicellular organisms in terms of abundance,
115 iii) their dominance increases also in terms of biomass with increasing water depth, ii) they account
116 for the major fraction of benthic abundance and biomass in all deep-sea ecosystems (Rex et al.,
117 2006; Gambi et al., 2017). Moreover, meiofauna have been widely utilised to investigate large-scale
118 biodiversity patterns and drivers, thus allowing a robust comparison with available literature
119 (Gambi et al., 2014; 2017; Danovaro et al., 2014).

120

121

122 **2. Materials and methods**

123 **2.1 Study area and data collection**

124 The deep Mediterranean Sea is characterized by stable and homoeothermic conditions below 300-
125 500 m, with bottom temperatures of 12.8-13.5 °C in the Western and 13.5-15.5 °C in the Eastern
126 basin (Emig and Geistdoerfer, 2004); differences in primary production and thus in organic matter
127 inputs to the seafloor (15-80 times higher in the Western than in the Eastern Basin; Danovaro et. al,
128 1999; Giordani et al., 2002) and in the benthic trophic state, with an eastward decreasing gradient
129 from mesotrophic/oligotrophic to ultra-oligotrophic conditions (Gambi et al., 2014; Giordani et al.,
130 2002; Pusceddu et al., 2009; 2010). In this study, we analysed data available in the literature on
131 meiofaunal abundance, biomass, richness of taxa and taxonomic composition (Supplementary Table
132 S1), in the Western, Central and Eastern Mediterranean sub-basins. The datasets span from
133 Balearic, Catalan and Ligurian margins in the Western Mediterranean Sea; South Adriatic margin in
134 the Central Mediterranean Sea and Cretan margin in the Eastern Mediterranean Sea. In addition, we
135 conducted a comparison with data available from the Portuguese margin in the North-Eastern
136 Atlantic Ocean. This region was selected as influenced by the deep Mediterranean waters outflow
137 from the Gibraltar strait, thus allowing to explore the impact of the regional setting with respect to
138 the potential connectivity among assemblages Mediterranean Sea and Atlantic Ocean.

139 In particular, we compared environmental, geomorphological, biological and ecological
140 features of 21 canyons (Lacaze-Duthiers, Cap de Creus, Sète, La Fonera, Blanes, Besòs, Foix,
141 Planier, Grand Rhône, Petit Rhône, Aude in the Catalan margin; Balearic and Minorca in the
142 Balearic margin, Calvi and Var in the Ligurian margin, B and C canyon in the South Adriatic
143 margin, Samaria canyon in the Cretan margin, plus Nazaré, Cascais and Setúbal in the Portuguese
144 margin) and 17 adjacent open slopes, at different sampling depths (Figure 1).

145 Overall, 200 samples within canyons and 84 along the open slopes were considered. Details
146 on the utilized datasets are reported in the Supplementary Table S1. We collected data on
147 meiofaunal total abundance and total biomass reported as n. ind 10cm⁻² (or m⁻²) and µg (or g) 10

148 cm^{-2} (or m^{-2}). All data were expressed as n. ind 10cm^{-2} and $\mu\text{g } 10 \text{ cm}^{-2}$, for meiofaunal abundance
149 and biomass, respectively. We addressed here that the data collected for the meta-analysis were
150 published from 1990 to 2016, from different research groups, with different sampling devices, and
151 possibly with different sample sizes/sampling effort. In this regard, these possible bias have to be
152 taken into account.

153 Cumulatively, we compiled an inventory of 284 samples of meiofaunal abundance, 118 of
154 biomass and 192 datasets of richness of higher taxa and 263 of taxonomic composition, obtained
155 from the abovementioned scientific literature and few unpublished data.

156 The unpublished data were obtained from samples collected in the Catalan and Cretan
157 margin, in October 2009 and June 2006, respectively. In the Catalan margin, the samples were
158 collected in the Cap de Creus canyon (at ca. 950, 1860 m water depth), Sete canyon (at ca. 2350 m
159 water depth) and along the southern open slope (at ca. 960 and 1850 m water depth). In the Cretan
160 margin, the samples were collected in the Samaria canyon (at ca. 1250, 2400, 3550, 3600 m water
161 depth), and along the western (at ca. 520, 1080, 1900 m water depth) and eastern open slopes (at ca.
162 210, 590, 1180, 2670 m water depth). Samples were collected at the same sampling stations
163 reported in Pusceddu et al. (2010).

164

165 **2.2 Data analyses**

166 **2.2.1 Meiofaunal abundance, biomass and biodiversity**

167 Differences between basins (NE Atlantic ocean and Mediterranean Sea), among continental margins
168 (Catalan, Balearic, Ligurian, Adriatic and Cretan margins in the Mediterranean Sea), between
169 canyons and adjacent open slopes within each margin, at different water depths in the meiofaunal
170 abundance, biomass and taxonomic composition were analyzed in either the uni- and multivariate
171 contexts, following different sampling designs. First, we used a 2-way sampling design comprising
172 “Basin” (fixed, 2 levels: Atlantic and Mediterranean) and “Depth range” (fixed, 5 levels: 150-500
173 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m), separately for canyons and open

174 slopes. Then, we used a 2-way sampling design comprising Margin-habitat (fixed, 10 levels:
175 Catalan canyon, Catalan slope, Balearic canyon, Balearic slope, Ligurian canyon, Ligurian slope,
176 Adriatic canyon, Adriatic slope, Cretan canyon and Cretan slope, nested in Margin) and “Depth
177 range” (fixed, 5 levels: 150-500 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m). When
178 a significant effect of the factor Depth range was observed, we applied also a 2-way design
179 comprising “Transect” (fixed, 19 levels: Foix, Blanes, Fonera, Cap de Creus, Lacaze-Duthiers, Petit
180 Rhône, Planier, Adriatic B and C, Samaria canyons, Blanes, Cap de Creus, Lacaze-Duthiers, Petit
181 Rhône, Calvi, Adriatic, Cretan Western and Eastern open slopes) and “Depth range” (fixed, 5
182 levels: 150-500 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m) in order to identify in
183 which specific canyon/slope the differences were observed.

184 All the analyses were carried out using the distance-based permutational analysis of variance
185 (PERMANOVA) and the tests were based on Euclidean distance for meiofaunal abundance and
186 biomass after standardization and square root transformation of data, and Bray Curtis similarity
187 matrixes for taxonomic composition, after standardization and fourth-root transformation. Data on
188 taxonomic composition were also tested after presence/absence transformation (Anderson, 2005;
189 McArdle and Anderson, 2001). Since PERMANOVA is sensitive to differences in multivariate
190 dispersion among groups, before the tests, a test of homogeneity of dispersion (PERMDISP) was
191 also performed to test the null hypothesis of equal dispersions among groups.

192 For both uni- and multivariate analyses, when significant effects of the considered factors
193 were observed, pair wise tests were carried out, to ascertain at which water depth range, the
194 significant differences were observed between basins, margins, canyons and slopes.

195 The meiofaunal diversity was assessed in terms of richness of higher taxa. The expected
196 number of taxa (ET) was also calculated (by means of the ES function in PRIMER 6+; Clarke and
197 Gorley, 2006), since it provides a standardization of the richness of taxa values according to the
198 sample size. The ET was calculated at different spatial scales. First, the ET was calculated at the
199 widest spatial scale in the different basins (N Atlantic and Mediterranean Sea) at similar

200 bathymetric ranges. Then the ET was calculated in the different habitats (canyons and open slopes)
201 in all sub-basins at similar bathymetric ranges and then in each transect at similar bathymetric
202 ranges. For each calculation, the meiofaunal assemblages were pooled together from all samples of
203 each bathymetric range in basins, habitats and transects, using the minimum number of individuals
204 retrieved in basins, habitats and transect for the ET calculation.

205 To visualize differences in the meiofaunal taxonomic composition, bi-plots after a Canonical
206 Analysis of Principal Coordinates (CAP) were also prepared (Anderson and Willis, 2003). To
207 assess the percentage dissimilarity (Gray, 2000) in the meiofaunal taxonomic composition,
208 SIMPER tests were also carried out.

209 Uni- and multivariate PERMANOVAs, pair wise, CAP, SIMPER analyses and ET
210 calculation were carried out using the routines included in the software PRIMER 6+ (Clarke and
211 Gorley, 2006).

212

213 **2.2.2 Environmental and geomorphological effect on meiofaunal assemblages**

214 Log-linear relationships between meiofaunal abundance, biomass and richness of taxa and water
215 depth and longitude were also investigated using linear regressions, in order to evaluate the
216 direction and scale of variations. We used a partial regression analysis according to the approach
217 reported by Gambi et al. (2017), in order to separate the effect of water depth and longitude.

