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Turnover diversity drives large-scale biodiversity patterns in bathyal sediments of the Mediterranean Sea

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Abstract

Understanding biodiversity patterns and how they are driven at different spatial scales is a crucial issue in ecological studies. This is particularly evident for the deep sea, the largest biome of the biosphere, where information on the scales of spatial variation is very scant. Here, we investigated deep-sea nematodes species richness, turnover and functional diversity, and life strategies at different spatial scales (from local to macro-regional) to identify the factors that shape regional (γ) and macro-regional (ε) deep-sea diversity. This study was conducted in several deep-sea habitats (canyons, open slopes, deep-water corals, and bathyal plains) over > 2000 km across the whole Mediterranean basin, at a fixed depth of ca. 1000 m. Our results indicate that the patterns of local (α) diversity across the deep Mediterranean follow the gradients of the trophic conditions, which decrease from the Western to the Eastern basins. For all of the sites and habitats, the α-diversity is generally low. Conversely, the turnover diversity changes significantly among habitats (β-diversity) and between regions (δ-diversity), showing values of dissimilarity (based on species presence/absence) between 59 % and 90 % for β-diversity and between 81 % and 89 % for δ-diversity. This suggests that patterns and values of regional (γ) and macro-regional (ε) diversity in the deep Mediterranean Sea are related to turnover diversity among habitats and between regions (β- and δ-diversity), rather than to the local biodiversity (α-diversity). These results indicate that the differences in β-diversity and δ-diversity are even more important than those for the α-diversity for the understanding of the drivers of biodiversity in the deep Mediterranean Sea. These data also allow us to conclude that habitat heterogeneity (and type) and gradients in environmental conditions, by promoting a high turnover diversity across the deep Mediterranean Sea, are crucial players for the nematode diversity levels.

1 Introduction

A comprehensive understanding of the patterns of biodiversity requires the identification of the drivers that generate these patterns and of the biodiversity components that respond to these drivers. High values of regional diversity can arise from a combina-
5 tion of local and turnover diversities (Loreau, 2000; Koleff and Gaston, 2002; Witman et al., 2004), or they can arise from one single component. The drivers of local (α) and habitat turnover (β) diversities are likely to be different, as α-diversity is generally associated with high abundance and high resource availability, whereas β-diversity can be more sensitive to the heterogeneity of the habitat and/or of the resource distribution
10 (Lambshead et al., 2002; Soininen et al., 2008; Levin et al., 2010).

Deep-sea ecosystems represent the most extensive biome of the Earth, as they cover ca. 65 % of the Earth surface and account for 95 % of its volume. Together with the rain forests, deep-sea ecosystems host the largest portion of the yet-to-be-discovered biodiversity and have key roles in global biogeochemical cycles (Danovaro
15 et al., 2010). For a long time, deep-sea ecosystems have been believed to be characterized by very low diversity (Grassle, 1989). However, research conducted over the last few decades has changed our perceptions (Rex and Etter, 2010). Despite the typically low abundance of the fauna of deep-sea ecosystems, their evenness and expected species richness are indeed amongst the highest on Earth (Danovaro et al.,
20 2010). We have also assumed for centuries that the deep-sea floors are characterized by flat and monotonous desert-like landscapes, although, due to the present availability of sophisticated technologies, we know that the deep-sea floors are far more complex and heterogeneous than was previously believed (Danovaro et al., 2009a, b, 2010; Ramirez-Llodra et al., 2010; Vanreusel et al., 2010; Ingels et al., 2011). However, the
25 patterns of deep-sea biodiversity and the factors that control these patterns remain controversial (Snelgrove and Smith, 2002; Danovaro et al., 2008a, 2010).

As observed for terrestrial ecosystems (Gaston, 2000), the presence of different habitats (such as canyons, open slopes, landslides, and bathyal and hadal plains) can

certainly influence the distributions of deep-sea species (Rex et al., 2006; Ramirez-Llodra et al., 2010; Vanreusel et al., 2010). Deep-sea canyons, for instance, are characterized by high hydro-dynamism, as they are "fast-track" corridors for materials and organisms that are rapidly transported from the land to the deep sea (Canals et al., 2006; Tyler et al., 2009; Pusceddu et al., 2010a, 2012). Some of these systems, such as seamounts, deep-water corals and cold seeps, contain many deep-sea species and have a high level of endemism, which are possibly linked to the peculiar environmental and geomorphological conditions (Raes and Vanreusel, 2006; Roberts et al., 2006; Vanreusel et al., 2009).

The Mediterranean region is a "hot-spot" of terrestrial biodiversity, with a high fraction of endemic species (Myers et al., 2000). Despite its small dimensions (0.82 % of the global ocean surface, and 0.32 % of the global ocean volume), the Mediterranean Sea hosts approximately 17 000 marine species (7.5 % of the global marine biodiversity; Coll et al., 2010). This "miniature ocean" can therefore also be considered as a hot-spot of marine biodiversity, which is characterized by the co-occurrence of temperate and subtropical organisms.

In all deep-sea sediments, nematodes are the most abundant metazoan taxon, and they are ubiquitous in all of these habitats, with their dominance increasing with increasing water depth (typically > 80–90 % of the total faunal abundance in the deep sea, Danovaro et al., 2002). Nematodes are also characterized by high species richness, and they have key roles in benthic trophodynamics, which provides an excellent opportunity for the testing of ecological hypotheses (Danovaro et al., 2008b, 2010).

In the present study, we used marine nematodes as a model for comparing the patterns of local (α), regional (γ) and macro-regional (ε) diversity, as well as habitat (β) and regional turnover (δ) in different deep-sea habitats (canyons, open slopes, deep-corals and bathyal plains) over > 2000 km of the Mediterranean basin. The habitats investigated are characterized by different topographic settings, productivities and physical-chemical conditions, although they are located at approximately the same depth (ca. 1000 m). We tested the hypothesis that the key variable that generates

patterns of deep-sea biodiversity is the turnover diversity, which in turn is influenced by the spatial heterogeneity. We also determined the effects of increasing the spatial scale of observation on the turnover diversity.

