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

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ABSTRACT

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

1. Introduction

1.1 Deep Mediterranean Sea canyons

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

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

So far, in the Mediterranean Sea, more than 500 large submarine canyons have been documented (Canals et al., 2004; Weaver et al., 2004; Harris and Whiteway, 2011; Würtz, 2012a). Recent worldwide studies indicate that the Mediterranean canyons are typically different from any other marine region (Harris and Whiteway, 2011), since they are: i) more closely spaced (14.9 km vs 33.0 km on global worldwide average), ii) more dendritic (12.9 limbs vs 4.8 limbs per 100,000 km^2), iii) shorter (mean length of 26.5 km vs 43.4 km), iv) steeper (mean slope of 6.5° vs 5.1°) and v) smaller in depth range (mean depth: 1613 m vs 1992 m) than canyons occurring in all other oceans.

1.2 Biodiversity in Mediterranean deep canyons

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

1.3 Aim of the study

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

2. Materials and methods

2.1 Study area and data collection

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

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

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

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

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

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

2.2 Data analyses

2.2.1 Meiofaunal abundance, biomass and biodiversity

Differences between basins (NE Atlantic ocean and Mediterranean Sea), among continental margins (Catalan, Balearic, Ligurian, Adriatic and Cretan margins in the Mediterranean Sea), between canyons and adjacent open slopes within each margin, at different water depths in the meiofaunal abundance, biomass and taxonomic composition were analyzed in either the uni- and multivariate contexts, following different sampling designs. First, we used a 2-way sampling design comprising "Basin" (fixed, 2 levels: Atlantic and Mediterranean) and "Depth range" (fixed, 5 levels: 150-500 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m), separately for canyons and open slopes. Then, we used a 2-way sampling design comprising Margin-habitat (fixed, 10 levels: Catalan canyon, Catalan slope, Balearic canyon, Balearic slope, Ligurian canyon, Ligurian slope, Adriatic canyon, Adriatic slope, Cretan canyon and Cretan slope, nested in Margin) and “Depth range” (fixed, 5 levels: 150-500 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m). When a significant effect of the factor Depth range was observed, we applied also a 2-way design comprising “Transect” (fixed, 19 levels: Foix, Blanes, Fonera, Cap de Creus, Lacaze-Duthiers, Petit Rhône, Planier, Adriatic B and C, Samaria canyons, Blanes, Cap de Creus, Lacaze-Duthiers, Petit Rhône, Calvi, Adriatic, Cretan Western and Eastern open slopes) and “Depth range” (fixed, 5 levels: 150-500 m, 500-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m) in order to identify in which specific canyon/slope the differences were observed.

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

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

The meiofaunal diversity was assessed in terms of richness of higher taxa. The expected number of taxa (ET) was also calculated (by means of the ES function in PRIMER 6+; Clarke and Gorley, 2006), since it provides a standardization of the richness of taxa values according to the sample size. The ET was calculated at different spatial scales. First, the ET was calculated at the widest spatial scale in the different basins (N Atlantic and Mediterranean Sea) at similar bathymetric ranges. Then the ET was calculated in the different habitats (canyons and open slopes) in all sub-basins at similar bathymetric ranges and then in each transect at similar bathymetric ranges. For each calculation, the meiofaunal assemblages were pooled together from all samples of each bathymetric range in basins, habitats and transects, using the minimum number of individuals retrieved in basins, habitats and transect for the ET calculation.

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

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

2.2.2 Environmental and geomorphological effect on meiofaunal assemblages

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

To determine whether the meiofaunal assemblages are influenced by canyons geomorphological characteristics, we carried out multivariate multiple regression analyses (DistLM forward, McArdle and Anderson, 2001) and produced distance-based Redundancy Analysis (db-RDA) plots. Canyons geomorphological characteristics were obtained from data reported in Harris and Whiteway (2011). For the purpose of this study we used data regarding: class (shelf-incising canyons having/not having heads with a clear bathymetric connection to a major river system, or blind canyons), status (size of tributaries to the main canyon thalweg), top and low heights (depth at 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 km^2, 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

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

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

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

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

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

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

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

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

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

Meiofaunal abundance, biomass and richness of taxa showed a significant negative log-linear relationship with the water depth in the Mediterranean Sea canyons and open slopes (Figure 3; 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 along continental margins) allows diversified assemblages, increasing the overall diversity at regional and basin scale (Bianchelli et al., 2010; Zeppilli et al., 2016).

