

**Deep-sea benthos
from Mediterranean
slopes and basins**

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Benthic communities in the deep Mediterranean Sea: exploring microbial and meiofaunal patterns in slope and basin ecosystems

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Abstract

The long held perception of the deep sea consisting of monotonous slopes and uniform oceanic basins has over the decades given way to the idea of a complex system with wide habitat heterogeneity. Under the prism of a highly diverse environment, a large dataset was used to describe and compare spatial patterns of the dominant small-size components of deep-sea benthos, metazoan meiofauna and bacteria, from Mediterranean basins and slopes. A grid of 73 stations sampled at five geographical areas along the central-eastern Mediterranean basin (central Mediterranean, northern Aegean Sea, Cretan Sea, Libyan Sea, eastern Levantine) spanning over 4 km in depth revealed a high diversity in terms of both metazoan meiofauna and microbial communities. The higher meiofaunal abundance and richness observed in the northern Aegean Sea highlights the effect of productivity on benthic patterns. Non parametric analyses detected no differences for meiobenthic standing stocks and major taxa diversity (α , β , γ and δ components) between the two habitats (basin vs. slope) for the whole investigated area and within each region, but revealed significant bathymetric trends: abundance and richness follow the well-known gradient of decreasing values with increasing depth, whereas differentiation diversity (β - and δ -diversity) increases with depth. In spite of a similar bathymetric trend observed for nematode genera richness, no clear pattern was detected with regard to habitat type; the observed number of nematode genera suggests higher diversity in slopes, whereas richness estimator Jack1 found no differences between habitats. On the other hand, δ -diversity was higher at the basin habitat, but no differences were found among depth ranges, though turnover values were high in all pairwise comparisons of the different depth categories. Results of multivariate analysis are in line with the above findings, indicating high within habitat variability of meiofaunal communities and a gradual change of meiofaunal structure towards the abyssal stations. In contrast to meiobenthic results, microbial richness is significantly higher at the basin ecosystem and tends to increase with depth, while community structure varies greatly among samples regardless of the type of habitat,

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depth or area. The results presented here suggest that differences in benthic parameters between the two habitats are neither strong nor consistent; it appears that within habitat variability is high and differences among depth ranges are more important.

1 Introduction

Covering more than 60 % of the Earth's surface and about 90 % of the oceans, the deep sea is the largest ecosystem on earth (Ramirez-Llodra et al., 2010). Yet the deep-sea floor remains largely unexplored in spite of the enormous technological advances and the intense research efforts of the past few decades. The recent breakthroughs in deep-sea research have nevertheless revealed a complex system with diverse geological, physical and biochemical characteristics that lead to wide variability of different habitats and benthic communities.

The deep sea consists of slopes and basins. The slopes are the steep part of the continental margins that connect the continental shelf with the deep-sea plains. Although of restricted size (roughly 10 %, Ramirez-Llodra et al., 2010), slopes are essential ecosystems for the functioning of the oceans and the globe as they constitute the region where the continent-to-ocean transfer of water, sediment and energy takes place. The sharp depth gradient of slopes is characterised by equally sharp environmental gradients, such as temperature and food availability. As an important component of continental margins, slopes are also characterised by high habitat heterogeneity and host diverse communities (Levin and Sibuet, 2011). In contrast, oceanic basins lack environmental gradients and are relatively uniform, appearing similar to deserts; for that they were for long considered constant and stable environments. However, evidence now exists that basins are dynamic environments that sustain considerable regular and episodic disturbances, such as seasonal phytodetritus deposition and benthic storms (Rex and Etter, 2010).

As most of the deep sea is heterotrophic, food supply to deep-sea benthos is derived ultimately from surface production. Primary productivity of the euphotic zone varies in

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space and time and so does the organic matter arriving at the deep seafloor; this may in turn lead to spatio-temporal variability in the benthos. The variability of benthic communities along the continental margins is mostly related to depth, which however may reflect changes in food supply, sediment characteristics or other factors. While benthic standing stocks decrease exponentially down the continental margin and reach extremely low levels in the abyssal plain (Rex et al., 2006), deep-sea biodiversity is among the highest on Earth (Ramirez-Llodra et al., 2010 and references therein). A unimodal diversity-depth pattern with a midslope diversity maximum has been recognised for benthos, though this trend and the depth where diversity peaks are not universal and may vary among basins, regions, benthic components or taxa (Rex and Etter, 2010; Ramirez-Llodra et al., 2010, and references therein). Hence, by increasing sampling and extending research to include more taxa and more areas of the deep oceans will help elucidate this basic bathymetric trend of benthic diversity.

In the Mediterranean the continental shelf is very narrow and therefore the largest part of this enclosed sea is classified as deep sea. Though Mediterranean ecosystems are among the most studied areas of the world, deep-sea fauna research lags behind those of other areas (Danovaro et al., 2010). Nonetheless, considerable work carried out over the last three decades on the deep Mediterranean meiofauna has advanced our knowledge on the smallest but most abundant metazoans of the sediments (extensive bibliographic references reported in Danovaro et al., 2010; Gambi et al., 2010). Following major trends in ecology, recent investigations have sought for latitudinal, longitudinal and bathymetric patterns of meiofauna (Lampadariou and Tselepidis, 2006; Danovaro et al., 2009a, 2010; Gambi et al., 2010), while few study differences in meiofaunal patterns among deep-sea habitats (Danovaro et al., 2009a,b; Vanreusel et al., 2010; Gambi et al., 2010). Danovaro et al. (2009a) in a study including samples from Mediterranean slopes and basins found that meiofaunal diversity in slopes was higher than in deep-sea plains. This differs from the results reported by Vanreusel et al. (2010) that found no differences between these two habitats and contradicts partly the results

of Netto et al. (2005) that found higher diversity in basins southeast of Brazil only when nematode genera diversity was considered.

Microbial benthic community studies are a recent addition to deep-sea research in the Mediterranean. A high level of bacterial richness has been recorded in the Mediterranean Sea (Luna et al., 2004; Polymenakou et al., 2005a,b, 2009), which is comparable to other deep-sea sediments (Li et al., 1999a,b; Bowman and McCuaig, 2003). Contrary to what has been found for the larger benthic components, microbial community parameters do not change with depth but remain constant (Rex et al., 2006; Danovaro et al., 2010). Recent studies dealing with bacterial diversity estimates have revealed that many bacteria found in the deep sea are similar to those living in soil or shallow water (Li et al., 1999a,b; Polymenakou et al., 2005a, 2009; Kouridaki et al., 2010; Schauer et al., 2010; Zinger et al., 2011). On the other hand, there is little evidence to support ubiquitous dispersal and a biogeographical pattern of sediment bacteria (Polymenakou et al., 2005b). Only recently, Zinger et al. (2011) performed an analysis of 9.6 million bacterial V6-rRNA amplicons for 509 samples that span the global ocean's surface to the deep-sea floor in order to investigate global patterns of bacterial diversity. Their analysis has shown remarkable horizontal and vertical large-scale patterns in microbial communities. Overall, benthic communities appeared more diverse than pelagic communities, and a substantially higher diversity of bacterial populations was recorded in the deep-sea sediments compared to open ocean surface waters, vents and anoxic ecosystems (Zinger et al., 2011).