2 Methods

2.1 Study area and sampling

Sediment samples were collected from three regions of the Mediterranean Sea: the North-Western, Central and Eastern basins. In each region, samples were collected from the different habitats at approximately 1000 m in depth, from a total of 18 sampling areas (Fig. 1; Table 1).

In the North-Western Mediterranean, the samples were collected from two different canyons (i.e. Cap de Creus and Lacaze-Duthiers canyons) and from two open slopes adjacent to the two canyons (northern and southern open slopes); all of these sites are located in the Gulf of Lions.

In the Central Mediterranean, the samples were collected from two canyons (the B and C Bari canyons) and from two open slopes adjacent to the canyons (northern and southern open slopes), along the South Adriatic margin. Samples were also collected from two sites that are characterised by deep-water coral rubble (northern and southern deep-coral sites) along the Ionian margin, and from one site in a bathyal plain (Central Mediterranean bathyal plain).

In the Eastern Mediterranean, the samples were collected from one canyon (Samaria canyon) and from two adjacent open slopes (Eastern and Western open slopes), along the Cretan margin, and from four sites along the bathyal plain. The geographical coordinates and water depths of all of these sampling sites are given in Table 1.

The sampling was carried out during several oceanographic cruises, from September 1989 to May 2006, using different research vessels. At all of the sampling sites, replicate sediment samples were collected (two independent deployments at each site),

using a NIOZ-type box corer that allows the recovery of apparently undisturbed sediment samples. Three sediment cores (internal diameter, 3.6 cm) from independent deployments (whenever possible) of the box corer were analysed for their nematode species diversities (from the 0–1 cm sediment layer). Sediment samples for organic matter analysis (the top 1 cm from 3 different cores from each site) were preserved at $-20\,°C$ until analysis in the laboratory.

2.2 Nematode biodiversity

All of the meiofaunal organisms, including the nematodes, had previously been extracted from the sediment. The sediment samples had been sieved through a 1000 µm mesh, with a 20 µm mesh then used to retain the smallest organisms. The fraction remaining on the 20 µm sieve was re-suspended and washed three times ($800 \times g$, 10 min, room temperature) in Ludox HS40 colloidal silica (density, $1.31\,g\,cm^{-3}$; according to Heip et al., 1985; Danovaro, 2010). All of the animals that remained in the supernatant were again passed through a 20 µm mesh net, washed with tap water, stained with $0.5\,g\,L^{-1}$ Rose Bengal solution, and sorted under a stereomicroscope (magnification, $40 \times$), according to Danovaro (2010). For the nematode diversity analysis, 100 nematodes for each of the three replicates (or all of the nematodes when the abundance was lower than 100 specimens per sample) were mounted on slides, following the formalin-ethanol-glycerol technique to prevent dehydration (Seinhorst, 1959; Danovaro, 2010). The nematodes were identified to species level according to the presently used manuals (Platt and Warwick, 1983, 1988; Warwick et al., 1998; Deprez et al., 2005) and the recent literature dealing with new nematode genera and species. All of the unknown species were indicated as sp_1, sp_2, sp_3, ... sp_n.

The nematode diversity was estimated using the species richness (SR), as the total number of different species identified at each site. Each replicate sampling from each site was analysed separately; the biodiversity at each site was determined cumulatively as the total number of species retrieved from the three independent samplings. As species richness is strongly affected by sample size, the expected number

of species, ES(X), was also considered, which provides a standardisation of the values of the species richness according to the sample size. At each site, the species abundance data were used to construct the rarefaction curves (Sanders, 1968; Hurlbert, 1971), and the expected number of species for a theoretical sample of 100 specimens, ES(100), was chosen to facilitate the comparisons among habitats and regions.

The species diversity (H', using log-base 2, expressed as H'^2) was also measured by the Shannon-Wiener information function, and the evenness was measured by the Pielou index (J; Pielou, 1975). These indices were calculated from the sum of the individuals of the three replicates of each of the sampling sites, using PRIMER v6.0+ (Plymouth Marine Laboratory, UK; Clarke and Gorley, 2006).

We measured local (α-diversity), regional (γ-diversity) and macro-regional (ε-diversity) species richness as the numbers of different nematode species within each site (local), region and macro-region (i.e. the whole Mediterranean basin; Gray, 2000; Danovaro et al., 2009a).

We also measured the turnover diversity between sites (β-diversity; sensu Gray 2000) and between regions (δ-diversity). The β-diversity and δ-diversity were measured using the similarity percentage analysis (SIMPER) routine that is included in the PRIMER v6.0+ software as the percentage of the dissimilarity between sites and regions, respectively, calculated from resemblance matrices based on Bray-Curtis dissimilarity using a presence/absence matrix.

The trophic composition of the nematode assemblages was defined according to the Wieser classification (Wieser, 1953). Nematodes were divided into four groups: no buccal cavity or a fine tubular one-selective (bacterial) feeder (1A); large but unarmed buccal cavity non-selective deposit feeders (1B); buccal cavity with scraping tooth or teeth, epistrate or epigrowth (diatom) feeders (2A); and buccal cavity with large jaws, predators/omnivores (2B). Moens et al. (1999) proposed a modified feeding-type classification based on: (1) microvores; (2) ciliate feeders; (3) deposit feeders sensu strictu; (4) epigrowth feeders; (5) facultative predators; and (6) predators. However, in the present study, the Wieser classification was preferred because it is still widely

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used and because no information is available for most of the genera encountered in deep-sea systems.

The Index of Trophic Diversity (ITD) was calculated as the 1-ITD, where ITD $= g_1^2 + g_2^2 + g_3^2 \ldots + g_n^2$, g is the relative contribution of each trophic group to the total number of individuals, and n is the number of trophic groups (Gambi et al., 2003). For $n = 4$ (as in the present study), the 1-ITD ranges from 0.00 to 0.75.

To determine the colonisation strategies of the nematodes, the maturity index (MI) was calculated according to the weighted mean of the individual genus scores, as $\Sigma v(i)f(i)$, where v is the colonisers-persisters (c-p) value of the genus i, as given in the Appendix of Bongers et al. (1991), and $f(i)$ is the frequency of that genus.