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

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

The specific features of canyon fauna has been previously reported from several Mediterranean margins, in particular on canyons off the Alboran, Catalan, Malta, and Turkey coasts (Özturk et al., 2012; Vella and Vella, 2012; Watremez, 2012; David and Di-Méglio, 2012; Madurell et al., 2012; Company et al., 2012; Baro et al., 2012). In the Mediterranean sea, one of the most relevant aspects is the relationship between the number of species, the number of individuals of 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).

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 constrains 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) constrains 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

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

4.3 Influence of canyons geomorphological characteristics on meiofaunal assemblages

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

Faunas inhabiting such complex environments are thus influenced by multiple factors, which include hydrodynamic conditions and current regimes, topography and habitat heterogeneity, amount, origin and quality of sedimentary organic matter, sedimentation processes and turbidity 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

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

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Caption of figures

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

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

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

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

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

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

		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	44.81
		500-1000	33.1	41.99
		1000-2000	32.8	40.19
	Ligurian	150-500	28.4	31.54
	Adriatic	150-500	25.5	26.54
		500-1000	26.7	18.62
	Cretan	1000-2000	28.9	36.51
		2000-3000	15.8	0
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

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

	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	***

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

A)	Variable	F	P	% Prop explained variance
Abundance	class	20.6	***	12.7
	depth	17.8	***	9.2
	sinuosity	10.4	**	6.0
	height dif	9.3	***	4.5
	length	9.1	***	4.0
	slope	5.1	**	2.4
	status	4.4	*	1.9
	top height	3.9	*	1.8
	margin type	2.4	ns	1.0
	parts at 1500m	1.8	ns	0.7
	density	1.1	ns	0.5
	dendricity per 100k km^{-2}	0.9	ns	0.4
Biomass	class	18.0	***	11.4
	status	8.8	***	5.9
	density	8.3	***	5.6
	canyon density	5.9	***	4.1
	margin type	5.2	***	3.6
	parts at 1500m	4.3	**	3.0
	height dif	3.8	**	2.6
	slope	3.8	**	2.6
	top height	3.8	**	2.6
	dendricity per 100k km-2	3.2	**	2.2
	dendricity	3.2	**	2.2
	sinuosity	3.1	*	2.2
	low height	3.0	**	2.1
	length	1.9	ns	1.3
	depth	1.8	ns	1.3

B)	Variable	F	P	% Prop explained variance
Richness of taxa	class	25.8	***	18.2
	height dif	20.6	***	12.4
	depth	10.3	**	5.8
	top height	8.0	*	4.0
	canyon density	9.4	*	3.8
	sinuosity	7.6	**	3.6
	length	6.6	**	3.5
	status	6.1	*	2.7
	slope	4.8	*	2.1
	margin type	0.7	ns	0.3
Taxonomic composition (presence/absence)	class	20.4	***	13.3
	density	18.1	***	10.5
	sinuosity	5.5	***	3.1
	margin type	5.5	**	2.7
	canyon density	5.0	**	2.4
	depth	4.4	**	2.4
	top height	4.2	**	2.2
	slope	3.4	*	1.8
	dendricity per 100k km-2	3.3	*	1.7
	status	2.3	ns	1.1
	length	2.3	ns	1.1
	height dif	2.0	ns	0.9
Taxonomic composition	depth	32.8	***	17.0
	status	11.8	***	8.1
	margin type	10.8	***	6.9
	low height	5.9	**	2.9
	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