218 To determine whether the meiofaunal assemblages are influenced by canyons
219 geomorphological characteristics, we carried out multivariate multiple regression analyses (DistLM
220 forward, McArdle and Anderson, 2001) and produced distance-based Redundancy Analysis (db-
221 RDA) plots. Canyons geomorphological characteristics were obtained from data reported in Harris
222 and Whiteway (2011). For the purpose of this study we used data regarding: class (shelf-incising
223 canyons having/not having heads with a clear bathymetric connection to a major river system, or
224 blind canyons), status (size of tributaries to the main canyon thalweg), top and low heights (depth at
225 which the canyon commences/ends), height difference (difference between top and low heights),

average length and slope, margin type (active or passive margin), parts of the canyon at 1500 m or deeper water depth), dendricity (n. of canyon limbs), dendricity per 100,000 km², sinuosity, spacing (calculated based on the number of canyons within a 370 km circular window) and canyon density per km (Harris and Whiteway, 2011). More in detail, among the worldwide raw data on canyons geomorphological characteristics (reported in the Supplementary material of Harris and Whiteway, 2011), those corresponding to the geographic coordinates of the meiofaunal data used for the meta-analysis, were extracted. Then, the coordinates of geomorphological features and meiofaunal data were reported in GIS. Only the geomorphological data coordinates fitting with the meiofaunal data coordinates were used for the analyses.

DistLM forward, dbRDA analyses were carried out using the routines included in the software PRIMER 6+ (Clarke and Gorley, 2006).

3. Results

3.1 Meiofaunal abundance and biomass: basin, habitat and bathymetric effects

The output of PERMDISP is reported in Supplementary Table S2. The output of PERMANOVA and pair wise analyses, testing for the effect of Basin at different bathymetric ranges on meiofaunal abundance and biomass, in canyons and open slopes, are reported in Supplementary Table S3. Higher values of meiofaunal abundance in N Atlantic Ocean than in Mediterranean Sea were observed below 3000 m water depth for canyons, whereas higher values of biomass were observed below 500 m water depth for canyons and at all the bathymetric ranges for the open slope (Supplementary Table S3).

In the Mediterranean Sea, meiofaunal abundance in canyons was higher than in the open slopes at 150-500 m water depth in the Ligurian margin (more specifically in the Calvi canyon). In all the considered margins, a decreasing pattern of meiofaunal abundance with increasing water depth was observed for both canyons (except for Adriatic, and more specifically along Cap de

251 Creus, Lacaze-Duthiers, Petit Rhône and Samaria canyons) and open slopes (more specifically
252 along slopes adjacent to Blanes, Cap de Creus and Calvi canyons) (Supplementary Table S4).

253 Higher values of meiofaunal biomass were observed in canyons than in open slopes only at
254 500-1000 m water depth in the Adriatic margin. In Catalan and Adriatic margins a decreasing
255 pattern of meiofaunal biomass with increasing water depth was observed for both canyons (more
256 specifically along Cap de Creus and C) and open slopes (along slopes adjacent to Lacaze-Duthiers
257 and Adriatic canyons) (Supplementary Table S4).

258

259 **3.2 Meiofaunal richness of taxa and taxonomic composition: basin, habitat and bathymetric** 260 **effects**

261 The richness of higher taxa, the number of total individuals and the number of individuals used for
262 ET calculation are reported in the Supplementary Table S5. Similar values of expected richness of
263 meiofaunal taxa in Mediterranean than in N Atlantic Ocean were observed for canyons and slopes
264 at all the bathymetric ranges (Supplementary Table S5).

265 The output of PERMANOVA and pair wise analyses, testing for the effect of Basin at
266 different bathymetric ranges on meiofaunal taxonomic composition, in canyons and open slopes, is
267 reported in Supplementary Table S3. Significant differences in the taxonomic composition between
268 N Atlantic Ocean and Mediterranean Sea canyons were observed between 1000 and 3000 m or
269 below 2000 m water depth when data were presence/absence transformed, whereas no differences
270 were observed for open slopes (Supplementary Table S3, Figure 2). The percentage dissimilarity in
271 the taxonomic composition (Table 1) between N Atlantic and Mediterranean ranged from 87 to 98%
272 in canyons and from 82 to 99% in open slopes. When data are presence/absence transformed, the
273 percentage dissimilarity ranged from 41 to 64% in canyons and from 41 to 62% in open slopes. The
274 percentage dissimilarity increased with increasing bathymetric range in both canyons and open
275 slopes (Table 1).

276 In the Mediterranean Sea, over a total of 16 available comparisons between canyons and
277 adjacent open slopes at the same depth range, the expected richness of taxa was higher in the
278 canyons than in the adjacent open slopes in 5 cases, was the same in 8 cases and in 3 cases was
279 higher in the adjacent open slope than in the canyon (Supplementary Table S5). The cumulative
280 expected richness of taxa reported within each margin was higher in canyons than in the open
281 slopes at similar depth ranges except for Ligurian and Cretan margins, where the richness of taxa
282 was higher in slopes (Supplementary Table S5).

283 In the Mediterranean Sea, differences between canyons and open slopes in the meiofaunal
284 taxonomic composition were observed at 150-500 m (in Ligurian margin, Calvi canyon) and 1000-
285 2000 m (in Catalan margin, Cap de Creus and Blanes canyons). Significant differences were also
286 observed among bathymetric ranges along canyons and slopes in Catalan (along Blanes, Lacaze-
287 Duthiers and Petit-Rhône canyons, and open slopes adjacent to Cap de Creus). When data were
288 presence/absence transformed, significant differences were also observed Calvi slope.
289 (Supplementary Table S4).

290 In the Mediterranean Sea, the overall percentage dissimilarity between canyons and adjacent
291 slopes was 34-45% (at 500-1000 and 2000-3000 m water depth, respectively) and 25-46% when
292 data were presence/absence transformed (2000-3000 and 150-500 m, respectively). The highest
293 dissimilarity between canyons and adjacent slopes was observed in the Catalan margin (Table 1). In
294 all margins, the dissimilarity was highest when the data were presence/absence transformed (except
295 for Adriatic at 500-1000 m and Cretan at 2000-3000 m water depth).

296

297 **3.3 Environmental drivers of meiofaunal assemblages in N Atlantic and Mediterranean deep** 298 **canyons**

299 Meiofaunal abundance, biomass and richness of taxa showed a significant negative log-linear
300 relationship with the water depth in the Mediterranean Sea canyons and open slopes (Figure 3;
301 Table 2). Conversely, no significant relationships were observed in the N Atlantic canyons and open

slopes (Figure 3; Table 2). Meiofaunal abundance, biomass and richness of taxa showed a significant negative log-linear relationship with increasing longitude in the Mediterranean Sea canyons and open slopes (Figure 4; Table 2).

The results of the multivariate multiple regression analyses (DistLM forward) conducted on the variance of the meiofaunal abundance, biomass, expected richness of taxa and taxonomic composition in canyons are reported in Table 3. Canyons geomorphological characteristics significantly explained the variance of meiofaunal assemblages, cumulatively accounting for ca. 42% for the abundance, 50% for the biomass and 40% taxonomic composition (also after presence/absence transformation) and more than 56% for the richness of taxa.

dbRDA analyses indicate that the geomorphological characteristics explained, cumulatively for the first 2 axis, 39% of the variance in the meiofaunal taxonomic composition and 35% when the data are presence/absence transformed (Figure 5).

4. Discussion

4.1 Meiofaunal assemblages and biodiversity in deep Mediterranean canyons

Habitat heterogeneity has been suggested as one of the key factors influencing the structure and biodiversity of deep-sea benthic communities, including meiofaunal assemblages (Gage and Tyler, 1991; Etter and Grassle, 1992; Lambshead et al., 1995; Galéron et al., 2000; Soltwedel, 2000; Levin et al., 2001; Baguley et al., 2006). The results of our meta-analysis indicate weak differences in meiofaunal abundance and biomass between canyons and slopes at all depth ranges in each investigated Mediterranean continental margin. This reflects the results of previous studies conducted on datasets limited to specific canyons/margins, which reports controversial patterns (Bianchelli et al., 2010; Romano et al., 2013). Moreover, our data report similar or even higher values of expected richness of taxa in canyons than in the adjacent slopes in most cases and at all depth ranges, confirming that habitat diversification (the alternation of canyons and open slopes

327 along continental margins) allows diversified assemblages, increasing the overall diversity at
328 regional and basin scale (Bianchelli et al., 2010; Zeppilli et al., 2016).