2.3 Quantity and biochemical composition of sediment organic matter

Chlorophyll *a* and phaeopigment analyses were carried out according to methods reported in Pusceddu et al. (2009) and Danovaro (2010). Total phytopigments were defined as the sum of chlorophyll a and phaeopigments (reported as $mg\,gDW^{-1}$). The protein, carbohydrate and lipid contents of the sediments were determined spectrophotometrically (Pusceddu et al., 2009, 2010b). A detailed description of the analysis of the sedimentary organic matter is reported by Danovaro (2010). All of the analyses were performed as 3 replicates, with about 1 g of surface sediment (0–1 cm sediment depth) for each sample. The protein, carbohydrate and lipid sediment contents were converted into carbon equivalents using the conversion factors 0.49, 0.40 and 0.75 $mg\,C\,mg^{-1}$, respectively, and their sum was defined as the biopolymeric organic carbon (Pusceddu et al., 2009, 2010b). The concentration of biopolymeric carbon (biopolymeric C) was chosen as indicator of the quantity of the sedimentary organic matter.

2.4 Statistical analyses

The differences in the nematode diversity indices among the regions were analysed using one-way analysis of variance (ANOVA). The test used the regions (North-Western,

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Central and Eastern Mediterranean) as the single sources of variance (with $n = 3$ fixed levels). The differences in the nematode diversity indices among habitats were analysed separately for each region, using one-way analysis of variance (ANOVA) and the sampling sites as the single source of variation (with $n = 4$–7 fixed levels). When significant differences were encountered, Student-Newman-Keuls (SNK) post-hoc comparison tests were also carried out (at $\alpha = 0.05$), to determine the patterns of variability among regions or habitats. The ANOVA and SNK tests were carried out using GMAV software (WinGMAV5, University of Sidney, Australia).

Analysis of similarity was performed based on the Bray Curtis similarity matrices obtained after the presence/absence transformation of the data, to assess the differences in the compositions of the nematode assemblages between sites within the same habitat, between habitats within the same region, and among regions. Analysis of similarity was carried out using the analysis of similarity (ANOSIM) routine included in the PRIMER v6.0+ software (Clarke and Gorley, 2006).

To determine how potential trophic resources and local diversity explained the differences in regional diversity, non-parametric multivariate multiple regression analyses were carried out based on Bray-Curtis distances, using the routine distance-based linear model (DISTLM) forward (McArdle and Anderson, 2001). The forward selection of the predictor variables was carried out with tests by permutation; p-values were obtained using 4999 permutations of the raw data for the marginal tests (tests of individual variables), while for all of the conditional tests, the routine used 4999 permutations of the residuals under a reduced model. We used the concentrations of the main sedimentary organic matter compounds (phytopigment, protein, carbohydrate, lipid and biopolymeric C) as indicators of the trophic resources (Pusceddu et al., 2010b), and the α- and β-diversity as the components of the local biodiversity.

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3   Results

3.1   Nematode diversity for the different deep-sea habitats of the Mediterranean Sea

The different indices of nematode biodiversity are reported in Table 2: SR, ES(100), and H′^{2}. The α-diversity is expressed as the species richness within a single site, and this varied from 11 to 81. However, the results of the present study reveal significant differences between sites for the species richness and ES(100) only for the North-Western Mediterranean Sea (ANOVA, $p < 0.01$; Table 3). The post-hoc comparisons reveal higher values for Cap de Creus canyon than for the Lacaze-Duthiers canyon and the northern and southern open slopes (SNK, $p < 0.05$; Table 3). Moreover, the maturity index shows significant differences among the habitats within the Eastern Mediterranean (ANOVA, $p < 0.01$; Table 3), with the highest values for two sites along the bathyal plains (sites A13 and A14; SNK, $p < 0.05$; Table 3).

The patterns of the nematode species richness found for each habitat (i.e. the habitat diversity) are illustrated in Fig. 2. Within both the Western and the Eastern Mediterranean, the habitat diversity for the open slopes, canyons, deep-water corals and bathyal plain have similar values. In the Central Mediterranean, however, the nematode diversity for the bathyal plains is lower than for the canyons and open slopes.

The average β-diversity between the habitats for each region is shown in Fig. 2. The SIMPER analysis reveals that on average the β-diversity between the sampling sites or habitats increased when moving from the North-Western Mediterranean (ca. 59 %) to the Central Mediterranean (60 %–90 %) to the Eastern Mediterranean (83 %–95 %; Table 4). The ANOSIM analysis reveals significant differences in the composition of the nematode species assemblages among the deep-sea habitats and among the sampling sites belonging to the same habitat (ANOSIM, $p < 0.05$; Table 4).

The portion of exclusive species found for each habitat was always > 50 % (Fig. 3), and the complete list of these exclusive species for the North-Western, Central and Eastern Mediterranean Sea are reported in Appendix S1 of the Supplement. The

rarefaction curves reveal a higher expected species number for the North-Western and Central Mediterranean than for the Eastern Mediterranean (Fig. 4). When different habitats are compared, a higher expected species number is seen for the open slopes, canyons and deep-water corals, than for the sediments of the bathyal plains.

5 Our data also reveal a saturation pattern of expected species in the Eastern Mediterranean, whilst non-saturation conditions are seen for the Western Mediterranean deep basin.

3.2 Regional and macro-regional deep-sea nematode diversity for the Mediterranean Sea

10 The one way analysis of variance (ANOVA) reveals that on average, all of the diversity indices were significantly higher for the Western and Central Mediterranean than for the Eastern Mediterranean (Table 3, Fig. 5a, b), while the species evenness (the Pielou index) shows the highest values for the Eastern Mediterranean (Fig. 5c). Significant differences are also seen in terms of the functional (trophic) diversity and life strategy

15 among these three regions (Table 3). However, these two variables showed opposite patterns, with the highest values of trophic diversity for the Western Mediterranean, and highest values of the maturity index for the Eastern Mediterranean (ANOVA, $p < 0.05$; Fig. 5d). Comparing these different deep-sea habitats, the maturity index shows the highest values along the bathyal plain (Table 2).