To expand knowledge of deep-sea community spatial patterns we examine the dominant small fractions of benthos, meiofauna and bacteria. A large and detailed dataset from the central-eastern Mediterranean basin is used for describing and comparing basin and slope ecosystems over large scale including different geographical areas. We pay special attention to the potential role of productivity for the observed patterns because food availability has been invoked as a major factor of benthic trends in the Mediterranean (Danovaro et al., 1995; Tselepides et al., 2000; Tselepides and Lampadariou, 2004; Lampadariou and Tselepides, 2006). More specifically, we aimed at

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investigating: (1) whether benthic parameters based on meiofaunal metazoan major taxa, nematode genera and bacteria species differ between basins and slopes, (2) whether there are major shifts in benthic parameters along depth ranges, (3) whether the observed patterns are similar between the two studied habitats, within different subregions and among the different benthic components, and (4) whether the patterns resulted from the current synthesis data are consistent with patterns of deep-sea fauna parameters worldwide.

2 Methods

2.1 Study area and sampling

The Mediterranean Sea, an oligotrophic marine system with increased salinity, is the largest and deepest enclosed sea on Earth. The Strait of Sicily divides the Mediterranean in two basins, the western and the central-eastern basins. It is characterised by many complex structural features, such as canyons, cold seeps, seamounts and mud volcanoes, and several steep environmental gradients, among which an eastward increasing salinity and temperature gradient and a southward and eastward decreasing productivity gradient. Due to the narrow continental shelf the largest part of the Mediterranean is classified as deep sea.

In the course of 10 multidisciplinary European collaborations, benthic samples were collected during 12 oceanographic surveys at different depths in the central-eastern basin of the Mediterranean Sea (Table 1). Overall, a grid of 73 stations located at slope and basin ecosystems were sampled at 5 regions along the Mediterranean: the central Mediterranean, the northern Aegean Sea, the Cretan Sea, the Libyan Sea and the eastern Levantine (Fig. 1, Table S1). At each station, sediment samples were collected by means of multiple-core sampler, which allowed for undisturbed sediment surface sampling. All analyses were focused on the sediment surface, where the bulk of meiofauna metazoan and bacteria is gathered. Meiofaunal samples were first treated with

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6% MgCl₂ to relax tissues and subsequently preserved by adding 10% formalin. Sediment samples for microbial analysis were kept frozen at -20 °C.

2.2 Laboratory treatment

In the laboratory, meiofauna samples from 69 stations were sieved through 500/1000 and 30 µm mesh sieves. The fauna retained on the 30 µm sieve was extracted by either triplicate centrifugation or triplicate flotation, using in both cases Ludox TM colloidal silica solution of 1.18 specific gravity. After extraction, meiofauna samples were stained with Rose Bengal and sorted to higher taxon level under a stereomicroscope. Nematode community analysis was based on samples from 22 out of the 69 stations. For nematode identifications, subsampling was performed so that at least 200 nematodes per sediment core were selected. After subsampling, specimens were slowly evaporated in anhydrous glycerol, evenly spread on microscope slides and identified to genus level using the pictorial keys of Platt and Warwick (1983, 1988), Warwick et al. (1998) as well as relevant literature dealing with new species and genera from the Mediterranean (e.g. Schuurmans Stekhoven Jr, 1950; Soetaert and Decraemer, 1989; Soetaert and Vincx, 1987).

Total microbial community DNA was extracted from approximately 1 g of sediment material per station (UltraClean Soil kit, MoBio, Carlsbad, CA, USA) and 16S rRNA gene libraries were successfully constructed for 16 of the sampled stations (19 samples) by targeting the hypervariable V5-V6 region with the following set of primers: 802f (5'-GATTAGATACCCBNGTA-3') and 1027r (5'-CGACRRCCATGCANCACCT-3', Claesson et al., 2010). The sequences of the partial 16S rRNA genes were produced by using a Roche GS-FLX 454 pyrosequencer (Roche, Mannheim, Germany). Sequences that were shorter than 200 bp in length were removed. Taxonomy was assigned using the Ribosomal Database Project classifier. Pyrosequencing data were submitted to NCBI Sequence Read Archive with the study accession number SRA054862.

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2.3 Data analyses

In the present study, meiofaunal and nematode diversity refer to taxon richness (TR, number of meiofaunal taxa) and genus richness (NR, number of nematode genera), respectively. Following Whittaker's scheme (1972), we calculated TR and NR separately for three levels of inventory diversity (the diversity of a defined geographic unit): (i) for each station, identified either as basin or slope habitat, as a univariate measure of alpha diversity, (ii) for each habitat within each of the five studied areas as a univariate measure of gamma (landscape/large area) diversity and (iii) for the whole data set that corresponds to epsilon diversity (biogeographic province diversity). The first order Jackknife estimator (Jack1) was also calculated using EstimateS v. 8.2.0 (Colwell, 2006) as an estimator of true nematode richness for the whole meiobenthic data set and for each habitat.

Differentiation diversity (the rate of change in species composition) can be measured in many different ways. Following the concept of Anderson et al. (2006), we measured beta and delta diversity using multivariate dispersion based on Jaccard dissimilarity. Beta diversity was measured (i) as the variability in taxa/genera composition among stations per habitat for each depth range/area and (ii) as the variability in taxa/genera composition among stations per depth range within each habitat. In a similar context, delta diversity was considered as the variability in taxa/species composition among all stations for each habitat and for each depth range. Besides being flexible on the measure of dissimilarity used, the method proposed by Anderson et al. (2006) has the advantage of testing for differences in differentiation diversity through a multivariate test for homogeneity in dispersions (PERMDISP, Anderson, 2006). Another facet of differentiation diversity, the turnover of taxa/genera between habitats and between depth ranges was also measured and for consistency was presented as Jaccard dissimilarity.

Hypothesis testing for differences in meiofauna abundance (overall and of nematodes and copepods), richness (TR and NR) and meiofauna and nematode structure was done using permutational multivariate analysis of variance (PERMANOVA). Of

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central interest was the relationship of meiofaunal parameters with habitat type i.e. basin and slope. Nevertheless, since it is well known that water depth affects marine sediment communities, it was necessary to consider depth range as a factor in the analysis. Thus, the overall experimental design consisted of two fixed factors: habitat, with two levels (basin, slope) and depth, with eight levels (< 500 m, > 3500 m and six categories in between of 500 m resolution). p-values were obtained using 9999 permutations of residuals under a reduced model. DISTLM routine, a permutational regression analysis, was performed for exploring relationships between multi- or univariate variables and depth. These analyses were based on Bray-Curtis dissimilarities of square-root transformed abundances, except from richness, for which Euclidean distances on untransformed data are considered more appropriate. To explore whether the observed bathymetric and habitat heterogeneity patterns apply to the whole Mediterranean, the permutational analyses were also applied to data sets from each area separately. PERMDISP routine was applied for measuring and exploring differences in differentiation diversity (measured as multivariate dispersion). Non-metric multi-dimensional scaling (nMDS) ordinations were used to illustrate spatial patterns of meiofauna structure. All analyses were performed with PRIMER v6 with PERMANOVA+ add-on software (Clarke and Gorley, 2006; Anderson et al., 2008).

For microbial diversity analysis, sequences were assigned to OTUs (operational taxonomic units) using the QIIME software at 3% sequence divergence (species level) according to Schloss and Handelsman (2005). Individual-based rarefaction curves at a distance level of 3% (species level) and the commonly used for microbial diversity analysis Chao1 richness estimator were calculated using the rarefaction calculator (<http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>).

3 Results

3.1 Meiofaunal standing stocks

Average meiofaunal densities in the sediment surface ranged from 2 ind/10 cm² in the deep basin of the central Mediterranean (2837 m depth) to 1249 ind/10 cm² in the northern Aegean basin (1271 m depth). As expected, nematodes predominated in all stations, habitats and areas, with an average percentage contribution ranging from 75 % to 88 % in the basins of Levantine and Cretan Sea, respectively, and from 72 % to 95 % in the Levantine and Central Mediterranean slopes (Fig. 2). Other meiofauna taxa of some importance were copepods (4–16 %), polychaetes (0.2–2 %), tardigrades (0.2–4 %) and the group of soft bodied animals (turbellarians, gnathostomulids) (0.5–4 %) (Fig. 2).