329 In this regard, we also observed similar expected richness of taxa in Mediterranean Sea and
330 in the NE Atlantic margins at all bathymetric ranges, both in canyons and open slopes, confirming
331 that the deep Mediterranean Sea is not biodiversity depleted (Bianchelli et al., 2010; Coll et al.,
332 2010; Danovaro et al., 2010). The Mediterranean Sea, indeed, is recognized as hot spot of
333 biodiversity, with a highly heterogeneous distribution of taxonomic groups in the different regions,
334 comprising meiobenthic assemblages in deep-sea habitats (Coll et al., 2010).

335 The meta-analysis conducted on the meiofaunal taxonomic composition revealed high
336 dissimilarity levels in the meiofaunal assemblages between canyons and open slopes in the
337 Mediterranean Sea, with % dissimilarity even higher when data were presence/absence transformed.
338 These results suggest that in Mediterranean canyons specific faunal assemblages may be
339 preferentially observed, and this is true not only for macro- and mega- (e.g., benthic megafauna,
340 corals, crustaceans, fishes, mammals, Öztürk et al., 2012; Vella and Vella, 2012; Watremez, 2012;
341 David and Di-Méglio, 2012; Madurell et al., 2012; Company et al., 2012; Baro et al., 2012), but
342 also for meiofauna. This specificity in assemblages occurrence in the Mediterranean canyons is also
343 confirmed by the high levels of dissimilarity of meiofaunal taxonomic composition between NE
344 Atlantic and Mediterranean canyons. Such differences increase at increasing water depth. Overall,
345 these results suggest that sea floor heterogeneity allows diversified assemblages across different
346 habitats and margins, increasing the overall diversity at regional and basin scale.

347 The specific features of canyon fauna has been previously reported from several
348 Mediterranean margins, in particular on canyons off the Alboran, Catalan, Malta, and Turkey coasts
349 (Öztürk et al., 2012; Vella and Vella, 2012; Watremez, 2012; David and Di-Méglio, 2012; Madurell
350 et al., 2012; Company et al., 2012; Baro et al., 2012). In the Mediterranean sea, one of the most
351 relevant aspects is the relationship between the number of species, the number of individuals of
352 endemic species and the ecological features of submarine canyons (Palanques et al., 2005). Indeed,

no individual canyon is identical to another, and this is reflected by differences in fauna between canyons even located along the same continental margin, also for meiofaunal assemblages (Hecker, 1990; Rogers et al., 2002). Regarding the habitat heterogeneity, the most complex Mediterranean region is the Catalan margin, one of the areas of the world oceans with the higher canyon density per 100 km (Würtz, 2012b). In this region, it has been demonstrated an isolation effect related to peculiar hydrodynamic processes, canyon morphology and ecological differences, which has led to high faunal diversification and even speciation processes, particularly for Foix, Lacaze-Duthiers, La Fonera (Palamòs) and Planier canyons (Gili et al., 1999; Palanques et al., 2005; Würtz, 2012b).

361

4.2 Patterns and environmental drivers of meiofaunal assemblages in deep Mediterranean canyons and slopes

The regression analyses revealed that meiofaunal abundance, biomass and richness of taxa display a significant negative relationship with water depth in both Mediterranean canyons and slopes, whereas no significant relationships were observed in the NE Atlantic margin. We report here that the decline of meiofaunal biomass with increasing water depth is more evident in open slopes than in canyons, suggesting that the environmental constraints related to water depth (e.g., increasing pressure, decrease of food supply with the increasing water depth) may have a different effect depending on the deep-sea habitat considered. Moreover, the decline of meiofaunal biomass with increasing water depth is more evident than the decline of abundance only in open slopes, suggesting that environmental (or even trophic or anthropogenic) constraints acting inside canyons (as example, massive and pulsing food supply, deep currents and tides characteristics) can determine a shift of the size of individuals, leading to a differential miniaturization at greatest depths in canyons and in open slopes (Pusceddu et al., 2013; 2014; Gambi et al., 2017).

At basin scale, our results indicate that meiofaunal assemblages were characterised also by significant differences among the investigated deep Mediterranean regions. Indeed, at basin spatial scale, meiofaunal abundance, biomass and richness of taxa displayed clear decreasing patterns from

379 Western to Eastern deep Mediterranean sea. This gradient in meiofaunal variables has been
380 repeatedly observed in the deep Mediterranean basin (Danovaro et al., 2008; Gambi and Danovaro,
381 2006; Gambi et al., 2014) and reflects the differences in the trophic conditions already observed in
382 previous studies, also in the deep sea sediments (Danovaro et al., 1999; Gambi and Danovaro, 2006;
383 Bianchelli et al., 2010; Pusceddu et al., 2010). Here, the decreasing patterns of meiofaunal
384 abundance, biomass and richness of taxa from Western to Eastern Mediterranean Sea has been
385 observed both for canyons and open slopes, suggesting that, at basin scale, one of the main drivers
386 for deep-sea benthic assemblages variables is the trophic status of the region, whatever the
387 considered habitat (Bianchelli et al., 2010; Pusceddu et al., 2010).

388

389 **4.3 Influence of canyons geomorphological characteristics on meiofaunal assemblages**

390 The multivariate multiple regression analysis showed that in canyon systems, their
391 geomorphological characteristics are responsible for the observed variability among such complex
392 and peculiar habitats. During the last decade the intense exploration of the deep ocean, along with
393 the refinement of the available technologies has revealed the presence of a wide variety of different
394 geomorphological features of the submarine canyons, resulting in a wide variety of topographic
395 structures also at small spatial scales (i.e., within each canyon). In this regard, due to their high
396 spatial and temporal variability in their morphological, hydrographic and sedimentological
397 characteristics, canyons have been recently recognized as extreme environments (Zeppilli et al.,
398 2018), since they comprise complex, highly heterogeneous environments that encompasses a
399 patchwork of environmental and trophic conditions with different degrees of stability (Tyler et al.
400 2009; Amaro et al. 2016).

401 Faunas inhabiting such complex environments are thus influenced by multiple factors,
402 which include hydrodynamic conditions and current regimes, topography and habitat heterogeneity,
403 amount, origin and quality of sedimentary organic matter, sedimentation processes and turbidity
404 events and anthropogenic impacts (Danovaro et al., 1999; Baguley et al., 2006; Ingels et al., 2009;

2011a; b; 2013; Pusceddu et al., 2014; Ramalho et al., 2014; Amaro et al., 2016; Román et al., 2016; Thistle et al., 2017). Among the investigated drivers, previous studies revealed the strong influence of trophic resources in shaping meiobenthic assemblages in deep-sea canyons (Soltwedel et al., 2005; Ingels et al., 2011a; b; 2013) and indicated that up to the 30% of the variability in assemblages traits was explained by environmental variables, including the amount and nutritional quality of sedimentary organic matter (Bianchelli et al., 2010; Román et al., 2016).

The results of the present study indicate that ca. 40% of the variability in the meiofaunal taxonomic composition was explained by the geomorphological characteristics of canyons. In particular, beside the water depth, the characteristics more influencing the meiofaunal taxonomic composition are class (shelf-incising with correlation - or not - to river systems or blind canyons), density (number of canyons in the same area) and status (thalweg or tributary systems) of the canyons. Conversely, other characteristics (such as sinuosity, top and low height), even having a significant effect, explained lower % of the taxonomic composition variability. Even more in details, different geomorphological characteristic are responsible for the presence/absence of the taxa, whereas others are responsible for their composition. Overall, our data suggest that the complex combination of geomorphological characteristics is responsible for high % of the taxonomic composition variability but also suggest that most of the variance depends on variables not considered in the present study (supposedly, sediment features and trophic resources; Soltwedel et al., 2005; Bianchelli et al., 2010; Ingels et al., 2011a; b; 2013; Román et al., 2016).

The role of the seafloor heterogeneity in shaping meiobenthic assemblages has also been observed for other deep seabed morphologies, which are inhabited by different meiofaunal assemblages in term of taxonomic composition and may influence faunal distribution more than other factors as trophic resources (Zeppilli et al., 2016).

Deep-sea canyons have been repeatedly proposed as biodiversity hotspots (Vetter and Dayton, 1998; Curdia et al., 2004; Ingels et al., 2009; Bianchelli et al., 2010; Amaro et al., 2016; Román et al., 2016). Data presented here indicate that this is particularly true for the Mediterranean

431 Sea, where canyons are typically different from any other marine region worldwide from a
432 geomorphological point of view (Harris and Whiteway, 2011). Our meta-analysis also demonstrates
433 that deep-sea Mediterranean canyons contribute significantly to enhance the deep-sea biodiversity
434 at both regional and whole-basin scale thus representing crucially important deep-sea habitats
435 deserving appropriate protection.