20 Despite, the generally low α-diversity, there is high β-diversity both between the different sites belonging to the same habitat, and between the different habitats (Fig. 6a). Such high values are responsible for the high γ-diversity (i.e. regional diversity; Fig. 6b), which shows the highest values in the Central Mediterranean (210 species) and the lowest in the Eastern Mediterranean (120 species), as illustrated in Fig. 7.

25 The turnover of nematode species among the different regions (the δ-diversity) is always $> 80\%$, with the largest difference in species compositions between the Central and Eastern Mediterranean (89 %), and lowest between the North-Western and the

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Central Mediterranean (81 %). The resulting overall species richness (ε-diversity) of the deep Mediterranean Sea at 1000 m depth was 280 species (Fig. 7).

Concentrations of all sedimentary organic matter compounds are reported in the Appendix S2 (Supplement). The results of the multivariate multiple regression analyses (DISTLM) carried out using the sedimentary organic matter compounds and the α-diversity and β-diversity show that most of the variance seen for the regional diversity can be significantly explained by the α-diversity and β-diversity (28 % and 32 %, respectively; Table 5).

4 Discussion

4.1 The α-diversity and β-diversity of nematodes in the deep Mediterranean Sea

The data from the present study indicate that three main features characterize the local (α) biodiversity in the deep-sea sediments of the Mediterranean Sea: (i) low diversity values, either expressed as species richness or expected species number; (ii) very limited differences in biodiversity within each sampling site or habitat, expressed either in terms of the species richness or ES(100); and (iii) minor differences between habitats within the same region. One single main exception was the North-Western Mediterranean Sea, where the sediments of the Cap de Creus canyon displayed a significantly higher level of α-diversity than the adjacent open slope. However, this can be considered an exception that is related to the specific environmental characteristics of this active and dynamic canyon (Canals et al., 2006). As large differences in the α-diversity between deep-sea sites are expected to be quite common in several oceanic regions (García et al., 2007; Ingels et al., 2009), these data would suggest an apparent homogeneity (and scarceness) of deep-sea biodiversity in the Mediterranean Sea.

The present study also shows that whichever index is considered (species richness or expected species number), the nematode species diversity decreases significantly

when moving eastwards, thus suggesting that the patterns observed are independent of the number of sampling sites within each region. However, the evenness (the Pielou's index) shows opposite patterns, with the highest values observed in the Eastern Mediterranean Sea.

Previous studies that were conducted from the deep North-Eastern Atlantic to the Central and Eastern Mediterranean Sea have revealed that the nematode species richness decreases eastwards (Danovaro et al., 2008a, 2009a, b; Vanreusel et al., 2010). Although these investigations were conducted at greater water depths (i.e. 3000–4000 m; Danovaro et al., 2008a), our results here indicate that such a decreasing longitudinal pattern in the nematode α diversity is a particular feature of the whole deep Mediterranean Sea.

Several factors have been invoked to explain patterns in benthic biodiversity in deep-sea systems, including the quantity and availability of trophic resources, the hydrodynamic conditions, and topographic features (García et al., 2007; Danovaro et al., 2009a; Bianchelli et al., 2010). As the deep-sea sediments of the Mediterranean Sea are characterised by very low organic matter concentrations (García et al., 2008; Pusceddu et al., 2009), and as the sites investigated generally have very low amounts of bioavailable organic matter (Pusceddu et al., 2010b; Dell'Anno et al., 2012), the results of this study would confirm that the low α-diversity of the deep Mediterranean Sea is primarily the result of the scarcity of available food resources (Danovaro et al., 2009a). This is consistent with the high meiofaunal abundance and α-diversity of the Cap de Creus canyon at this 1000 m water depth, which is characterised by favourable trophic and environmental conditions that have probably promoted colonisation by a higher number of nematode species (Canals et al., 2006; Pusceddu et al., 2010a, 2012).

Conversely, the comparison of the α-diversity at larger spatial scales (i.e. amongst basins, instead of among habitats or sites), shows the presence of clear differences between the sites of the Western, Central and Eastern Mediterranean basins, with the α-diversity in the Western Mediterranean up to eight-fold higher than in the Eastern

Mediterranean. These differences can be easily attributable to the known decreasing gradient of food availability from the Western to the Eastern Mediterranean.

The analysis of the rarefaction curves reveals that the number of species retrieved, for instance, from the open slopes of the Western Mediterranean, does not have a threshold level, whereas the rarefaction curves of the biodiversity of the same habitat in the Eastern Mediterranean saturated rapidly (i.e. reached a threshold level). This means that an increase in the sampling size in the Eastern Mediterranean would not increase the α-diversity of the sample, and that the differences seen between the open slopes of the Western and Eastern Mediterranean are real and might further increase with increasing sampling size (expressed as the number of individuals collectively collected from each site).

Conversely to what is seen for the α-diversity, the turnover (β) diversity between both the sites and habitats is consistently very high, ranging from 59 % (in the North-Western Mediterranean) to 93 % (in the Eastern Mediterranean). These data indicate the presence of major differences in the compositions of the nematode species assemblages when either comparing different deep-sea sites belonging to the same habitat, or between different habitats. These data are consistent with recent observations on specific deep-sea habitats, such as seamounts or coral banks, versus the adjacent open slopes (Pusceddu et al., 2010a, b; Bongiorni et al., 2010; Lopez-Fernandez et al., 2012a, b). However, while high β-diversity is expected when we compare deep-sea hot-spots of biodiversity with the surrounding sediments (i.e. following the concept of different species in different habitats), our data suggest that high levels of β-diversity are the rule in the deep-sea sediments of the Mediterranean Sea. This has important implications, because an average β diversity of 80 % based on the presence/absence matrix means that when comparing two samples, eight out of 10 of the species in one sample will be absent in the second sample, leading to much higher species richness at larger spatial scales. In addition, a high fraction of the species are exclusively found in each habitat investigated. The canyons of the Western Mediterranean have the highest levels of exclusive species (ca. 30 %), although the deep-water corals in

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the Central Mediterranean also have higher percentages of exclusive species than the canyons, open slopes and bathyal plains (20 %, 17 %, 13 % and 10 %, respectively). In the Eastern Mediterranean, the bathyal plain had a higher percentage of exclusive species than the open slope and canyon (34 %, 23 % and 17 %, respectively).