Irrespective of the type of habitat, depth or area, meiofaunal abundance followed the pattern of nematode abundance. The lowest values were recorded at basin stations in all five areas (Fig. 3), while the highest values were observed at slope stations only in the central Mediterranean and the Libyan sea. The lowest copepod abundances were also observed at basin stations in the five Mediterranean regions (0–6 ind/10 cm² at Central Mediterranean and northern Aegean basins), whereas the highest values (5 ind/10 cm² at Cretan Sea to 93 ind/10 cm² at northern Aegean) were found in slope stations except from the central Mediterranean and the northern Aegean. PERMANOVA results (Table 2) indicated differences in metazoan meiofaunal abundance between the two habitats only for two depth ranges (1000–1500 m and 2500–3000 m), but significant differences were detected in relation to depth, more pronouncedly at the basin habitat where meiofaunal abundance changed gradually from the shallower stations (up to 1000 m) to the deeper ones (> 3000 m). PERMANOVA analysis applied to data sets from each of the five regions separately could not distinguish meiofaunal abundances between the two habitats either (statistics not shown). Similar results were obtained based on benthic copepod abundance, which showed a sharper depth gradient clearly

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distinguishing between the very shallow stations (< 500 m) and those down to 1500 m as well as from the rest (Table 2).

DISTLM results complemented those of PERMANOVA, indicating that depth explains a significant amount of the variation in meiofaunal abundance (Table 3), which appears to decrease with depth (Fig. 4a). The variation explained was higher for basin as compared to slope habitat (Table 3). The same bathymetric pattern was also observed for copepod abundances (Table 3) and in all the studied Mediterranean areas except from the central part (statistics not shown).

3.2 Diversity

3.2.1 Meiofaunal taxa

Overall, 27 meiofaunal taxa were encountered in all studied areas and habitats (ϵ -diversity). Of these, only nematodes and copepods were found at all stations and samples, which along with polychaetes, tardigrades and halacaroids were found at all areas and habitats. Cnidarians were found only in slope stations, whereas aplacophorans, cumaceans, echinoderms and scaphopods were restricted to basin stations. The latter were found only at one station (northern Aegean, 1224 m depth).

Gamma diversity of the five studied regions was high (Fig. 5a) reaching the highest value in the Aegean Sea (24 and 23 taxa at the northern Aegean and the Cretan Sea, respectively) whereas, the lowest value was found at the central Mediterranean area (13 taxa, Fig. 5a). TR ranged from two to 18 in the central Mediterranean and the northern Aegean basin, respectively and from three to 16 at deep-sea slopes of the Libyan sea (α -diversity, Fig. 4b). With the exception of eastern Levantine, values of TR were higher at the basin habitat (Fig. 5a). Nevertheless, PERMANOVA results showed statistically significant differences in TR among depth ranges and not habitat (Table 2) pointing to similar bathymetric patterns with that of meiofaunal abundance. Indeed, DISTLM results for TR (Table 3) showed that depth explains a significant amount of the variation in the number of meiofaunal taxa, which decrease with increasing water

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depth (Fig. 4b). However, this bathymetric pattern could not be observed in all the Mediterranean regions but only within the Aegean and the Libyan seas (statistics not shown). Similar to meiofaunal abundance trends, variability in TR explained by depth was also higher in the basin habitat (Table 3).

3.2.2 Nematodes

A total of 155 genera were encountered in the 22 samples where nematode community analysis was conducted. Among these, three genera were found in all stations (*Acantholaimus*, *Halalaimus*, *Sphaerolaimus*) and six more genera were found in all areas and habitats (*Daptonema*, *Metasphaerolaimus*, *Microlaimus*, *Oxystomina*, *Pselionema*, *Syringolaimus*). 48 genera were restricted to one station of which 46 were found only in one sample.

Similar to TR, γ -diversity of nematodes peaked in the northern Aegean sea (108 genera, Fig. 5b), but it was lowest at the most eastern part of the basin, the Levantine (22). Likewise, α -diversity ranged from 13 in the eastern Levantine basin to 77 in the northern Aegean slope (Fig. 4c), and as opposed to TR, PERMANOVA results indicated differences in the number of nematode genera between habitats (Table 2); this pattern could not however be verified for each of the studied areas separately except from the Cretan Sea. Because the different depth ranges were not present in both habitats, depth was not included in the PERMANOVA design for nematode community analysis; nevertheless, DISTLM results indicated a significant dependence of NR on depth for the whole nematode data set and for the basin habitat, which explains more than 60% of its variability (Table 3). Similar to the rest of the univariate variables, NR decreases with depth (Fig. 4c).

The number of nematode genera predicted by the species richness estimator Jack1 for the whole investigated area, the basin and the slope habitat (mean \pm SD: 160 ± 10 , 128 ± 12 and 127 ± 11 , respectively) is very close to the one observed in the data set (155, 123 and 126). This estimator showed a clear sign of approaching an asymptote for the slope habitat (Fig. 6) despite the fact that the number of samples for this habitat

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is comparably low (12). As opposed to NR, Jack1 predicts no difference in nematode genera number between the two habitats as the confidence intervals of the two curves overlap (not shown in Fig. 6).

3.2.3 Microbial diversity

Pyrosequencing analysis produced 55213 16S rRNA pyrotags and a total of 9587 different OTUs were finally identified from the 19 samples analysed for microbial diversity. Richness was much higher at the basin compared to the slope habitat accounting for 7969 and 3329 different OTUs, respectively. Chao1 richness estimator predicted 19489 different microbial species, an extremely high microbial richness comparable to values found in the highly diverse soil environments.

DISTLM analysis indicated a marginally significant dependence of microbial diversity on depth for the whole microbial data set (Table 3), suggesting that, opposite to the rest of the benthic parameters, microbial richness tends to increase with depth (Fig. 4d). Nevertheless, this trend could not be verified separately for each of the two habitats.

3.3 Diversity change and community structure

3.3.1 Meiofaunal taxa

Delta diversity based on meiofaunal major taxa (Table 4) was similar at both habitats (PERMDISP $p > 0.05$) and rather high, suggesting greater variability in meiofaunal taxa composition within (> 38 %) than between habitats (22.22 %). At smaller scale (within depth ranges), beta diversity of the two habitats did not differ either (PERMDISP $p > 0.05$ for all depth categories) but variability appears to increase with depth for both basin and slope (Table 4). On the other hand, meiofaunal taxa turnover between the two habitats (Table 4) increases down to 1500 m depth after which it appears to stabilize close to a high value (~ 55 %). The same bathymetric trend was also observed

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when Jaccard dissimilarity was measured between the two habitats for stations of the same area and of similar depth (data not shown).

When the different depth ranges were tested (Table 4), differences in delta diversity were detected (PERMDISP $p < 0.01$) due to the low variability in meiofauna composition among the very shallow stations (< 500 m, 13.27 %; PERMDISP p of pairwise tests < 0.05 for all comparisons of the first depth range). Statistically significant differences were also found for beta diversity of depth ranges for the basin habitat but not for slope. Jaccard dissimilarity between depth ranges for the whole data set (delta diversity) was relatively increasing for depth categories deeper than 1500 m, indicating higher compositional differences in meiofaunal taxa towards greater depths. This pattern of bathymetric increase was stronger within the slope habitat but was not observed for basins (beta diversity), where values were rather high (89 % of values > 30 %) regardless of the depth category.