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767 **Caption of figures**

768 **Figure 1.** Location of the sampling sites in the deep Mediterranean Sea and Portuguese margin (NE
769 Atlantic Ocean) canyons and open slopes.

770 **Figure 2.** CAP analysis output reporting the taxonomic composition of meiofaunal assemblages at
771 different bathymetric ranges in NE Atlantic ocean vs Mediterranean canyons (A) and opens
772 slopes (B), and in canyons vs open slopes in the Mediterranean Sea (C).

773 **Figure 3.** Regression analyses of meiofaunal abundance (A), biomass (B) and richness of higher
774 taxa (C) against depth in Mediterranean and NE Atlantic canyons and open slopes. Only
775 significant regressions are indicated.

776 **Figure 4.** Regression analyses of meiofaunal abundance (A), biomass (B) and richness of higher
777 taxa (C) against longitude in Mediterranean canyons and open slopes. Significant regressions
778 are indicated.

779 **Figure 5.** dbRDA ordination after DistLM forward analysis, describing the relationship between the
780 canyons geomorphological characteristics and meiofaunal taxonomic composition (A), also
781 after presence/absence transformation (B) .

782

783 **Table 1.** Dissimilarity % in the meiofaunal taxonomic composition, also after presence/absence
784 transformation, among basins and between canyons and open slopes in investigated Mediterranean
785 continental margin.

786

		Bathymetric range (m)	% dissimilarity	% dissimilarity (presence/absence)
N Atlantic vs Mediterranean	canyon	150-500	88.9	40.8
		500-1000	86.6	38.7
		1000-2000	91.8	43.6
		2000-3000	89.2	42.7
		3000-4000	97.8	64.4
	open slope	150-500	82.1	41.11
		500-1000	86.9	48.38
		1000-2000	89.9	43.86
		2000-3000	99.6	62.39
	Mediterranean canyon vs slope	Catalan	150-500	34.5
			500-1000	33.1
			1000-2000	32.8
		Ligurian	150-500	28.4
		Adriatic	150-500	25.5
			500-1000	26.7
		Cretan	1000-2000	28.9
			2000-3000	15.8
Mediterranean canyon vs slope (avg % dissimilarity)		150-500	38.2	46.02
		500-1000	34.2	42.56
		1000-2000	34.8	41.81
		2000-3000	45.8	25.08

787

788

789 **Table 2.** Regression analyses of meiofaunal abundance, biomass and richness of higher taxa against
790 depth and longitude. $P < 0.001 = ***$, $P < 0.01 = **$, $P < 0.05 = *$, ns = not significant.

791

	Regression	Equation	n	R ²	P-value
Against depth	Log10 abundance (ind. cm⁻²)				
	Mediterranean canyons	$y = -2.0E-04x + 3.1$	175	0.0938	***
	Mediterranean open slopes	$y = -1.0E-04x + 3.0$	70	0.0718	*
	Atlantic canyons	$y = 1.0E-05x + 2.8$	25	0.0018	ns
	Atlantic open slopes	$y = 3.0E-05x + 2.6$	14	0.0201	ns
	Log10 biomass (µgC 10cm⁻²)				
	Mediterranean canyons	$y = -2.0E-04x + 2.0$	60	0.0955	*
	Mediterranean open slopes	$y = 4.0E-04x + 2.3$	37	0.358	***
	Atlantic canyons	$y = -7.0E-06x + 2.4$	10	0.0032	ns
	Atlantic open slopes	$y = -2.0E-05x + 2.6$	11	0.0143	ns
	Log10 Richness of taxa (n. taxa)				
	Mediterranean canyons	$y = -1.0E-04x + 1.1$	117	0.1304	***
	Mediterranean open slopes	$y = -1.0E-04x + 1.2$	50	0.1416	**
	Atlantic canyons	$y = 1.4E-03x + 1.0$	14	0.0002	ns
	Atlantic open slopes	$y = -5.0E-06x + 1.0$	11	0.0093	ns
Against longitude	Log10 abundance (ind. cm⁻²)				
	Mediterranean canyons	$y = -2.2E-02x + 3.0$	175	0.0567	***
	Mediterranean open slopes	$y = -3.9E-02x + 3.2$	70	0.4342	**
	Log10 biomass (µgC 10cm⁻²)				
	Mediterranean canyons	$y = -2.6E-02x + 1.8$	60	0.1515	**
	Mediterranean open slopes	$y = -3.9E-02x + 2.0$	37	0.4738	***
	Log10 Richness of taxa (n. taxa)				
	Mediterranean canyons	$y = -7.6E-03x + 0.9$	117	0.0326	*
	Mediterranean open slopes	$y = -1.6E-02x + 1.1$	50	0.3733	***

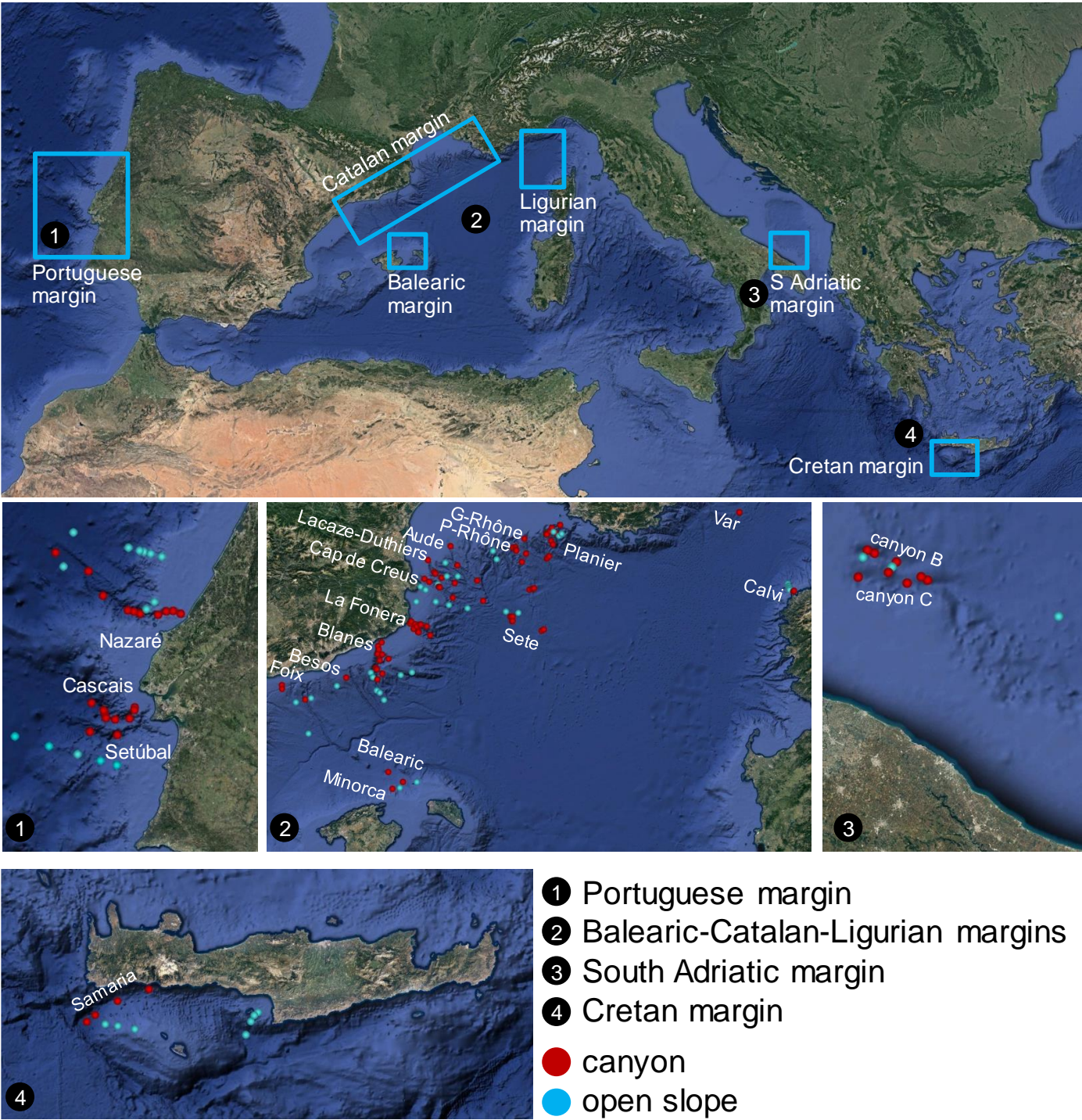
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794 **Table 3.** Output of DISTLM forward analyses, testing for geomorphological characteristics of the
795 N Atlantic and Mediterranean Sea canyons. $P < 0.001 = ***$, $P < 0.01 = **$, $P < 0.05 = *$, ns = not
796 significant.