Altogether, the data obtained in the present study are supportive of the hypothesis that different habitats, such as deep canyons, open slopes, basins and deep-water corals, host particular assemblages, and that the higher the number of habitat in a region, the higher the number of exclusive (and potentially endemic) species. Given the low α-diversity, it is the high β-diversity (both between different sites and habitats) that is the main driver of the high γ-diversity at the regional level. This is evident for all of the three regions investigated here, although it is less evident in the Western Mediterranean, which has the highest α-diversity. Conversely, the Central-Eastern Mediterranean has a much higher β-diversity, and this can explain why the ultra-oligotrophic Eastern Mediterranean shows a regional (γ) diversity that is identical to that of the much richer Western Mediterranean, while that of the Central Mediterranean is the highest of the γ-diversities.

4.2 Functional diversity across deep-sea habitats

Analysis of the functional traits and diversities is essential to better understand the effects of species richness and composition on the functioning of deep-sea ecosystems (Danovaro et al., 2008b). Here, we analysed the changes in the trophic diversity using a widely recognised and simple indicator: the functional (trophic) diversity as a comparison of the three regions. The analysis of variance shows limited differences among the sites and habitats within a given region, although there is a clear decrease in the functional diversity moving from the Western to the Eastern Mediterranean. A skewed trophic diversity in the Eastern Mediterranean might be the result of the lower amounts of food sources and/or of the dominance of specific trophic groups. Indeed, an in-depth analysis also revealed the presence of a decreasing gradient in the relative abundance of predators when moving from the Western Mediterranean to

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the Eastern Mediterranean (see Appendix S3, Supplement). A higher abundance of predators can be explained by the larger availability of prey, as evident from a comparison of the samples coming from the Western Mediterranean versus the Eastern Mediterranean.

5   The analysis of the life strategies of the nematode assemblages (measured as the maturity index) in these three regions shows the highest values of the maturity index in the Eastern Mediterranean, which suggests that this region is colonised by a larger fraction of persistent species (K-strategists). This finding deserves further investigation, to explore potential links between the nematode life strategies and their functional

10 diversity.

4.3   The nematode γ-diversity, δ-diversity and ε-diversity in the deep Mediterranean Sea

The multivariate, multiple regression analyses indicate that the α-diversity and the β-diversity are the two most important variables for an explanation of the variance of the

15 γ-diversity. In addition, this analysis of the nematode biodiversity reveals significant differences in species compositions between the different deep-sea regions, which are highlighted by the δ-diversity (measured as the turnover of nematode species among the different regions), which was always $> 80\,\%$. This suggests that each deep-sea region is characterised by a specific nematode assemblage and species composition.

20 High δ-diversity amongst different oceanic regions (e.g. the Mediterranean Sea vs. the Atlantic Ocean) are expected, due to the significant differences in deep-water temperatures (ca. 10 °C warmer in the Mediterranean Sea at 1000 m in depth) and trophic conditions (Danovaro et al., 2009a). For the Western, Central and Eastern Mediterranean deep basins, such high δ-diversity cannot be explained only by differences in

25 temperature, which are typically generally close to 0.1 °C to 3.0 °C (Danovaro et al., 2010). Furthermore, we can also hypothesize that variations in the environmental variables that act between the different sites within the same habitat can be very important in the patterns of deep-sea biodiversity. Indeed, several studies have shown that both

physical-chemical variables and trophic resources (i.e. temperature, bottom salinity, grain size, and a combination of phytopigments, protein and biopolymeric C concentration) can have key roles in the structuring of the deep-sea nematode biodiversity (Danovaro et al., 2009a). However, the Mediterranean Sea is characterised by an extremely complex geological history, which led to the identification of ten biogeographic regions (Bianchi and Morri, 2000). As the three regions here have been characterised by different evolutionary histories in relation to the Messinian crisis, the role of the different geological histories and events that characterised the sea-floor at 1000 m in depth over the last 5 million years might be another key factor in such different species compositions amongst these different basins.

As a result of the large differences in the species compositions of the nematode assemblages observed among the North-Western, Central and Eastern Mediterranean regions, the overall species richness (ε-diversity) of the deep Mediterranean Sea (at 1000 m in depth) is very high: 280 nematode species are reported here at this fixed depth of 1000 m.

The data from the present study indicate that the differences in β-diversity and δ-diversity are even more important than those for the α-diversity for an understanding of the drivers of biodiversity in the deep Mediterranean Sea. These data also allow us to conclude that habitat heterogeneity (and type) and gradients in environmental conditions are crucial players for the nematode diversity levels, and they promote a high turnover diversity across the deep Mediterranean basin.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/17819/2012/ bgd-9-17819-2012-supplement.pdf.

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Table 1. Characteristics of the sampling sites in the present study.

Region	Habitat	Site	Latitude (° N)	Longitude (° E)	Water depth (m)
North-Western Mediterranean	Lacaze-Duthiers canyon	LD2	42.44	3.53	990
	Cap de Creus canyon	CC1	42.31	3.61	960
	Northern open slope	NS2	42.44	3.86	1022
	Southern open slope	SS2	42.13	3.78	985
Central Mediterranean	B Bari canyon	2	41.34	17.18	590
	C Bari canyon	9	41.31	17.26	721
	Northern open slope	11	41.23	17.59	908
	Southern open slope	77	39.75	19.19	1096
	Bathyal plain	St 7	36.61	12.25	1290
	Northern coral rubble	19	39.84	17.63	1084
	Southern coral rubble	33	39.83	17.61	1276
Eastern Mediterranean	Samaria canyon	11	35.19	23.93	1216
	Western open slope	12	35.01	23.70	1081
	Eastern open slope	5	34.95	24.59	1176
	Bathyal plain	A13	36.03	23.30	892
	Bathyal plain	A20	35.92	24.60	1078
	Bathyal plain	A14	36.05	23.43	1215
	Bathyal plain	A17	36.03	24.06	1147

Table 2. Nematode diversity indices in the habitats investigated in the present study.