Further non parametric multivariate analysis provides support to the above results with nMDS plot of all stations illustrating the high variability in meiofauna structure within each habitat (Fig. 7a) and a gradient of meiofaunal communities with depth (Fig. 7b). PERMANOVA results indicated differences in meiofaunal taxa community among depth ranges but not habitat (Table 2). Meiofauna composition differed between the shallower (up to 1500 m depth) and the deeper stations (> 2500 m), however, the difference in structure is gradual as successive depth ranges appear similar in terms of meiofauna taxa down to 2000 m depth. Similar to the univariate variables, DISTLM analysis indicated that depth explains a significant variation of meiofaunal major taxa community (Table 3). This holds also when the analysis is applied separately for each habitat (Table 3) and within each Mediterranean region except from the central part (statistics not shown).

3.3.2 Nematodes

Differentiation diversity analysis of nematode community was performed only at the level of the whole data set (delta diversity), as at smaller scales (within each habitat

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and within each depth range) not all levels of each factor were present. PERMDISP revealed strong differences in multivariate dispersions between the two habitats (PERMDISP $p < 0.05$) with higher delta diversity recorded at the basin habitat (Table 5, 46.54%). A rather high Jaccard dissimilarity value was also recorded between the two habitats (39.35 %) indicating high variability in nematode community structure not only within but also between habitats. In contrast, no differences in delta diversity were detected between the different depth ranges (PERMDISP $p > 0.05$) which ranged between 17.72 % at the shallowest depth range and 41.14 % at 2500–3000 m depth range (Table 5). However, Jaccard dissimilarity between depth categories ranged within high values for all pairwise comparisons (41–75.3 %) suggesting high variability in nematode genera between depth categories.

One-way PERMANOVA results did not indicate differences between the two habitats for nematode community either (Table 2), which is also depicted in the relevant nMDS plot (Fig. 7c). Similar to nematode diversity analysis, depth was not included in this experimental design due to the lack of all depth ranges within each type of habitat and vice versa. However, as illustrated in Fig. 7d, nematode communities of most bathyal stations (slope stations down to 1000 m depth and basin stations down to 2000 m) are grouped separately from the rest suggesting that depth has an effect on nematode community structure. Indeed, DISTLM results (Table 3) indicated a significant relation between nematode community and depth, which is stronger for the slope habitat.

3.3.3 Microbial communities

DISTLM analysis found no correlation of microbial community with depth for the whole data set and the basin habitat, though it suggests ($p = 0.045$) correlation of microbes with depth when the slope stations are only considered (Table 3). nMDS enhanced these results as the lack of apparent grouping could not reveal any spatial pattern or gradient (plot not shown). Jaccard dissimilarity between the two habitats (82 %), among depth ranges (> 77 %) and samples (> 78 %) was very high, clearly indicating high variability of microbial communities at all spatial scales.

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4 Discussion

4.1 Standing stocks in the deep sea

In the energy-poor environment of the deep sea, many community parameters seem linked to food supply. The Mediterranean Sea is an unusually oligotrophic system with particular low levels of productivity in the Eastern Basin (Psarra et al., 2000). The low nutrient input is further diminished before reaching the deep-sea floor due to the high water temperatures (12.8–15.5 °C, Coll et al., 2010) and therefore, the organic content of the Mediterranean deep sediments is extremely low (Danovaro et al., 1999). As a result, benthic standing stocks in the Mediterranean are expected to be depressed. Nevertheless, there are areas in the Mediterranean Sea which are more productive. Such an area is the northern Aegean Sea mainly due to riverine outflows and the influx of nutrient-rich Black Sea waters (Poulos et al., 1997; Lykousis et al., 2002). As a consequence, higher faunal densities are anticipated for this area. The meiofaunal abundances reported in the present synthesis are indeed lower from those of similar depths in other oceans (for an extensive reference report see Gambi et al., 2010) but comparable to those recorded from similar Mediterranean deep-sea sediments (Tselepides and Lampadariou, 2004; Lampadariou and Tselepides, 2006; Lampadariou et al., 2009; Gambi et al., 2010), yet they fall within a wider range of values (2–1249 ind/10 cm²). Our data also confirms the prediction of higher faunal densities in the northern Aegean Sea, as the higher meiofaunal density was measured in this area.

One of the best known gradients in marine sediments is that of abundance with water depth. Similar to all benthic groups, the relationship of meiofaunal density and depth has been found to be significant and negative (Rex et al., 2006). This general pattern has been mainly related to organic matter input, food limitation and food quality (Rex et al., 2006; Soltwedel, 2000), although it is also suggested to be locally influenced by a number of factors such as the hydrography of the area and the sediment type (Gambi et al., 2010; Rex and Etter, 2010). Our results are in agreement with this general bathymetric trend of abundance and indicate the existence of this pattern for

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meiofauna in all the eastern Mediterranean basins (all investigated areas except from central Mediterranean) irrespective of the type of habitat or investigated taxon.

In a pan-Mediterranean deep-sea meiofauna study Gambi et al. (2010) reported that meiobenthic abundances at slopes were higher than other investigated types of habitats, including basins. Our findings contradict these results but are in agreement with Netto et al. (2005) who found no differences between the two habitats in the deep sea off SE Brazil. Because slope stations are usually found in shallower areas higher meiofaunal abundances would be expected at this habitat. However, the high variability within each type of habitat probably related to environmental heterogeneity at smaller scale may be the reason that statistical analysis could not indicate differences.

4.2 Small-size benthos diversity

The number of meiobenthic metazoan taxa encountered in our study is higher than any other reported not only in the Mediterranean Sea but worldwide (Gambi et al., 2010 and references therein). This finding could be an artefact of the treatment of the data sets as in most review or synthesis papers ambiguous taxa are usually grouped together (e.g. different classes of Mollusca), especially when the data set is from different sources or research groups. In the case of the present synthesis, meiofauna classification was retained down to the lowest possible level as meiofaunal samples were treated by the same research group. Likewise, the number of nematode genera identified in the present study (155) is among the highest reported until now from the Mediterranean deep-sea (extensive bibliographic report in Miljutin et al., 2010) and most probably the highest, as only Soetaert and Heip (1995) found a higher number of genera (163), which however was based on deep-sea and shelf-break sites from the Mediterranean as well as from the North Atlantic.

At smaller scale, meiobenthic γ -diversity of the five studied areas was also high, regardless of the taxonomic level of the analysis, and peaked in the Aegean Sea. The lowest number of major meiofaunal taxa found at the central Mediterranean area is consistent with previous bibliographic reports (Gambi et al., 2010 and references therein),

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however it may be related to the lowest sampling effort from this region. On the other hand, the lower nematode genus richness in the most eastern part of the basin, the Levantine, may well depict the well-known west-eastward decrease of productivity and may also be an indication for a link between surface productivity and deep-sea nematode diversity (Lampadariou and Tselepides, 2006; Lamshead et al., 2000, 2002).

In a recent study on global patterns of marine microbial communities Zinger et al. (2011) obtained more than 120 000 OTUs, of which almost 41 000 were reported in the deep sea. In the Mediterranean deep-sea sediments, bacterial richness has been found to range from 13 to 1306 OTUs per gram of surface sediment (Luna et al., 2004; Polymenakou et al., 2005b, 2009), but estimations exceed 4000 species (Danovaro et al., 2010). In our study, microbial communities of the deep Mediterranean Sea were analyzed for the first time by applying the powerful tool of 454 pyrosequencing. This method is expected to increase significantly the estimates of microbial species richness (Danovaro et al., 2010) as it can detect the rare taxa that cannot be analyzed through the traditional Sanger based sequencing analysis. Indeed, a much higher number of bacterial OTUs (9587) than any previously reported from the Mediterranean deep-sea was detected in the present study, while Chao1 richness estimator predicted a number which is at least one order of magnitude higher from any previous estimates from the Mediterranean sediments (~ 1306 OTUs in Polymenakou et al., 2005b). From these results, it is evident that the deep Mediterranean sediments harbour an incredibly high microbial diversity.