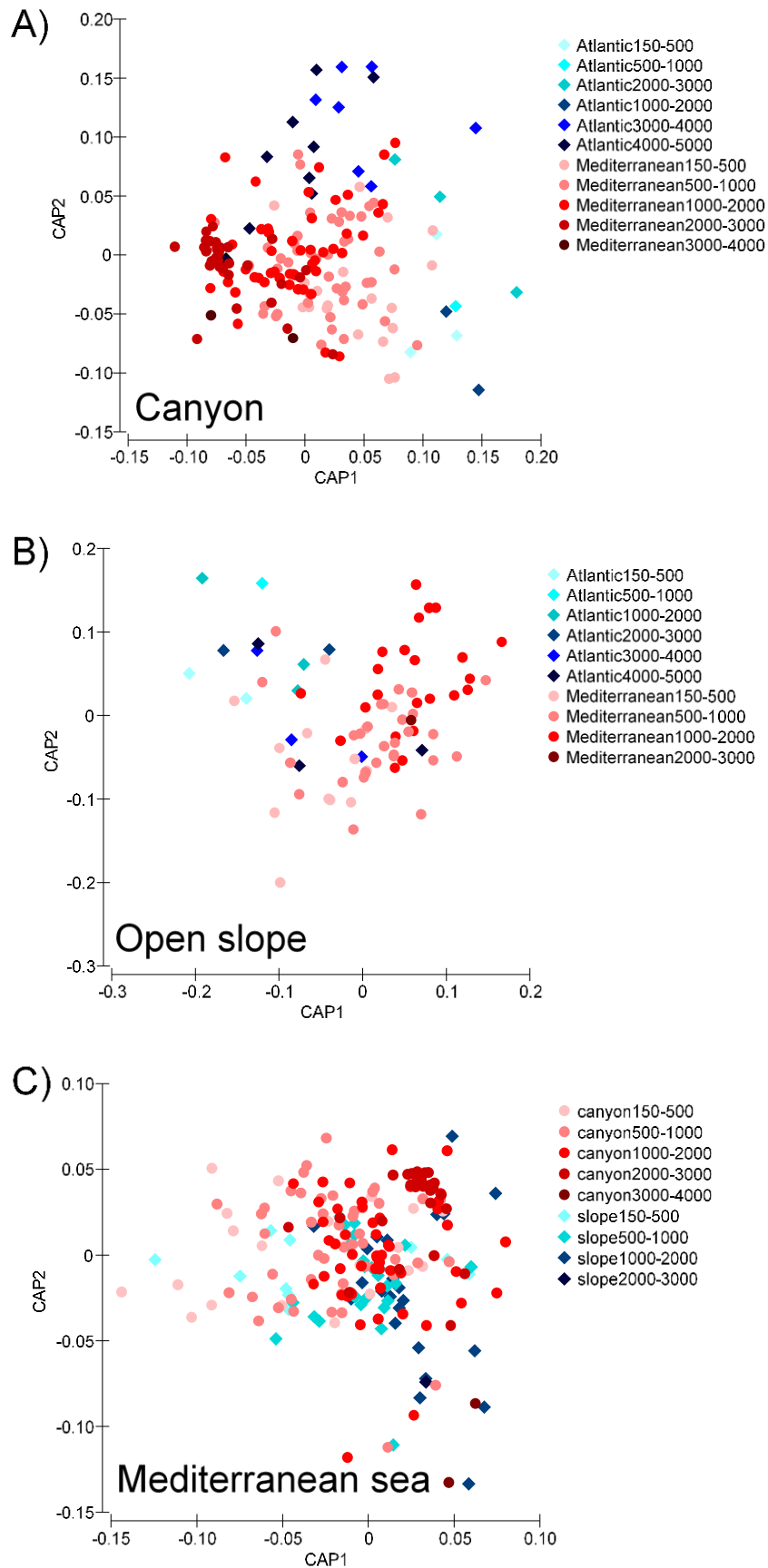
A)	Variable	F	P	% Prop explained variance	B)	Variable	F	P	% Prop explained variance
Abundance	class	20.6	***	12.7	Richness of taxa	class	25.8	***	18.2
	depth	17.8	***	9.2		height dif	20.6	***	12.4
	sinuosity	10.4	**	6.0		depth	10.3	**	5.8
	height dif	9.3	***	4.5		top height	8.0	*	4.0
	length	9.1	***	4.0		canyon density	9.4	*	3.8
	slope	5.1	**	2.4		sinuosity	7.6	**	3.6
	status	4.4	*	1.9		length	6.6	**	3.5
	top height	3.9	*	1.8		status	6.1	*	2.7
	margin type	2.4	ns	1.0		slope	4.8	*	2.1
	parts at 1500m	1.8	ns	0.7		margin type	0.7	ns	0.3
	density	1.1	ns	0.5	Taxonomic composition (presence/absence)	class	20.4	***	13.3
	dendricity per 100k km ⁻²	0.9	ns	0.4		density	18.1	***	10.5
Biomass	class	18.0	***	11.4		sinuosity	5.5	***	3.1
	status	8.8	***	5.9		margin type	5.5	**	2.7
	density	8.3	***	5.6		canyon density	5.0	**	2.4
	canyon density	5.9	***	4.1		depth	4.4	**	2.4
	margin type	5.2	***	3.6		top height	4.2	**	2.2
	parts at 1500m	4.3	**	3.0		slope	3.4	*	1.8
	height dif	3.8	**	2.6		dendricity per 100k km-2	3.3	*	1.7
	slope	3.8	**	2.6		status	2.3	ns	1.1
	top height	3.8	**	2.6		length	2.3	ns	1.1
	dendricity per 100k km-2	3.2	**	2.2		height dif	2.0	ns	0.9
	dendricity	3.2	**	2.2	Taxonomic composition	depth	32.8	***	17.0
	sinuosity	3.1	*	2.2		status	11.8	***	8.1
	low height	3.0	**	2.1		margin type	10.8	***	6.9
	length	1.9	ns	1.3		low height	5.9	**	2.9
	depth	1.8	ns	1.3		class	5.1	**	2.5
						height dif	5.1	**	2.4
						slope	2.0	ns	1.0
						parts at 1500m	1.8	ns	0.8
						density	1.6	ns	0.8
						dendricity	1.6	ns	0.7
						canyon density	1.1	ns	0.5
						dendricity per 100k km-2	0.3	ns	0.1

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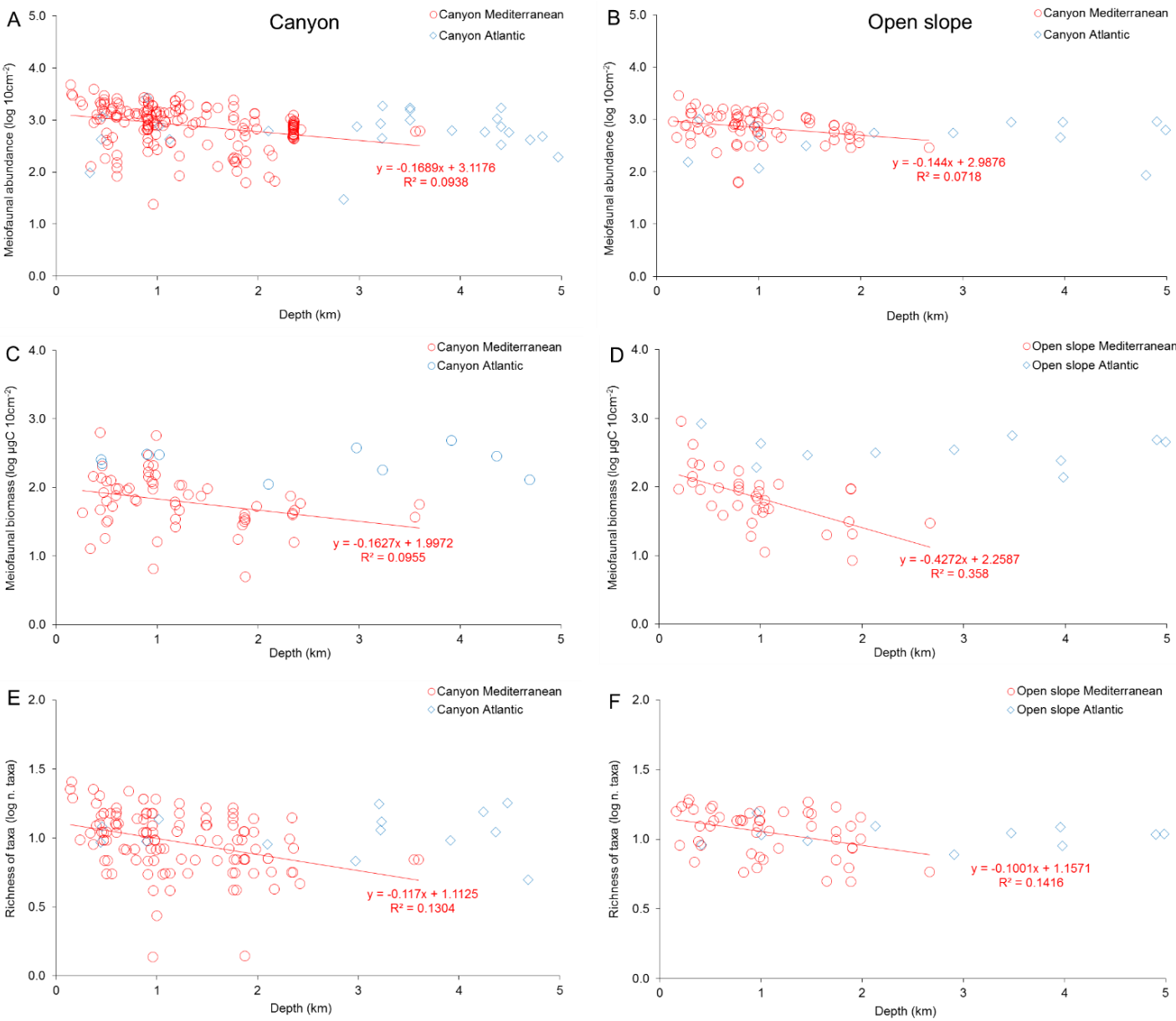
Figure 1.