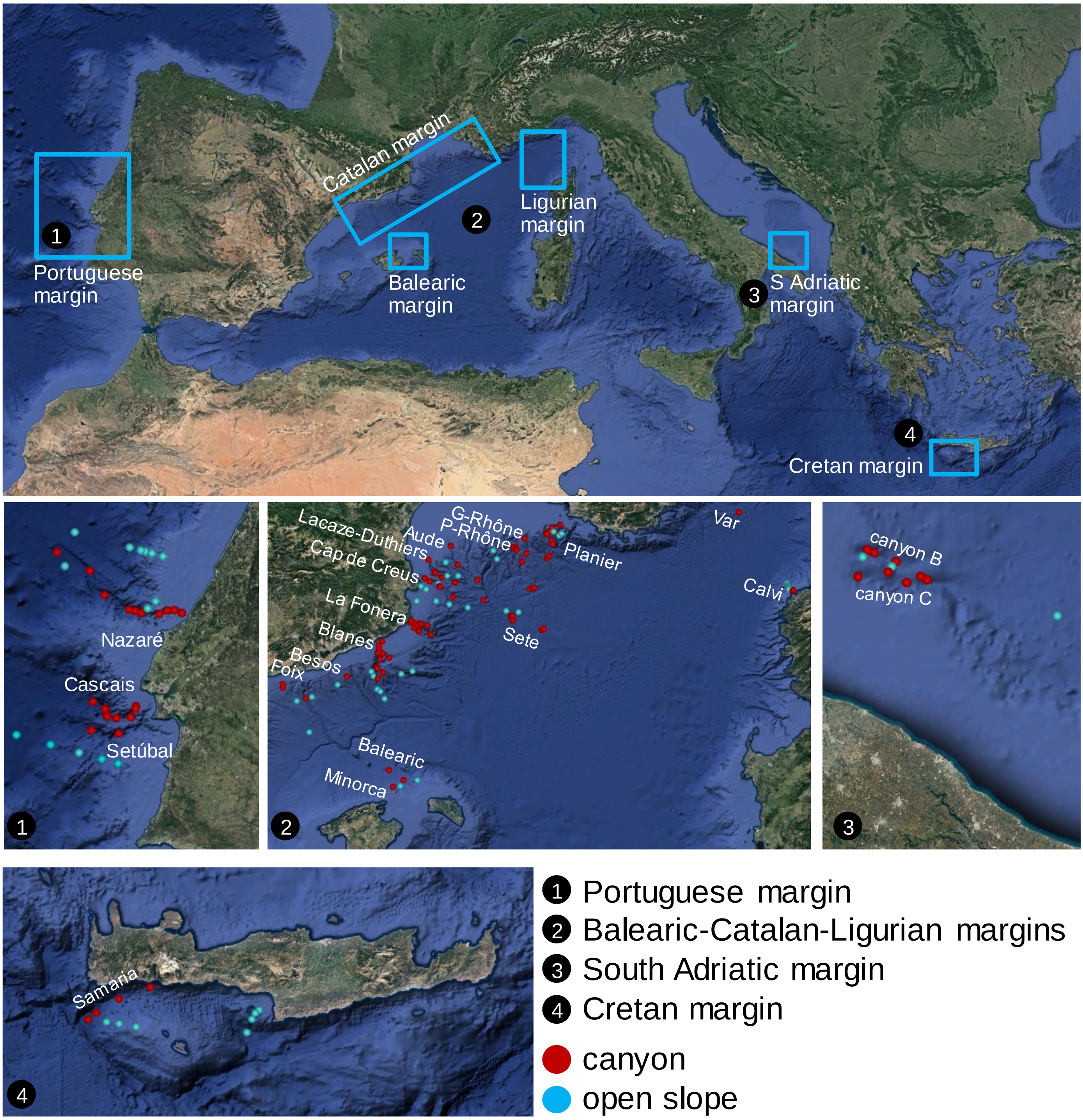
Catalan margin
1
Portuguese margin
2
Ligurian margin
Balearic margin
3
S Adriatic margin
4
Cretan margin
Lacaze-Duthiers
Aude
G-Rhône
P-Rhône
Planier
Var
Cap de Creus
Calvi
La Fonera
Sete
Blanes
Besos
Foix
Balearic
Minorca
Nazaré
Cascais
Setúbal
canyon B
canyon C
Samaria
1 Portuguese margin
2 Balearic-Catalan-Ligurian margins
3 South Adriatic margin
4 Cretan margin
● canyon
● open slope

Figure 1.