4.2.1 Bathymetric patterns of alpha diversity

Biodiversity research in the deep sea has largely concentrated on revealing bathymetric patterns of benthic communities. For many taxa, mainly macrobenthic, a parabolic pattern has been described (reviewed in Rex and Etter, 2010) with a maximum at intermediate depths, i.e. between 1500 and 2500 m, while several factors, such as surface productivity, geology, hydrology and evolutionary history of the area, are hypothesised for the explanation of the observed trends. On the other hand, bathymetric patterns of

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meiofaunal diversity have been generally found to be similar to that of abundance, with a decrease in richness with increasing depth for major taxa (Danovaro et al., 2008, 2009b; Gambi et al., 2010) and copepod species (Baguley et al., 2006), whereas nematode richness patterns are either absent or not consistent among different areas or habitat types (Lampadariou and Tselepidis, 2000; Danovaro et al., 2009a,b, 2010). Our results are in agreement with the general trend of meiobenthic diversity, as non parametric regression analysis revealed a highly significant negative correlation of TR and NR with depth within the whole investigated area and within each type of habitat. Moreover, the high variability explained by depth for the basin ecosystem suggests that the decrease in diversity with depth is sharper at the basin environments. The observed bathymetric pattern was not, however, discernible within each of the investigated areas, providing strong support to the suggestion of Danovaro et al. (2009a) that meiobenthic diversity patterns depend also on topographic and ecological features.

Although there is considerable gap in the study of spatial microbenthic patterns, it has been found that microbial diversity is similar among sediments of variable bathymetry and thus it is not affected by depth (Li et al., 1999a; Danovaro et al., 2010; Polymenakou personal observation). Contrary to those previous observations, our results suggest an increase of microbial richness with depth, which could not however be verified independently within each of the two habitats. In Tselepidis et al. (2007), the authors argue that high microbial diversity in the Eastern Mediterranean has evolved so that a system under starvation stress is able to utilise any quantity or quality of organic matter available. Clearly, more observations are required as well as the investigation of plausible explanatory factors before reaching a conclusive pattern. We could cautiously though speculate that the food-limited environment of the central-eastern Mediterranean basin might have been the stress factor that led to the evolution of a diverse community in order to use the available food resources more effectively.

4.2.2 Habitat-related diversity

Although much of the variability in deep-sea diversity has been closely related to depth gradient and depth-related factors, it is now greatly appreciated that the high complexity of the seafloor affects biodiversity levels and patterns (Levin et al., 2001; 2010; Vanreusel et al., 2010). Therefore, documenting and comparing the diversity of different types of habitats will help understand the complicated patterns of diversity in the deep sea. Slopes and deep-sea basins are two major habitats with inherent differences due to their wide variability in environmental settings. Thus, differences in the communities they host and in biological patterns could be found between these two habitats. Yet results based on recent meiobenthic studies are rather contradicting. Danovaro et al. (2009a) and Gambi et al. (2010) found higher diversity in slopes based on major taxa and nematode species of European margins and on major taxa from the Mediterranean, respectively; Vanreusel et al. (2010) based on nematode genera reported no differences between these two habitats on a global scale; and Netto et al. (2005) in a deep-sea study off SE Brazil showed that the results differ depending on the taxonomic level of analysis (higher diversity at slope for major taxa, no differences for nematode families, higher diversity at deep-sea basin for nematode genera).

Our detailed study suggests that no differences in diversity between the two habitats should be expected in the central-eastern basin of the Mediterranean. Although the number of major meiofaunal taxa was on average higher at the basin environment, the only exception being eastern Levantine, this difference was not statistically significant. Opposite to this, non parametric statistical analysis based on the observed number of nematode genera indicated that slopes are more diverse. Nevertheless, the results of true richness estimator Jack1 are consistent with the results based on major taxa suggesting no difference between the two habitats for nematode genera diversity as well. Despite the fact that more basin than slope samples were included in the analysis for nematode richness estimation, the shape of Jack1 curves reveals that whilst slope samples are sufficient for estimating nematode genera richness in the area (the curve

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reaching an asymptote), more basin samples are needed. This is rather a result to be expected as in deep-sea plains metazoan abundance is reduced and the animals are sparsely distributed pointing to the need of a more intense sampling in order to collect more rare species. This becomes even more imperative due to the patchy distribution of meiobenthic metazoan (Giere, 2009). It is also worth noting that the number of samples available for the nematode community analysis did not allow incorporating depth as a factor in the analysis. Thereby, no control for depth was possible and we cannot therefore preclude the possibility that the observed differences between the two habitats may be a consequence of differences in sampling depths. Apart from sampling effort, increased heterogeneity within the habitats may be another explanatory factor, as has been previously suggested (Levin et al., 2001; Vanreusel et al., 2010; Levin and Sibuet, 2012). Local variability in various environmental conditions within each habitat, including substrate structure, hydrology, food input and disturbance, results in higher habitat complexity with probably more microhabitat-specific species. As a result, within habitat variability may be higher than between habitats.

So far, comparative microbial studies of the two studied habitats are not available. The first report on benthic microbial communities from different types of ecosystems was provided very recently by Zinger et al. (2011). Similar to the study of Sogin et al. (2006), this study demonstrated that the deep-sea sediments were more diverse than other types of ecosystems, such as vents, anoxic habitats and open ocean surface waters. Our study is the first comparing microbial communities from basin and slope ecosystems and clearly indicates that the deep-sea basins harbour more diverse microbial communities than the slopes. Similar to the bathymetric pattern we observed for microbial richness, this excess of diversity in the deep-sea basins is difficult to be explained. Although environmental data are not considered here and available information on microbial communities is still very limited, the higher microbial richness of the basin may be explained on the basis of the source-sink hypothesis proposed by Rex et al. (2005), according to which, deep-sea basins act as sinks of food sources, therefore offering higher availability and variability of food, which ultimately is shaped into

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biodiversity. On the other hand, slope environments, in particular the steeper slopes, are known to experience strong perturbations due to current flow, landslides, or other sediment instability factors (Canals et al., 2009), which may affect benthic communities.

4.2.3 Turnover: patterns of change in diversity and community structure

Local diversity in deep-sea sediments is not only high but also quite variable (Rex and Etter, 2010). Following the discussion on diversity results, turnover diversity underlines the observed richness patterns. The high delta diversity of the two habitats for both levels of taxonomic analysis clearly indicates the high variation in meiofaunal composition in basin and slope ecosystems. When focusing exclusively on nematode community, the variation should also be expected to be higher within the basin habitat. As has already been stated, the deep sea is characterized by a wide variation of habitats due to local topographic and other environmental features, which may also account for differences in meiofaunal communities. Indeed, differentiation diversity in marine sediments has been positively related to environmental heterogeneity (Ellingsen, 2002; Ellingsen and Gray, 2002; Anderson et al., 2006).

At smaller scale (within depth range), beta diversity of the two habitats ranges at low to moderate values (23–40%), yet it shows a bathymetric trend of increasing values with depth, suggesting that meiofauna community varies more as we move deeper. This is in agreement with the findings of Ellingsen (2002) that several measures of beta diversity correlate with depth. In a rather similar way, meiofaunal taxa turnover between the two habitats increases down to mid-slope depths (~ 1500 m) after which the variation in meiofaunal taxa between basin and slope appears to be equally high, pointing to constantly high meiofaunal differences between habitats closer to the abyssal zone.