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809 **Figure 2.**

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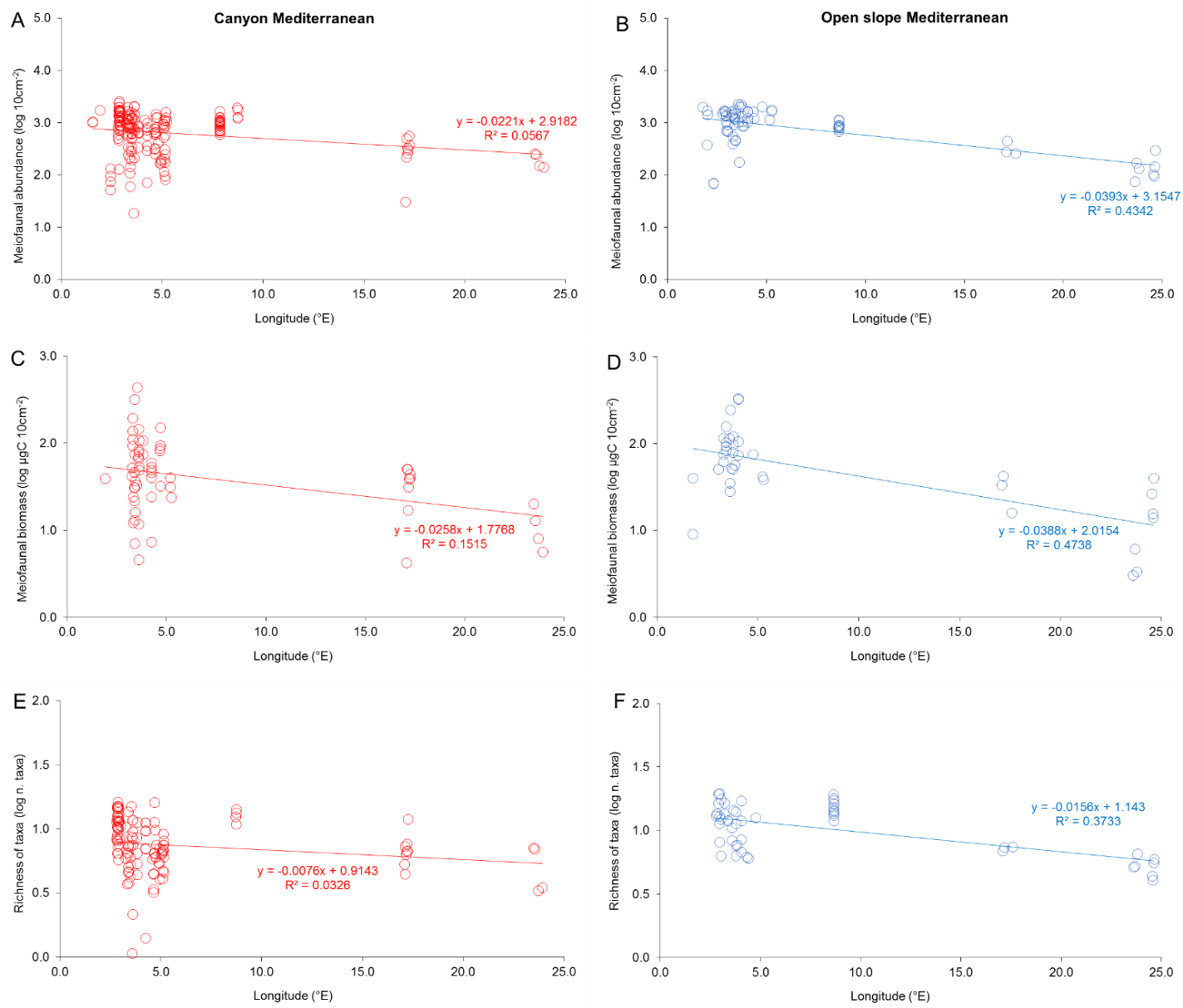
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813 **Figure 3.**

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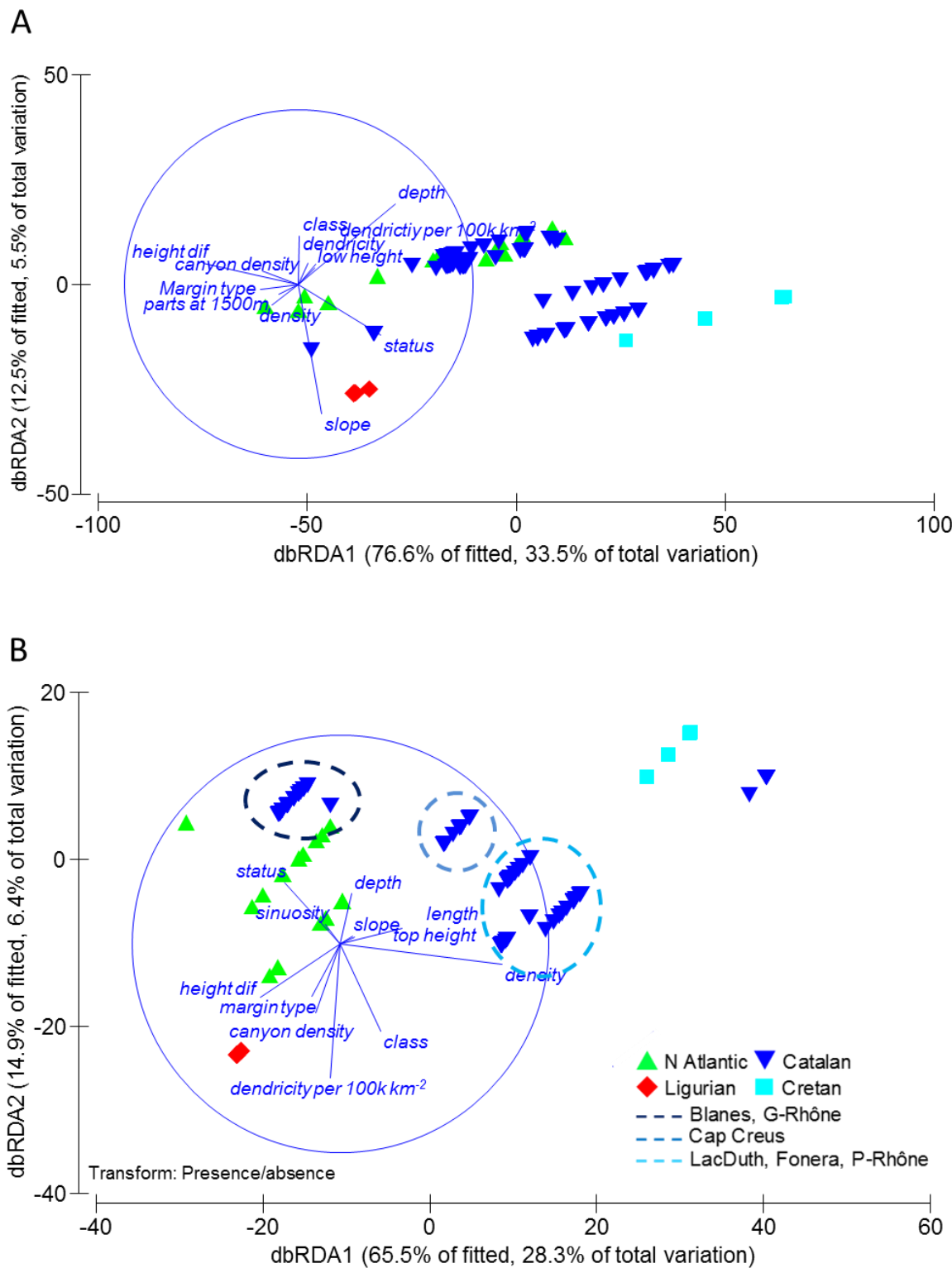
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818 **Figure 4.**

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824 **Figure 5.**

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827 **Supplementary Table S1.** Datasets utilized in the present study. Indicated are also the number of samples (n) analyzed within canyons and open
828 slopes in each dataset.