Region	Habitat	Site	SR	ES (100)	H'^2	J	1-ITD	MI
North-Western Mediterranean	Lacaze-Duthiers canyon	LD2	62	39.14	25.98	0.86	0.69	2.60
	Cap de Creus canyon	CC1	81	47.56	31.45	0.88	0.71	3.04
	Northern open slope	NS2	66	43.00	29.36	0.90	0.73	2.90
	Southern open slope	SS2	68	42.33	27.64	0.86	0.69	2.73
Central Mediterranean	Bari canyon B	2	56	40.85	26.82	0.89	0.65	2.77
	Bari canyon C	9	81	50.13	32.23	0.89	0.66	2.83
	Northern open slope	11	61	39.72	23.46	0.81	0.61	2.93
	Southern open slope	77	45	44.76	26.13	0.93	0.67	3.07
	Bathyal plain	St 7	57	40.02	27.46	0.90	0.73	2.91
	Northern coral rubble	19	73	48.62	30.62	0.89	0.66	3.11
	Southern coral rubble	33	61	45.71	27.44	0.88	0.65	2.78
Eastern Mediterranean	Samaria canyon	11	48	42.52	24.70	0.89	0.60	3.06
	Western open slope	12	35	35.00	21.42	0.90	0.63	3.20
	Eastern open slope	5	22	22.00	17.90	0.95	0.74	3.00
	Bathyal plain	A13	30	28.87	21.99	0.96	0.67	2.98
	Bathyal plain	A20	11	11.00	10.56	0.94	0.66	3.44
	Bathyal plain	A14	16	16.00	15.05	0.97	0.64	2.77
	Bathyal plain	A17	12	12.00	12.25	0.98	0.73	3.06

SR, species richness;
ES(100), expected species number for 100 individuals;
H'^2, Shannon's index;
J, species evenness;
1-ITD, index of trophic diversity;
MI, maturity index.

Table 3. One-way ANOVA. A: To test the differences in the diversity indices among the Mediterranean regions investigated. B: Separately for each of the regions investigated, testing for changes among the different deep-sea habitats.

ANOVA test	SR F	P	SNK	ES(100) F	P	SNK	H'^2 F	P	SNK	J F	P	SNK	1-ITD F	P	SNK	MI F	P	SNK
A) Region	18.0	***	W Med > C Med > E Med	17	***	W Med > C Med > E Med	9.7	***	W Med, C Med > E Med	4.1	*	E Med > W Med, C Med	3.4	*	W Med > C Med, E Med	3.5	*	E Med > W, C Med
B) North-Western Mediterranean	4.1	*	CCreus > LacDuth, N and S slope	3.7	*	CCreus > LacDuth, N and S slope	0.3	ns	ns	2.0	ns	ns	0.6	ns	ns	1.8	ns	ns
Central Mediterranean	2.2	ns	ns	2.2	ns	ns	1.4	ns	ns	1.8	ns	ns	2.2	ns	ns	0.7	ns	ns
Eastern Mediterranean	2.4	ns	ns	2.3	ns	ns	3.6	ns	ns	1.4	ns	ns	0.3	ns	ns	1.6	*	Bathyal plain A13, A14 > Samaria, E and W slope, bathyal plain A17, A20

W Med, North-Western Mediterranean; C Med, Central Mediterranean; E Med, Eastern Mediterranean.
CCreus, Cap de Creus canyon; LacDuth, Lacaze Duthiers canyon; N slope, northern open slope; S slope, southern open slope; W slope, western open slope; E slope, eastern open slope.
SR, species richness; ES(100), expected species number for 100 individuals; H'^2, Shannon's index; J, species evenness; SNK, Student-Newman-Keuls test; F, ANOVA F statistic; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

Table 4. Results of SIMPER and ANOSIM analyses for the dissimilarities in the nematode species compositions between the different deep-sea habitats and sampling sites in all the regions investigated in the present study.

		SIMPER % Dissimilarity	ANOSIM P
North-Western Mediterranean	Canyon vs. open slope	58.7	*
	Cap de Creus vs. Lacaze-Duthiers canyon	59.3	*
	Northern vs. Southern open slope	59.4	*
Central Mediterranean	Canyon vs. open slope	76.9	**
	Canyon vs. coral rubble	86.0	**
	Canyon vs. bathyal plain	78.2	**
	Open slope vs. coral rubble	87.1	**
	Open slope vs. bathyal plain	86.7	***
	Coral rubble vs. bathyal plain	84.3	**
	B vs. C canyon	59.9	ns
	Northern vs. Southern open slope	90.1	***
	Northern vs. Southern coral rubble	79.0	**
Eastern Mediterranean	Canyon vs. open slope	83.3	***
	Canyon vs. bathyal plain	92.8	***
	Open slope vs. bathyal plain	93.1	***
	Western vs. Eastern open slope	95.0	***
	A13 vs. A14 vs. A17 vs. A20 bathyal plain	88.0	***

*** $p < 0.001$; ** $p < 0.01$; *$p < 0.05$; ns, not significant.

Table 5. Multivariate multiple regression analysis carried out on the γ-diversity.

Variable	SS	F	P	Explained variance (%)	Cumulative explained variance (%)
β-diversity	994.09	12.41	**	32.48	32.48
α-diversity	864.23	6.30	*	28.24	60.72
Carbohydrate	186.16	2.90	ns	6.08	66.80
Phytopigment	142.85	1.84	ns	4.67	71.47
Biopolymeric C	142.15	1.89	ns	4.64	76.11
Lipid	49.65	0.60	ns	1.62	77.73
Protein	40.15	0.50	ns	1.31	79.04