Rex and Etter (2010) in their synthesis book on deep-sea biodiversity conclude that the rate of change in species composition is especially pronounced along depth gradients in the deep sea, and they further state that the rate of faunal replacement is roughly proportional to the rate of change in depth, therefore being higher in the bathyal zone and lower in the abyssal plain. In our study, the overall high values of nematode

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Jaccard dissimilarity between depth ranges, and the increase of Jaccard dissimilarity with depth in the case of major taxa composition indicate that in the Mediterranean Sea meiofaunal composition differs more towards the abyss. This is further supported by PERMDISP results as the rate of change in major taxa composition is low within the shallower stations (< 1000 m) and differs from the other depth categories, whereas no statistically significant differences in either delta or beta diversity were indicated among depth ranges deeper than 500 m. A roughly similar result was also obtained based on nematode genera, with no differences in the low to moderate values of delta diversity among all depth categories. In a study on diversity from Atlantic and Mediterranean margins (Danovaro et al., 2009b), dissimilarity results used for exploring differences among habitats and areas appear similar to ours when major taxa composition is considered, with lowest values of beta diversity within the group of 500 m depth stations and higher and rather similar values of dissimilarity for deeper stations (1000 and 2000 m). When nematode composition changes are investigated, dissimilarity values are increased also, and with the exception of the very high dissimilarity at the shallow stations of the Portuguese margin, they appear similar among all three depth categories in Mediterranean slopes. The observed differences within and between the two studies clearly indicates that the beta diversity component of meiofaunal communities needs further and substantial investigation in order to clarify bathymetric patterns of different taxa in various environmental settings.

All the above results are summarised and depicted in the ordination plots with the observed differences and gradients statistically supported by non parametric multivariate analysis. Indeed, meiofaunal community varies greatly within each of the two investigated habitats and is greatly affected by depth. More specifically, its structure was found to differ significantly between the bathyal and the abyssal stations; nevertheless, the change is gradual, with assemblages of nearby depth categories appearing more similar than distant ones, in particular with regard to major taxa composition. Moreover, the fact that the deeper stations (> 3000 m) group together suggest a stable synthesis of major meiofaunal taxa in abyssal sediments. A similar pattern was also

reported by Danovaro et al. (2008) that found nematode assemblages to differ among three depth categories (1000, 3000, 4000 m) in the Mediterranean Sea. Apparently, the limited number of stations and consequently the few depth categories involved in that study could not have allowed the detection of the bathymetric gradient reported here.

5 In their comprehensive study on global patterns of marine microbes, Zinger et al. (2010) found less variable communities in the deep sea sediments compared to the coastal environment and suggested that this is due to the lower environmental dynamics of the nutrient-poor deep sea. In contrast, our results indicate a highly variable microbial community in the Mediterranean deep-sea exceeding 77% in dissimilarity
10 even between samples of the same habitat, area or similar bathymetry. Although further investigation is needed to unravel patterns of microbial diversity, the results of our study support the idea of a dynamic deep-sea environment characterised by habitat heterogeneity and regular or episodic disturbances.

5 Conclusions

15 Deep-sea slopes and basins are two habitats with inherent differences due to their wide variability in environmental settings. Nonetheless, existing heterogeneity within each habitat owing to local/regional features and variation in environmental conditions may lead to higher “within” than “between” habitat variability. Indeed, the results presented here indicate high within habitat variability of all meiobenthic variables and suggest
20 that neither strong nor consistent differences should be expected between basin and slope ecosystems in the deep Mediterranean Sea. In contrast, depth appears once more as an overriding correlate with changes in deep-sea benthos, in particular within the basin habitat. Meiofaunal abundance and richness clearly diminish with depth and community structure changes gradually from the shallower bathyal to the abyssal sediments. This shift in meiobenthic community along the depth gradient is also evident
25 in β - and δ -diversity components that are not only high within and between the investigated depth ranges but also appear to increase with depth. Depth has an effect on

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microbial richness as well, but opposite to the metazoan patterns it appears to increase in the deep Mediterranean basin. Though depth is recognised as a major parameter affecting deep-sea patterns it must be borne in mind that several other depth-related factors may drive the observed patterns.

5 **Supplementary material related to this article is available online at:**
**[http://www.biogeosciences-discuss.net/9/17539/2012/
bgd-9-17539-2012-supplement.zip](http://www.biogeosciences-discuss.net/9/17539/2012/bgd-9-17539-2012-supplement.zip)**

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Table 1. Overview of projects, surveys and investigated areas involved in the present study.

Project/Expedition	Survey	Area	No of Stations	Depth range (m)
MATER	Mar-1997 Sep-1997	Northern Aegean, Cretan Sea	13	115–2273
METEOR 40	Dec-1997	Northern Aegean, Cretan Sea, Libyan Sea	8	1221–4261
TransMed	Jun-1999	Central Mediterranean, Eastern Levantine, Libyan Sea	4	2950–3870
ADIOS	Oct-2001	Central Mediterranean	3	2786–2837
BIODEEP	Aug-2001	Central Mediterranean	5	3080–3424
HERMES	May-2006	Cretan Sea, Eastern Levantine, Libyan Sea	10	508–3603
METEOR 71	Dec-2006 / Jan-2007	Eastern Levantine, Libyan Sea	4	2014–4392
BIOFUN	Jun-2009	Central Mediterranean, Libyan Sea	5	1204–3335
HERMIONE & REDECO (joint cruises)	Jan-2010 May-2010 May-2011	Eastern Levantine, Cretan Sea, Libyan Sea	21	874–3607

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Table 2. PERMANOVA results of the effects of habitat and depth for uni- and multivariate meiofaunal variables. Where statistical significant differences were indicated pairwise comparisons were done.

Variable	Source	F	p	A posteriori pairwise comparisons							
Meiofaunal abundance	Habitat x Depth	2.931	0.0046								
	Habitat	0.582	0.5592								
	Depth	6.287	0.0001	Within habitat: basin <500 500-1000 1000-1500* 2000-2500 2500-3000* 3000-3500 >3500 1500-2000							
				Within habitat: slope <500 500-1000 2000-2500 1000-1500 1500-2000 2500-3000							
Copepod abundance	Habitat x Depth	1.0318	0.3813								
	Habitat	1.583	0.1984								
	Depth	7.8645	0.0001	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500
Major taxa richness	Habitat x Depth	1.401	0.2374								
	Habitat	3.185	0.0768								
	Depth	7.936	0.0001	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500
Nematode richness ¹	Habitat	5.1425	0.0343								
Meiofaunal community	Habitat x Depth	1.5549	0.0582								
	Habitat	1.3677	0.2243								
	Depth	4.9251	0.0001	<500	500-1000	1000-1500	1500-2000	2500-3000	2000-2500	>3500	3000-3500
Nematode community ¹	Habitat	1.6703	0.0983								

* statistically significant differences between habitats for the specific depth range at p < 0.05

¹ One-way PERMANOVA (depth was not included in the experimental desing)

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Table 3. Results of DISTLM analysis for exploring relationships of benthic parameters with depth.