829

Reference	Total meiofaunal abundance		Total meiofaunal biomass		N. taxa		Taxonomic composition		Sampling device	Investigated margins
	n samples canyon	n samples slope	n samples canyon	n samples slope	n samples canyon	n samples slope	n samples canyon	n samples slope		
Accornero et al. (2003)	4	7	4	7	-	-	4	7	multiple-corer	Catalan
Bianchelli et al. (2010)	25	19	25	19	25	19	25	19	multiple-corer and box corer	Portuguese, Catalan, S Adriatic
Danovaro et al. (1999)	8	4	-	-	-	-	-	-	multiple-corer	Catalan, Balearic
de Bovée et al. (1990)	27	-	-	-	27	-	27	-		Catalan
Garcia et al. (2007)	5	3	-	-	-	-	5	3	multiple-corer	Portuguese
Grémare et al. (2002)	4	3	-	-	4	3	4	3	multiple-corer	Catalan
Guidi-Guilvard and Dallot (2014)	25	-	-	-	-	-	25	-	multiple-corer and maxicorer	Ligurian
Ingels et al. (2011a)	4	-	-	-	4	-	4	-	megacorer	Portuguese
Pusceddu et al. (2013)	13	6	13	6	13	6	13	6	multiple-corer and box corer	Catalan
Pusceddu et al. (2014)	13	-	13	-	13	-	13	-	multiple-corer	Catalan
Ramalho et al. (2014)	6	-	-	-	-	-	6	-	multiple-corer and megacorer	Portuguese
Riuax-Gobin et al. (2004)	8	7	8	7	-	-	8	7	multiple-corer	Catalan
Román et al. (2016)	22	10	-	-	22	10	22	10	multiple-corer	Catalan
Romano et al. (2013)	12	4	-	-	12	4	12	4	multiple-corer	Catalan
Rumolo et al. (2015)	4	2	-	-	-	-	4	2	multiple-corer	Catalan
Soetaert et al. (1991)	4	10	-	-	4	10	4	10	box corer	Ligurian
Soyer et al. (1987)	9	-	-	-	-	-	-	-	box corer	Catalan
This paper	7	9	7	9	7	9	7	9	box corer	Catalan, Cretan
N. samples tot	200	84	70	48	131	61	183	80		

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831

832 **Supplementary Table S2.** Results of PERMDISP conducted on meiofaunal abundance, biomass and taxonomic composition, testing for the
833 multivariate dispersion among groups (basins or habitats). When the PERMDISP output reports a significant P level, only the pair wise useful for
834 testing the hypothesis were reported.

835

			PERMDISP output	P	pair wise	P
Meiofaunal abundance	Atlantic vs Mediterranean	Canyons	F: 0.19259 df1: 1 df2: 198	0.658		
		Open slopes	F: 0.37599 df1: 1 df2: 82	0.559		
	Mediterranean	Canyon vs Open slope	F: 4.0642 df1: 9 df2: 235	0.001	Adriatic canyon vs Adriatic slope	0.603
					Catalan canyon vs Catalan slope	0.065
					Ligurian canyon vs Ligurian slope	0.309
					Cretan canyon vs Cretan slope	0.144
Meiofaunal biomass	Atlantic vs Mediterranean	Canyons	F: 1.0152 df1: 1 df2: 68	0.385		
		Open slopes	F: 2.6755 df1: 1 df2: 46	0.129		
	Mediterranean	Canyon vs Open slope	F: 2.0784 df1: 3 df2: 93	0.203		
Taxonomic composition (presence/absence)	Atlantic vs Mediterranean	Canyons	F: 0.26375 df1: 1 df2: 181	0.645		
		Open slopes	F: 2.4057 df1: 1 df2: 78	0.18		
	Mediterranean	Canyon vs Open slope	F: 9.8702 df1: 9 df2: 214	0.001	Adriatic canyon vs Adriatic slope	0.602
					Catalan canyon vs Catalan slope	0.134
					Ligurian canyon vs Ligurian slope	0.566
					Cretan canyon vs Cretan slope	0.023
Taxonomic composition	Atlantic vs Mediterranean	Canyons	F: 0.95016 df1: 1 df2: 181	0.406		
		Open slopes	F: 6.0921 df1: 1 df2: 78	0.055		
	Mediterranean (fourth-root transformation)	Canyon vs Open slope	F: 8.9218 df1: 9 df2: 214	0.001	Adriatic canyon vs Adriatic slope	0.646
					Catalan canyon vs Catalan slope	0.228
					Ligurian canyon vs Ligurian slope	0.608
					Cretan canyon vs Cretan slope	0.002

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840 **Supplementary Table S3.** Results of PERMANOVA and pair wise comparisons, testing for differences between basins at different bathymetric
841 ranges in canyons and adjacent opens slopes in A) meiofaunal abundance, B) biomass, C) taxonomic composition and D) composition after
842 presence/absence transformation. * = P<0.05; ** = P<0.01; *** = P<0.001; ns = not significant; na = not available, Atl = N Atlantic, Med =
843 Mediterranean Sea.

N Atlantic vs Mediterranean Sea		Source	df	MS	F	P	Bathymetric range				
							150-500m	500-1000m	1000-2000m	2000-3000m	3000-4000m
A) Abundance	Canyon	Basin	1	0.1	1.5	ns	na	ns	ns	ns	Atl > Med
		Bathymetric range	5	0.2	3.6	**					
		Basin X Bathymetric	3	0.2	2.7	*					
		Residuals	190	0.1							
	Open slope	Basin	1	0.1	0.8	ns	ns	ns	ns	ns	na
		Bathymetric range	5	0.1	1.0	ns					
		Basin X Bathymetric	3	0.3	2.1	ns					
		Residuals	74	0.1							
B) Biomass	Canyon	Basin	1	8.6	38.8	***	ns	Atl > Med	Atl > Med	Atl > Med	Atl > Med
		Bathymetric range	5	1.0	4.3	**					
		Basin X Bathymetric	4	0.1	0.3	ns					
		Residuals	59	0.2							
	Open slope	Basin	1	13.9	92.4	***	Atl > Med	Atl > Med	Atl > Med	Atl > Med	na
		Bathymetric range	5	1.0	6.9	***					
		Basin X Bathymetric	3	0.4	2.9	*					
		Residuals	38	0.2							
C) Taxonomic composition	Canyon	Basin	1	11991.0	3.6	***	ns	ns	Atl ≠ Med	Atl ≠ Med	ns
		Bathymetric range	5	5316.5	1.6	**					
		Basin X Bathymetric	4	4327.6	1.3	*					
		Residuals	172	3316.4							
	Open slope	Basin	1	7498.8	2.1	**	ns	ns	ns	ns	ns
		Bathymetric range	5	3604.8	1.0	ns					
		Basin X Bathymetric	3	3583.3	1.0	ns					
		Residuals	70	3625.4							
D) Taxonomic composition presence/absence	Canyon	Basin	1	6183.2	6.9	***	ns	ns	ns	Atl ≠ Med	Atl ≠ Med
		Bathymetric range	5	1041.3	1.2	ns					
		Basin X Bathymetric	4	994.2	1.1	ns					
		Residuals	142	899.1							
	Open slope	Basin	1	3435.0	3.1	*	ns	ns	ns	ns	ns
		Bathymetric range	5	805.7	0.7	ns					
		Basin X Bathymetric	3	1014.3	0.9	ns					
		Residuals	70	1102.6							