** $p < 0.01$; * $p < 0.05$; ns, not significant.

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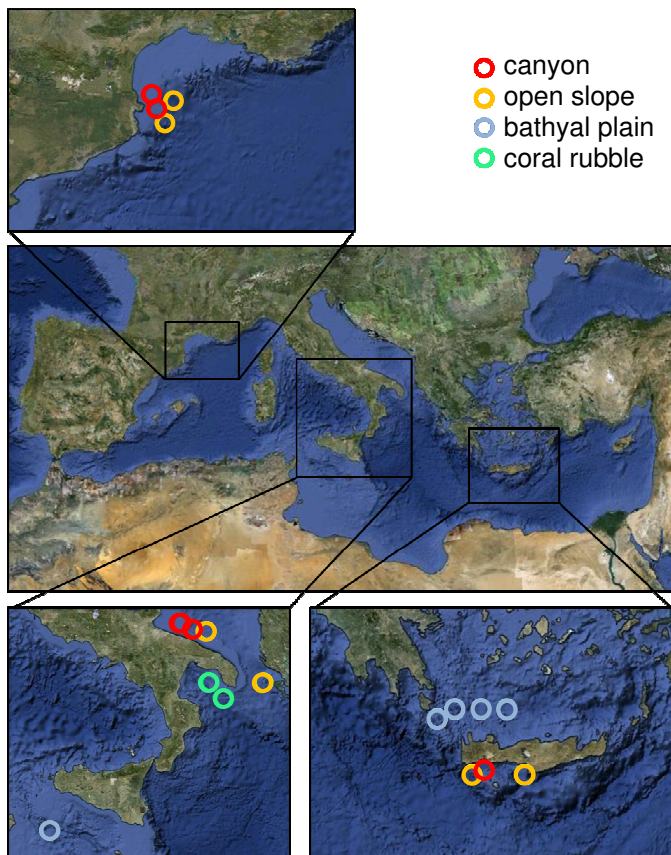
Fig. 1. Location and typology of the sampling sites in the deep Mediterranean Sea.