Variable	<i>F</i>	<i>p</i>	Variability
Overall			
Meiofauna abundance	43.261	0.0001	0.392
Copepod abundance	49.597	0.0001	0.425
Major taxa richness	44.478	0.0001	0.399
Nematode richness	35.299	0.0002	0.638
Microbial richness	4.851	0.0439	0.222
Meiofaunal community	30.290	0.0001	0.311
Nematode community	7.508	0.0001	0.273
Microbial community	1.278	0.1850	0.070
Basin			
Meiofauna abundance	31.111	0.0001	0.420
Copepod abundance	30.289	0.0001	0.413
Major taxa richness	48.147	0.0001	0.528
Nematode richness	19.624	0.0016	0.621
Microbial richness	0.072	0.7876	0.007
Meiofaunal community	21.238	0.0001	0.331
Nematode community	5.914	0.0006	0.330
Microbial community	0.69801	0.6189	0.065
Slope			
Meiofauna abundance	10.727	0.0015	0.328
Copepod abundance	26.752	0.0001	0.549
Major taxa richness	8.2169	0.0079	0.272
Nematode richness	5.6115	0.0682	0.483
Microbial richness	0.7223	0.4632	0.126
Meiofaunal community	9.7574	0.0003	0.307
Nematode community	4.3778	0.0055	0.422
Microbial community	1.7881	0.0448	0.263

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Table 4. Differentiation diversity based on major meiofaunal taxa Jaccard dissimilarity. Values within each habitat and within each depth range were calculated using multivariate dispersion. Dissimilarity increases from 0 to 100.

		δ -diversity								
<i>Within habitats</i>	Basin									
	Slope									
		42.00	38.45							
<i>Between habitats</i>		22.22								
<i>Within depth ranges</i>	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500		
	**	13.27	33.31	39.1	38.73	30.16	38.81	35.54	40.83	
<i>Between depth ranges</i>	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500		
	500-1000	26.09								
	1000-1500	30.77	22.22							
	1500-2000	33.33	16.67	22.22						
	2000-2500	47.62	36.36	46.15	43.48					
	2500-3000	28.57	18.18	30.77	18.18	31.58				
	3000-3500	35.00	39.13	42.31	31.82	38.89	26.32			
	>3500	45.45	41.67	38.46	34.78	42.11	38.10	36.84		
			β -diversity							
	<i>Within habitats</i>	Basin								
Slope										
		22.59	29.23							
		25.96	36.92							
		30.76	37.24							
		39.93	n/a							
<i>Between habitats</i>		<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500	
		16.67	40.91	50.00	40.91	57.14	55.56	n/a	n/a	
<i>Within depth ranges</i>	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500		
	Basin *	n/a	22.59	25.96	30.76	24.60	39.93	35.54	40.83	
	Slope	13.89	29.23	36.92	37.24	16.67	n/a	n/a	n/a	
<i>Between depth ranges</i>	<500	500-1000	1000-1500	1500-2000	2000-2500	2500-3000	3000-3500	>3500		
				Slope						
	<500	27.27	36.36	47.62	73.68	63.16				
	500-1000	33.33	19.05	38.10	70.00	60.00				
	1000-1500	36.36	43.48	22.22	66.67	55.56				
	1500-2000	36.36	36.36	38.46	57.14	53.33				
	2000-2500	47.37	47.37	54.17	40.91	25.00				
	2500-3000	26.32	35.00	44.00	22.73	31.58				
	3000-3500	33.33	42.11	36.36	36.36	38.89	26.32			
	>3500	45.00	52.38	39.13	31.82	42.11	38.10	36.84		

* statistically significant differences among levels at $p < 0.05$

** statistically significant differences among levels at $p < 0.001$

n/a: Few samples for running PERMDISP

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Table 5. Differentiation diversity based on nematode genera Jaccard dissimilarity. Values within each habitat and within each depth range were calculated using multivariate dispersion. Dissimilarity increases from 0 to 100.

		δ -diversity							
Within habitats	Basin	Slope							
*	46.54	40.67							
Between habitats	39.35								
Within depth ranges	< 500	500–1000	1000–1500	1500–2000	2000–2500	2500–3000	3000–3500	> 3500	
	17.72	n/a	37.96	35.74	28.07	41.14	39.43	29.63	
Between depth ranges	< 500	500–1000	1000–1500	1500–2000	2000–2500	2500–3000	3000–3500		
500–1000	44.00								
1000–1500	47.46	46.55							
1500–2000	47.06	50.49	47.86						
2000–2500	56.84	63.27	56.36	60.42					
2500–3000	65.00	65.66	61.06	56.99	53.25				
3000–3500	59.18	59.79	55.86	59.79	41.10	50.65			
> 3500	75.29	74.70	74.51	71.60	66.67	61.67	61.29		

* Statistically significant differences among levels at $p < 0.05$.

n/a: few samples for running PERMDISP.

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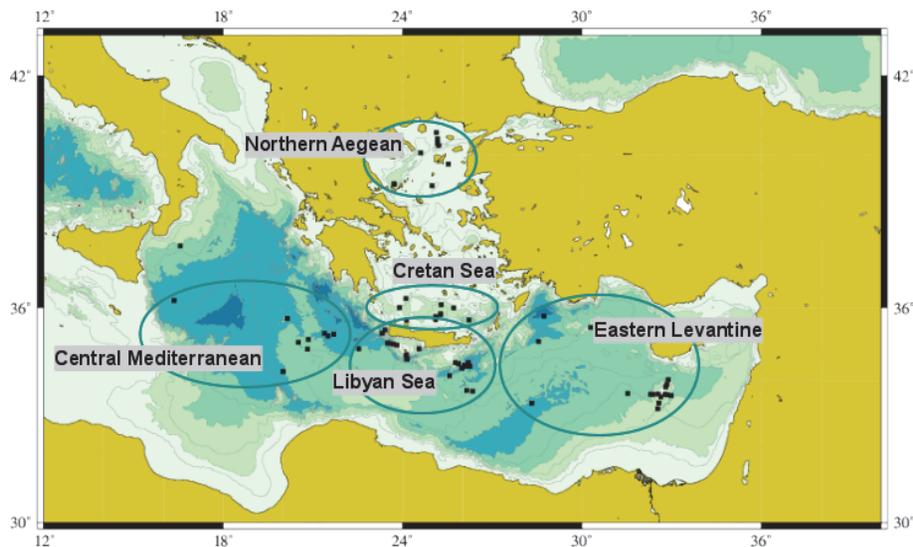


Fig. 1. Study areas and sampling stations along the Mediterranean Sea.

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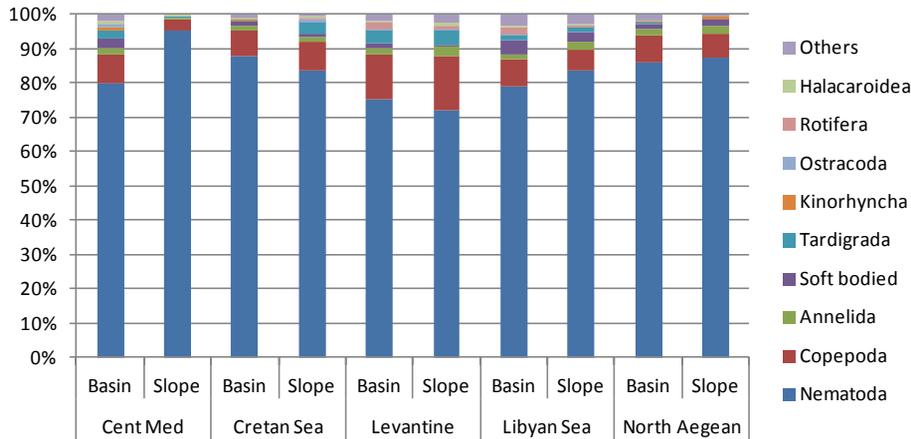


Fig. 2. Meiofauna composition per studied area and habitat.