844 **Supplementary Table S4.** Output of PERMANOVA and pair wise comparisons, testing for differences between canyons and open slopes at different
845 bathymetric ranges (indicated as Depth) and among bathymetric ranges along canyons/slopes, in the investigated Mediterranean Sea margins in A)
846 meiofaunal abundance, B) biomass, C) taxonomic composition and D) composition after presence/absence transformation. * = P<0.05; ** = P<0.01;
847 *** = P<0.001; ns = not significant; na = not available; Cat = Catalan, Lig = Ligurian, Adr = Adriatic, Cret = Cretan margins; C =canyon, S = open
848 slopes.

						canyon vs slope				along bathymetric ranges			
	Source	df	MS	F	P	150-500m	500-1000m	1000-2000m	2000-3000m	Catalan	Ligurian	Adriatic	Cretan
A) Abundance	Habitat	9	0.27	6.97	***	Lig C>S (Calvi)	ns	ns	ns	along C (-) (LacDuth,Cap Creus,P-Rhône); along S (-) (Blanes,CapCreus slope)	along S (-) (Calvi)	ns	along C (-)
	Depth	4	0.18	4.73	**								
	Habitat x Depth	11	0.02	0.63	ns								
	Residuals	220	0.04										
B) Biomass	Habitat	7	0.42	2.54	*	ns	Adr C>S	ns	ns	along C (-) (CapCreus); along S (-) (LacDuth slope)	na	along C (-) (C), S (-)	ns
	Depth	4	0.76	4.54	***								
	Habitat x Depth	8	0.13	0.75	ns								
	Residuals	77	0.17										
C) Taxonomic composition	Habitat	9	2292.00	4.73	***	Lig C≠S (Calvi)	ns	Cat C≠S (capCreus,Blanes)	ns	along C (Blanes,LacDuth, P-Rhône), along S (CapCreus)	ns	ns	ns
	Depth	4	1354.00	2.79	***								
	Habitat x Depth	11	774.25	1.60	*								
	Residuals	199	484.53										
D) Taxonomic composition (presence/absence)	Habitat	9	2600.30	3.41	***	Lig C≠S (Calvi)	ns	ns	ns	along C (Blanes,LacDuth); along S (CapCreus)	along S (Calvi)	ns	ns
	Depth	4	1561.20	2.05	*								
	Habitat x Depth	11	1265.00	1.66	**								
	Residuals	199	763.20										

849

850 **Supplementary Table S5.** Richness and Expected richness of taxa (ET) of meiofaunal taxa at different depth ranges in N Atlantic and Mediterranean
851 canyons and open slopes (A), Atlantic and Mediterranean margins canyons and open slopes (B) and in each canyon (C) and slope (D). Reported are
852 also the total number of individuals retrieved and the number of individuals used for the ET calculation.

853

A)	Depth range (m)	N	Richness	ET
Atlantic canyon ET (111)	150-500	2231	9	4.4
	500-1000	492	9	4.4
	1000-2000	901	14	3.9
	2000-3000	1565	10	3.9
	3000-4000	4400	23	4.4
	4000-5000	2380	21	4.4
Mediterranean ET (111)	150-500	16134	30	4.8
	500-1000	29593	28	4.5
	1000-2000	17835	24	4.3
	2000-3000	11962	15	3.3
	3000-4000	111	4	2.0
Atlantic slope ET (549)	150-500	818	7	5.2
	500-1000	549	11	7.0
	1000-2000	980	11	7.3
	2000-3000	1415	12	6.8
	3000-4000	1449	13	6.2
	4000-5000	654	9	5.7
Mediterranean slope ET (549)	150-500	9759	24	8.0
	500-1000	19133	28	7.2
	1000-2000	9995	23	7.5
	2000-3000	23970	15	4.7

B)		Depth range (m)	N	Richness	ET
N Atlantic margin ET (492)	canyon	150-500	492	9	8.0
		500-1000	2231	9	6.0
		1000-2000	901	14	6.8
		2000-3000	1565	10	6.6
		3000-4000	4400	23	8.1
		4000-5000	2380	21	9.0
	slope	150-500	818	7	5.0
		500-1000	549	11	6.7
		1000-2000	980	11	7.0
		2000-3000	1415	12	6.5
		3000-4000	1449	13	6.0
		4000-5000	654	9	5.4
Catalan margin ET (2198)	canyon	150-500	8623	24	13.2
		500-1000	28148	26	11.4
		1000-2000	16323	24	11.7
		2000-3000	2198	14	11.0
	slope	150-500	7003	15	10.7
		500-1000	13981	21	9.4
		1000-2000	9467	18	11.5
Balearic margin ET (1160)	canyon	1000-2000	1416	3	3.0
	slope	500-1000	1160	3	3.0
Ligurian margin ET (368)	canyon	150-500	6607	18	7.4
		2000-3000	9704	4	3.9
	slope	150-500	1966	18	8.8
		500-1000	3111	18	8.2
		1000-2000	368	12	6.0
Adriatic margin ET (146)	canyon	150-500	905	11	4.5
		500-1000	1445	11	5.4
	slope	150-500	551	8	4.8
		500-1000	146	6	4.0
Cretan margin ET (23)	canyon	1000-2000	96	3	1.0
		2000-3000	59	2	1.8
		3000-4000	111	4	1.8
	slope	150-500	238	7	1.5
		500-1000	186	7	1.9
		1000-2000	160	5	2.0
		2000-3000	23	2	2.0

C) CANYONS		Depth range	N	Richness	ET
N Atlantic margin ET (212)	Cascais	150-500	492	9	6
		1000-2000	901	14	5
		2000-3000	1565	10	5
		3000-4000	1448	17	7
		4000-5000	831	13	6
	Nazaré	500-1000	2231	9	5
		3000-4000	2362	19	5
		4000-5000	968	14	5
	Setúbal	3000-4000	590	12	7
		4000-5000	581	15	7
Catalan margin ET (80)	Besos	500-1000	331	5	4
		150-500	2091	19	5
	Blanes	500-1000	7719	21	4
		1000-2000	3042	17	5
	Fonera	150-500	2544	8	3
		500-1000	5209	11	3
		1000-2000	397	5	3
	Cap De Creus	500-1000	5608	13	3
		1000-2000	2649	14	3
		2000-3000	830	7	2
	Lacaze-Duthiers	150-500	1392	14	4
		500-1000	8525	15	4
		1000-2000	3239	11	3
	Sete	2000-3000	254	5	4
		2000-3000	1034	10	3
		150-500	1406	7	3
	Petit Rhône	500-1000	757	6	3
		1000-2000	1642	7	3
		2000-3000	80	5	5
	Planier	150-500	1190	3	3
		1000-2000	5355	3	3
Balearic margin ET(1160)	Balearic	1000-2000	1416	3	3
Ligurian margin ET (368)	Calvi	150-500	6607	18	7
	Var	2000-3000	9704	4	4
Adriatic margin ET(146)	B	150-500	608	10	5
		500-1000	600	8	5
	C	150-500	298	8	4
		500-1000	845	11	5
Cretan margin ET(23)	Samaria	1000-2000	96	3	2
		2000-3000	59	2	2
		3000-4000	111	4	2

D) OPEN SLOPE		Open slope	Depth range (m)	N	Richness	ET
N Atlantic margin ET (212)	Cascais slope		1000-2000	769	11	5
			2000-3000	1415	12	5
			3000-4000	378	10	5
			4000-5000	368	8	5
			150-500	818	7	4
	Nazaré slope		500-1000	549	11	5
			1000-2000	212	7	5
			2000-3000	1072	10	4
			3000-4000	286	6	4
Catalan margin ET (80)	Foix slope		1000-2000	2121	3	3
	Besos slope		500-1000	83	5	5
	Blanes slope		500-1000	4777	15	3
			1000-2000	3277	15	4
	Cap de Creus slope		150-500	2415	11	3
			500-1000	3939	15	3
			1000-2000	2113	10	3
	Lacaze-Duthiers slope		150-500	3366	13	4
			500-1000	2533	3	3
			1000-2000	457	6	3
Balearic margin ET(1160)	Petit Rhône slope		150-500	1222	6	3
			500-1000	709	5	3
			500-1000	3440	3	3
	Planier slope					
	Balearic slope		500-1000	1160	3	3
	Calvi slope		150-500	1966	18	9
			500-1000	3111	18	8
			1000-2000	368	12	6
Adriatic margin ET(146)	Adriatic slope		150-500	551	8	5
			500-1000	146	6	4
Cretan margin ET(23)	Samaria slope		150-500	238	7	2
			500-1000	186	7	2
			1000-2000	160	5	2
			2000-3000	23	2	1