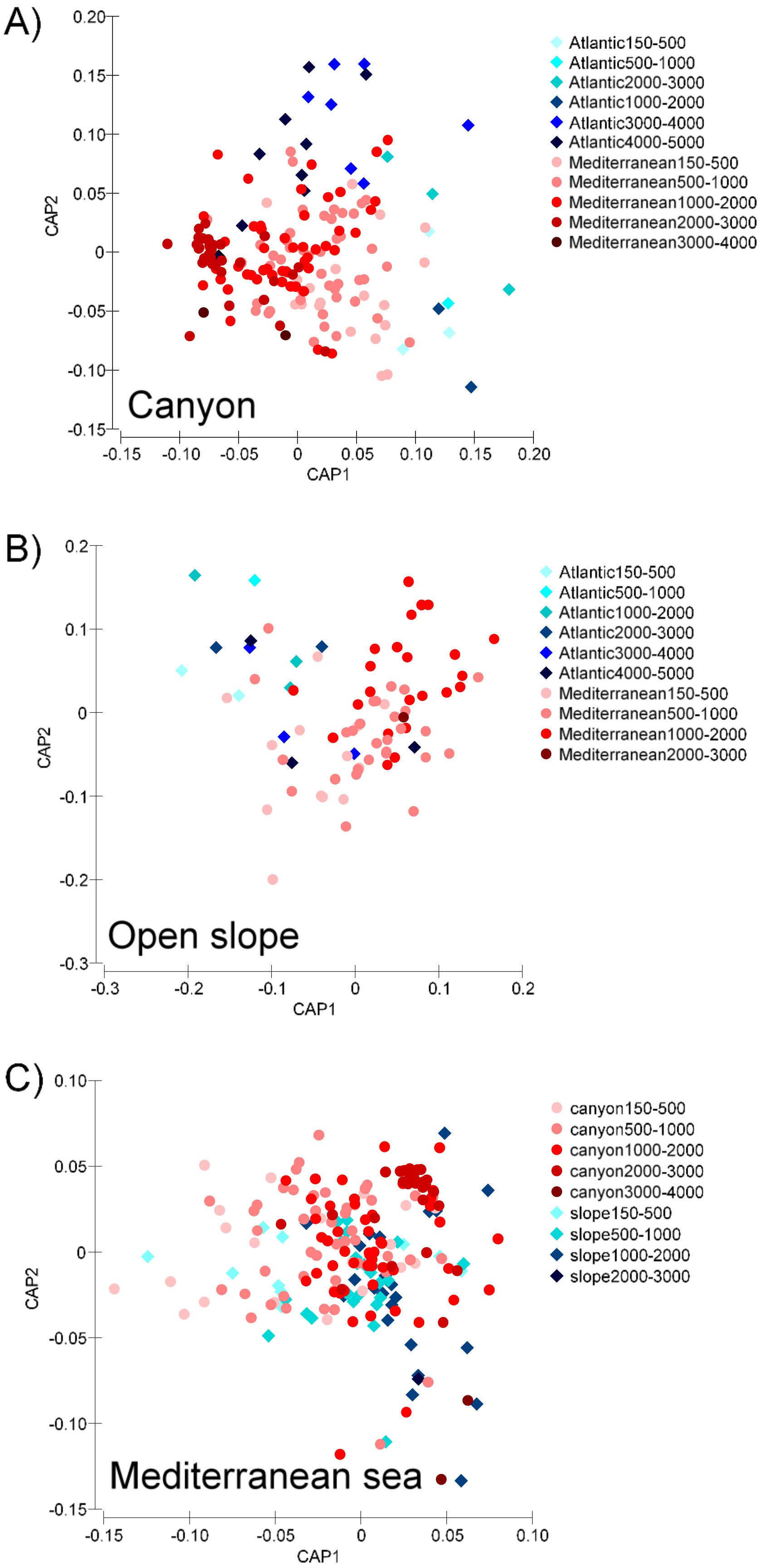
A)
0.20
0.15
0.10
0.05
0
-0.05
-0.10
-0.15
CAP2
-0.15
-0.10
-0.05
0
0.05
0.10
0.15
0.20
CAP1
Canyon
Atlantic150-500
Atlantic500-1000
Atlantic2000-3000
Atlantic1000-2000
Atlantic3000-4000
Atlantic4000-5000
Mediterranean150-500
Mediterranean500-1000
Mediterranean1000-2000
Mediterranean2000-3000
Mediterranean3000-4000
B)
0.2
0.1
0
-0.1
-0.2
-0.3
CAP2
-0.3
-0.2
-0.1
0
0.1
0.2
CAP1
Open slope
Atlantic150-500
Atlantic500-1000
Atlantic1000-2000
Atlantic2000-3000
Atlantic3000-4000
Atlantic4000-5000
Mediterranean150-500
Mediterranean500-1000
Mediterranean1000-2000
Mediterranean2000-3000
C)
0.10
0.05
0
-0.05
-0.10
-0.15
CAP2
-0.15
-0.10
-0.05
0
0.05
0.10
CAP1
Mediterranean sea
canyon150-500
canyon500-1000
canyon1000-2000
canyon2000-3000
canyon3000-4000
slope150-500
slope500-1000
slope1000-2000
slope2000-3000