- canyon
- open slope
- bathyal plain
- coral rubble

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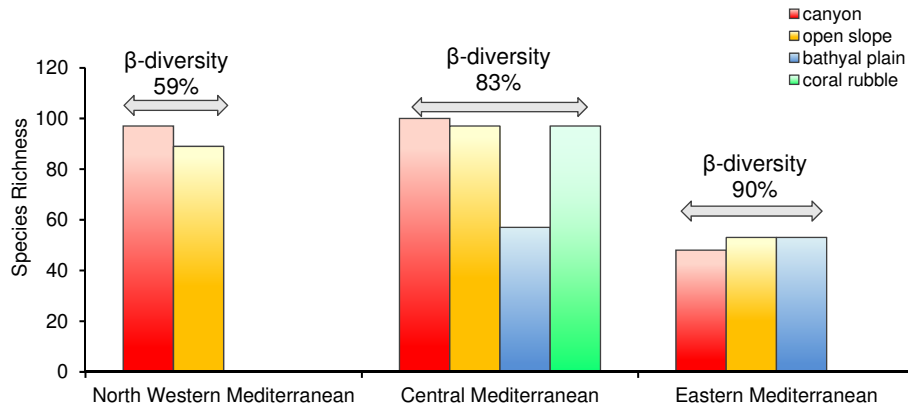
Fig. 2. Species richness of the nematodes in the different habitats in each of the regions investigated, with mean β diversity among the habitats in each investigated region also shown.
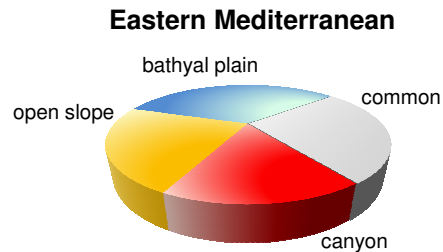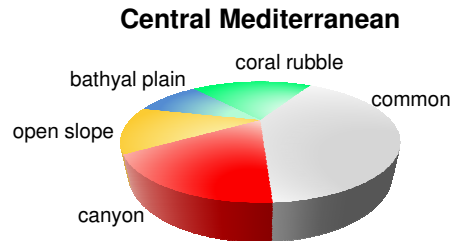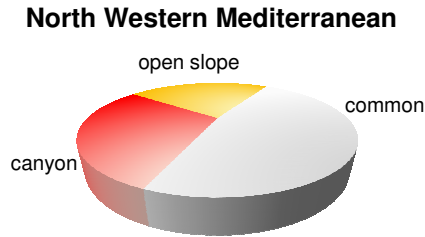
Fig. 3. Pie charts showing the relative importance of the exclusive species in each of the habitats investigated, along with the species in common to all of these habitats in the North-Western, Central and Eastern Mediterranean regions.
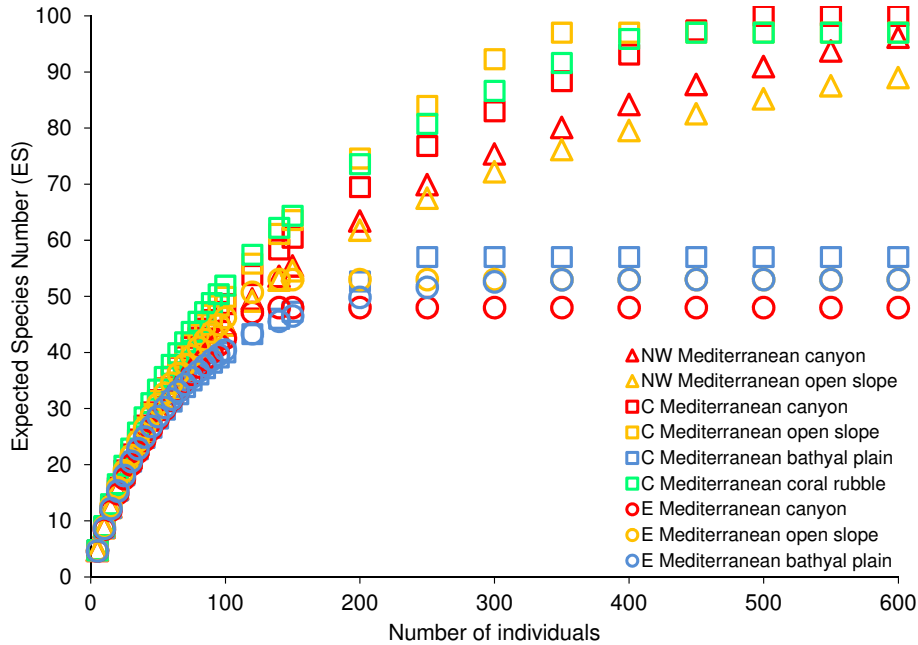
Fig. 4. Rarefaction curves for the nematode species in all of the habitats investigated.
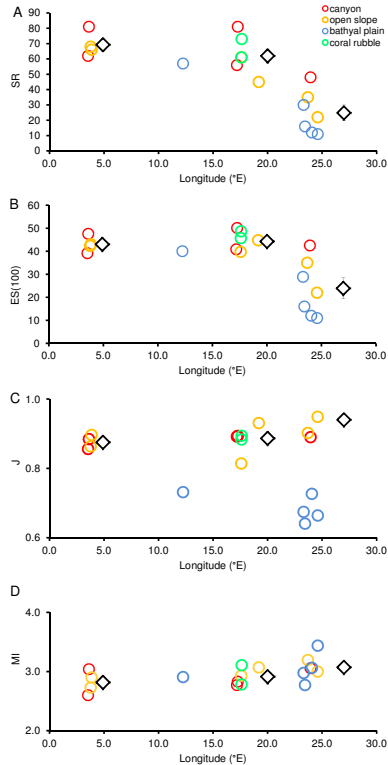
Fig. 5. α-Diversity in the different deep Mediterranean Sea regions: **(A)** Nematode species richness SR. **(B)** Expected species number ES(100). **(C)** Species evenness J (the Pielou index). **(D)** Maturity index. Black diamonds, mean data (±SE) for the individual regions investigated: the North-Western (ca. 5° longitude), Central (ca. 20° longitude) and Eastern (ca. 27° longitude) Mediterranean regions.
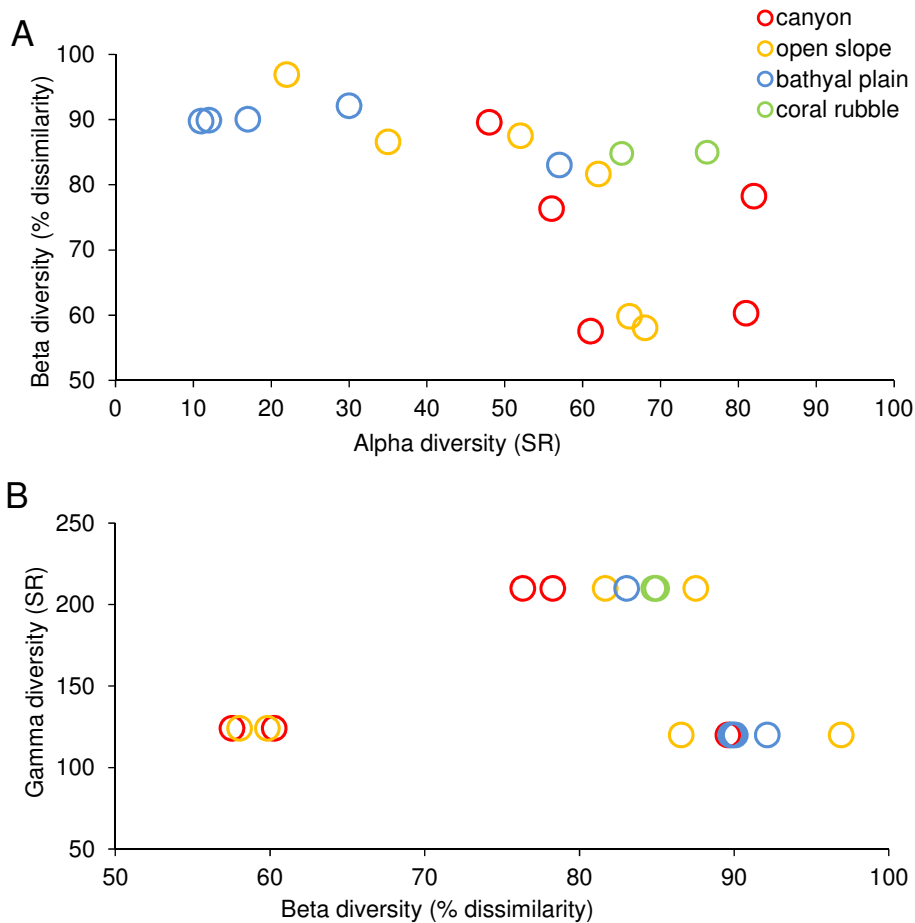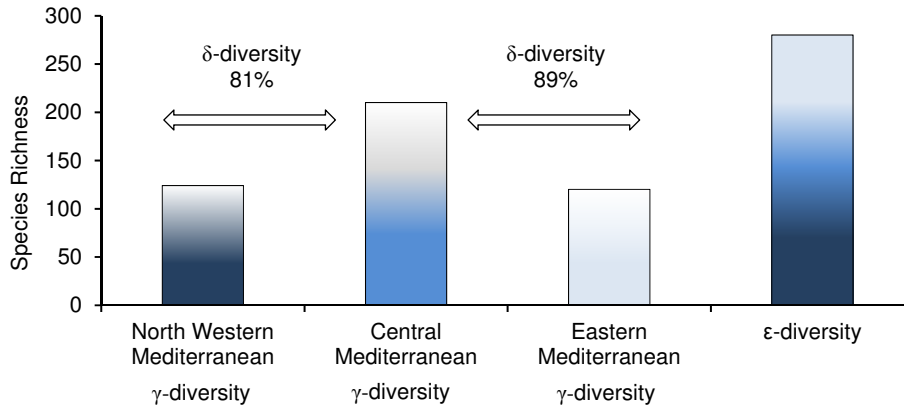
Fig. 6. Relation between: **(A)** α-diversity and β-diversity; and **(B)** β-diversity and γ-diversity, across the habitats (as indicated) of the deep-sea Mediterranean sites investigated.

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Interactive Discussion

Fig. 7. Nematode species richness at the different spatial scales, as the γ-diversity in each of the three regions investigated, the δ-diversity between these regions, and the ε-diversity (total species richness in this study) in the Mediterranean Sea.