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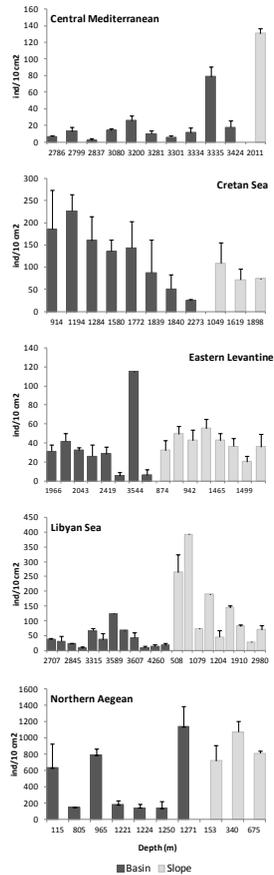


Fig. 3. Nematode abundance per studied area and habitat in relation to depth. Note in x-axis the arrangement of depth in increasing order for each habitat separately.

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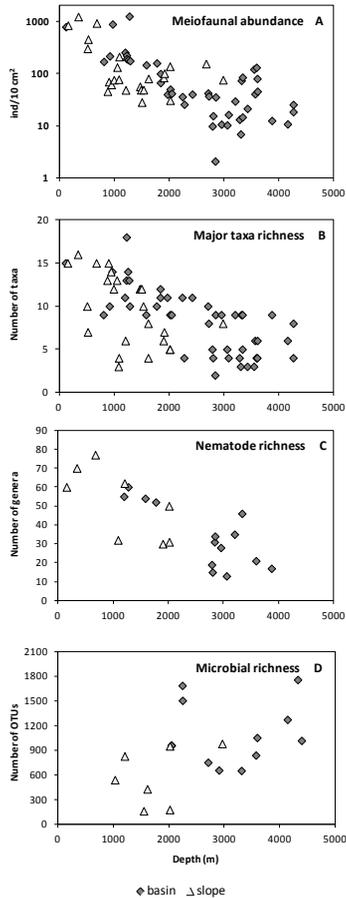


Fig. 4. Bathymetric gradient of **(A)** meiofaunal abundance ($n = 69$), **(B)** major taxa richness ($n = 69$), **(C)** nematode genus richness ($n = 22$) and **(D)** microbial richness ($n = 19$). Note the logarithmic scale for meiofaunal abundance.

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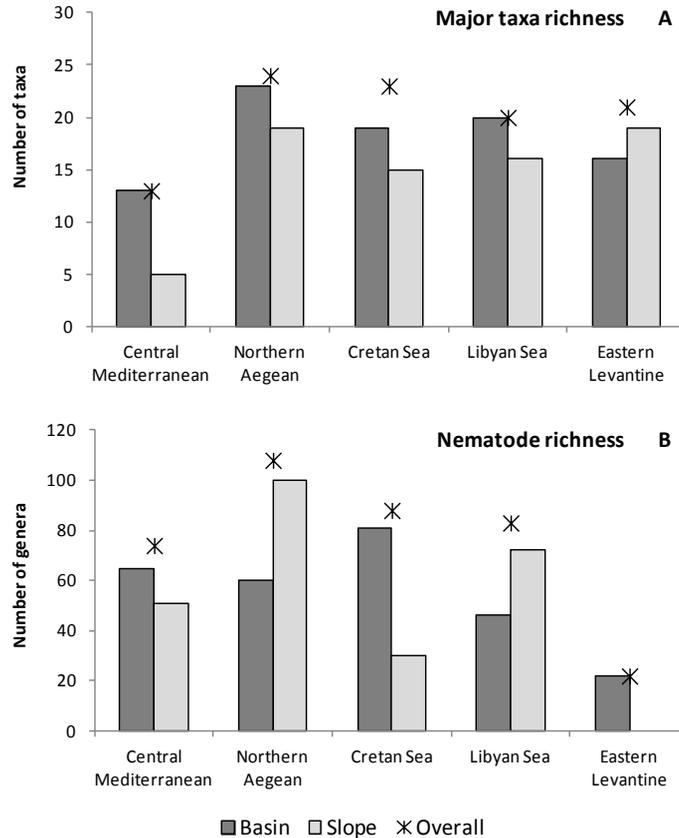


Fig. 5. Meiofaunal diversity per studied area and habitat based on **(A)** major meiofaunal taxa, **(B)** nematode genera.

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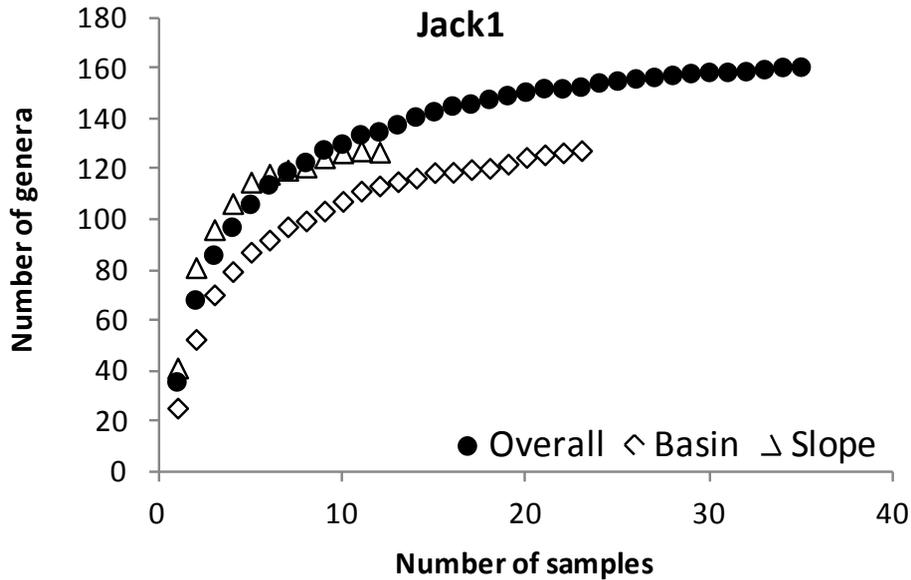


Fig. 6. Richness estimator Jack1 for nematode genera.

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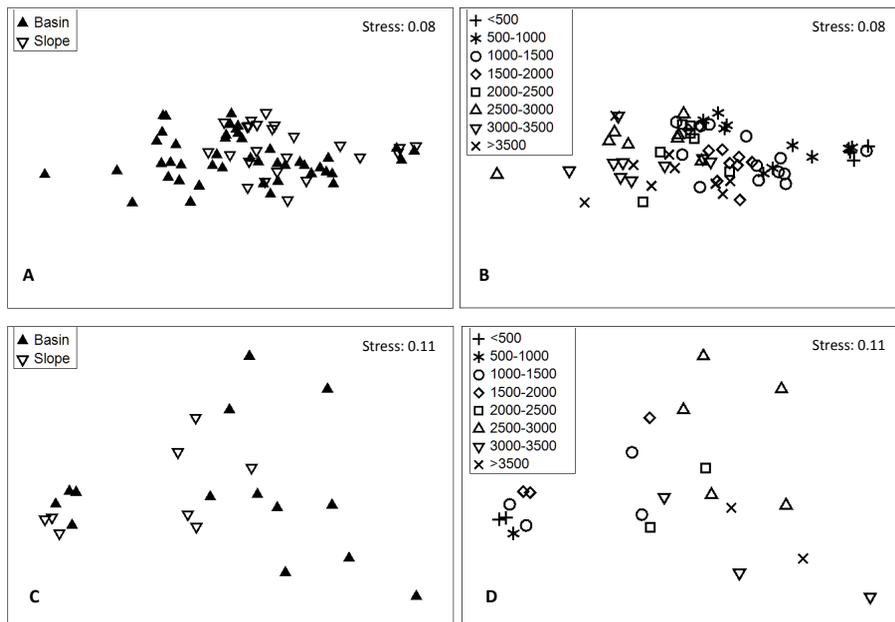


Fig. 7. nMDS ordination based on **(A–B)** major meiofaunal taxa and **(C–D)** nematode genera composition with symbols indicating **(A, C)** habitat and **(B, D)** depth.

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