Figure 2.

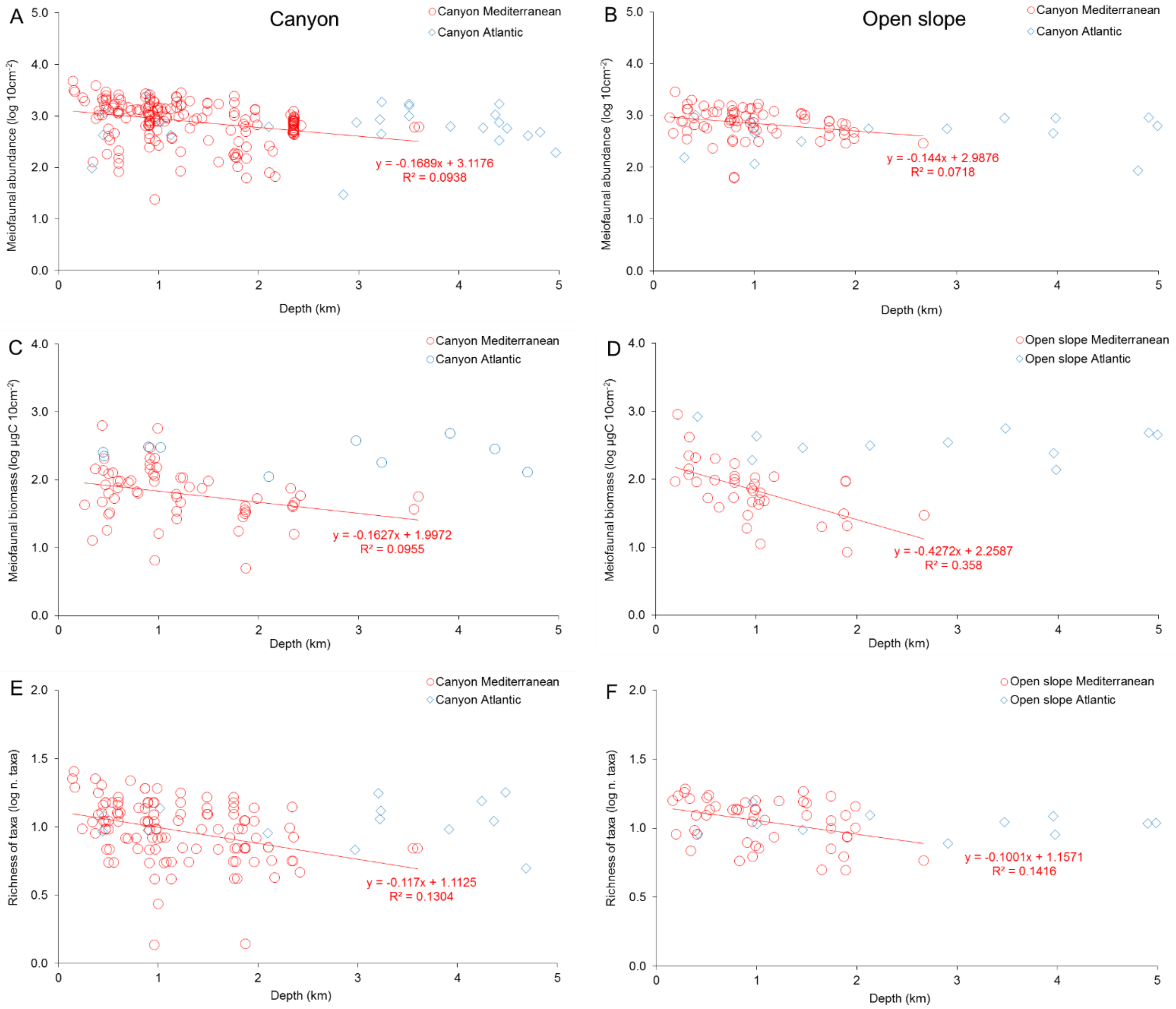
A
Canyon
Canyon Mediterranean
Canyon Atlantic
Meiofaunal abundance (log 10cm⁻²)
5.0
4.0
3.0
2.0
1.0
0.0
0
1
2
3
4
5
Depth (km)
y = -0.1689x + 3.1176
R² = 0.0938
B
Open slope
Canyon Mediterranean
Canyon Atlantic
Meiofaunal abundance (log 10cm⁻²)
Depth (km)
y = -0.144x + 2.9876
R² = 0.0718
C
Canyon Mediterranean
Canyon Atlantic
Meiofaunal biomass (log µgC 10cm⁻²)
Depth (km)
y = -0.1627x + 1.9972
R² = 0.0955
D
Open slope Mediterranean
Open slope Atlantic
Meiofaunal biomass (log µgC 10cm⁻²)
Depth (km)
y = -0.4272x + 2.2587
R² = 0.358
E
Canyon Mediterranean
Canyon Atlantic
Richness of taxa (log n. taxa)
2.0
1.5
1.0
0.5
0.0
Depth (km)
y = -0.117x + 1.1125
R² = 0.1304
F
Open slope Mediterranean
Open slope Atlantic
Richness of taxa (log n. taxa)
Depth (km)
y = -0.1001x + 1.1571
R² = 0.1416

Figure 3.

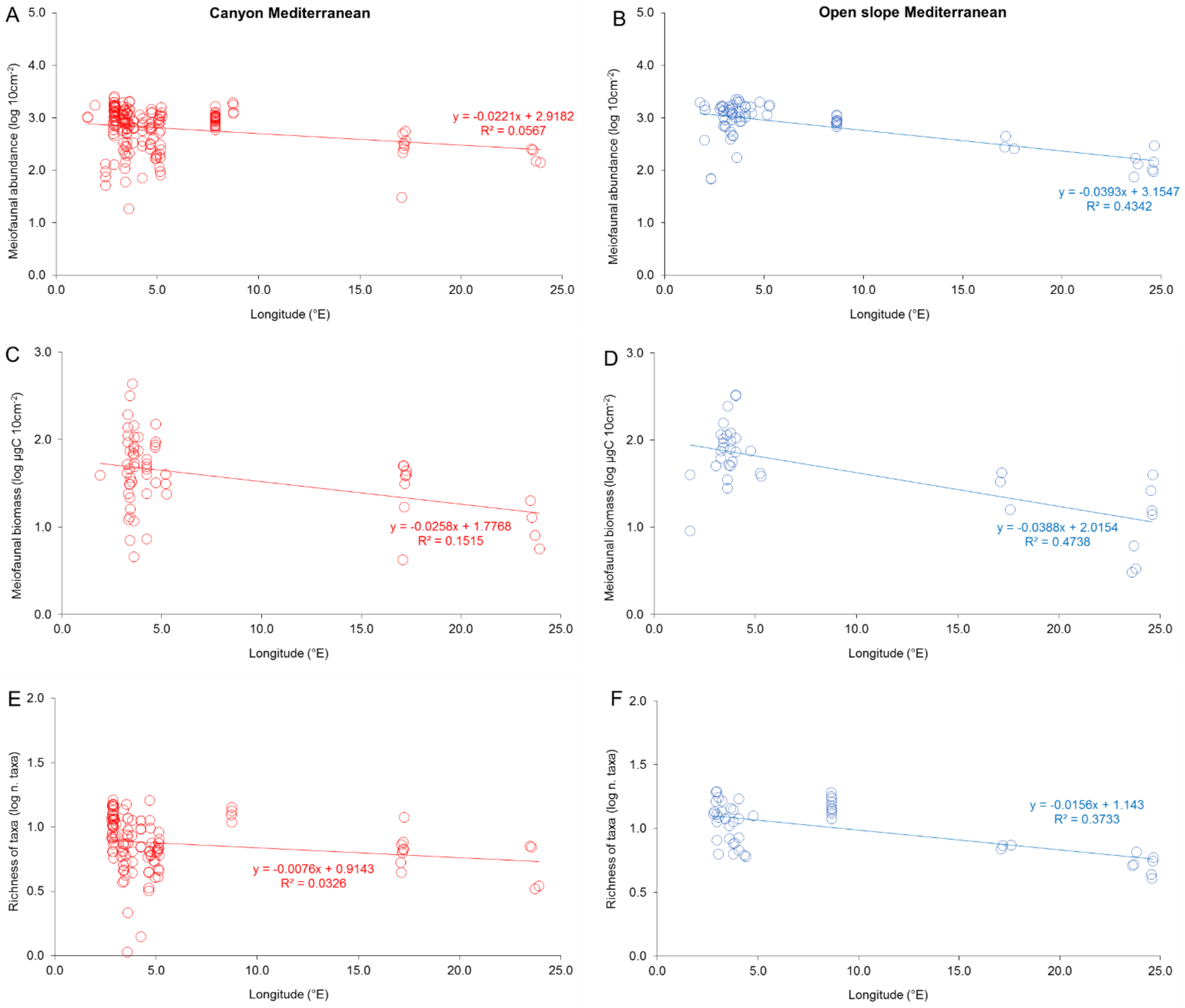
A
Canyon Mediterranean
Meiofaunal abundance (log 10cm⁻²)
y = -0.0221x + 2.9182
R² = 0.0567
B
Open slope Mediterranean
Meiofaunal abundance (log 10cm⁻²)
y = -0.0393x + 3.1547
R² = 0.4342
C
Meiofaunal biomass (log µgC 10cm⁻²)
y = -0.0258x + 1.7768
R² = 0.1515
D
Meiofaunal biomass (log µgC 10cm⁻²)
y = -0.0388x + 2.0154
R² = 0.4738
E
Richness of taxa (log n. taxa)
y = -0.0076x + 0.9143
R² = 0.0326
F
Richness of taxa (log n. taxa)
y = -0.0156x + 1.143
R² = 0.3733
Longitude (°E)
0.0
5.0
10.0
15.0
20.0
25.0

Figure 4.

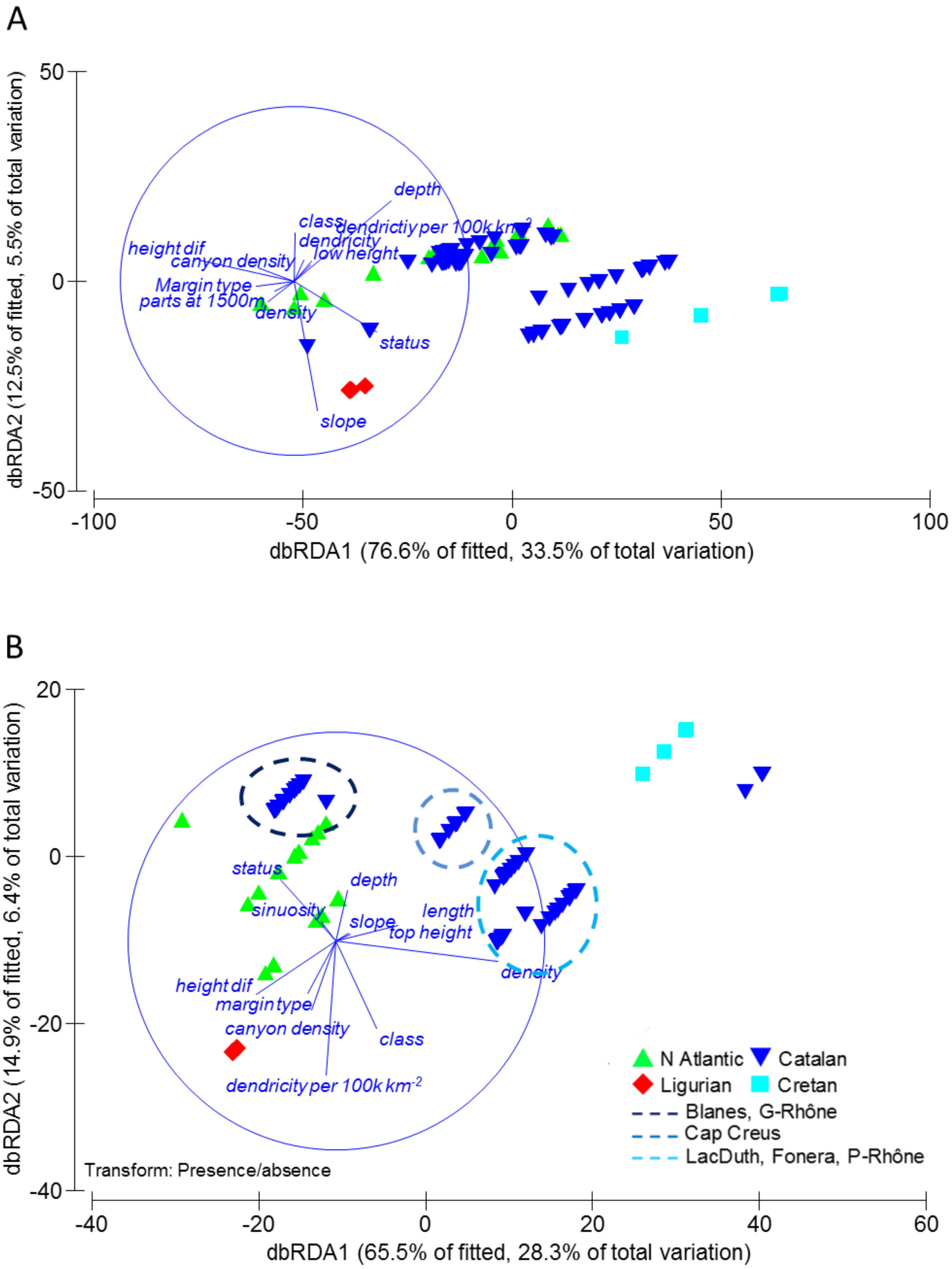
A
50
0
-50
-100
-50
0
50
100
dbRDA2 (12.5% of fitted, 5.5% of total variation)
dbRDA1 (76.6% of fitted, 33.5% of total variation)
depth
class
dendrictiy per 100k km-2
dendricity
low height
height dif
canyon density
Margin type
parts at 1500m
density
status
slope
B
20
0
-20
-40
-40
-20
0
20
40
60
dbRDA2 (14.9% of fitted, 6.4% of total variation)
dbRDA1 (65.5% of fitted, 28.3% of total variation)
status
depth
sinuosity
slope
length
top height
density
height dif
margin type
canyon density
class
dendricity per 100k km-2
N Atlantic
Catalan
Ligurian
Cretan
Blanes, G-Rhône
Cap Creus
LacDuth, Fonera, P-Rhône
Transform: Presence/absence

Figure 5.

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

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		

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

			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

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

								Bathymetric range				
N Atlantic vs Mediterranean Sea			Source	df	MS	F	P	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							

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

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

A)	Depth range (m)	N	Richness	ET
Atlantic canyon	150-500	2231	9	4.4
ET (111)	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	150-500	16134	30	4.8
ET (111)	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	150-500	818	7	5.2
ET (549)	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	150-500	9759	24	8.0
ET (549)	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	canyon	150-500	492	9	8.0
ET (492)		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	canyon	150-500	8623	24	13.2
ET (2198)		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	canyon	1000-2000	1416	3	3.0
ET (1160)	slope	500-1000	1160	3	3.0
Ligurian margin	canyon	150-500	6607	18	7.4
ET (368)		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	canyon	150-500	905	11	4.5
ET (146)		500-1000	1445	11	5.4
	slope	150-500	551	8	4.8
		500-1000	146	6	4.0
Cretan margin	canyon	1000-2000	96	3	1.0
ET (23)		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
	Blanes	150-500	2091	19	5
		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
		2000-3000	254	5	4
	Sete	2000-3000	1034	10	3
	Petit Rhône	150-500	1406	7	3
		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
	Nazaré slope	150-500	818	7	4
		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
	Petit Rhône slope	150-500	1222	6	3
		500-1000	709	5	3
	Planier slope	500-1000	3440	3	3
Balearic margin ET(1160)	Balearic slope	500-1000	1160	3	3
Ligurian margin ET (368)	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